INTEGRATING TRADITIONAL ECOLOGICAL KNOWLEDGE INTO ECOLOGY, EVOLUTION, AND CONSERVATION

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INTEGRATING TRADITIONAL ECOLOGICAL KNOWLEDGE INTO ECOLOGY, EVOLUTION, AND CONSERVATION

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Editorial: Integrating traditional ecological knowledge into ecology, evolution, and conservation

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Editorial on the Research Topic
Integrating traditional ecological knowledge into ecology, evolution, and conservation

Ecology and evolution are the core disciplines that investigate the processes that generate and maintain biodiversity in space and time. The theoretical and applied studies produced in these two disciplines represent pivotal information to set conservation biology priorities. Because humans represent one of the main factors contributing to land-use changes in world ecosystems, it is essential to include them in theoretical and applied studies. However, most of the current literature in ecology, evolution, and conservation (hereafter called "biodiversity disciplines") uses the variable "human" basically as the negative driver causing biodiversity loss. On the one hand, by including humans as the source of biodiversity loss, this literature provides relevant information to be broadly used in biodiversity management and conservation. On the other hand, disregarding that local populations depend on biodiversity for a living could hamper our ability to produce socially inclusive theories. In fact, recently the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services has argued that the traditional ecological knowledge is a missing component in applied sciences and in the decision-making process (see also IPBES, 2018; Jack et al., 2020; Albuquerque et al., 2021). This has raised two pertinent issues for promoting a program that incorporates local knowledge into biodiversity disciplines: (1) How can the fields of ethnobiology and biodiversity be integrated to better understand how landscapes, animals, and plants have been used and domesticated? (2) How can policies and conservation efforts be influenced by the ethnobiological evidence to help maintain biodiversity? In this Research Topic, several researchers looked into various facets of ethnobiology that might open up novel directions for explicitly merging biodiversity disciplines and traditional ecological knowledge. It contains 12 papers that address these issues in a variety of social-ecological systems.

One set of papers examined the patterns and processes involved in the use and domestication of landscapes, animals, and plants. Understanding how local populations' management and selection of resources can result in domestication is a long-standing concern of ethnobiology. In effect, for the conservation and sustainable use of biodiversity, it is essential to comprehend the multidimensional framework within which interactions between people and biodiversity have evolved. Tobes et al. investigate the ichthyological knowledge (with focus in ethnotaxonomy) of indigenous Kichwa people from the Ecuadorian Amazon showing that Kichwa classification is multidimensional and considers attributes like skin and scales, fishbones and spines, meat quality, body shape, diet, and salience. Ethnotaxonomic knowledge can provide important information about the stocks of economically and culturally important species, and makes it possible to elaborate workable monitoring plans involving fishing communities. The extent of human activities spans different spatial and temporal scales. The research by Ferreira et al. compiles information from a systematic review of small-scale populations' management practices in South American savannas. This is one of the first studies focused on the important dry forest formations of South America. The authors find evidence of different methods of biodiversity management, such as building niches that may result in the domestication of landscapes. The study of Ojeda-Linares et al. was performed in Mesoamerica, which is especially fruitful in studies focused on local ecological knowledge about plants to meet nutritional needs. What most calls attention in this paper is the union of this approach and genomic techniques to understand these processes in fermented beverages traditionally prepared in Mexico. The authors concluded that the traditional practices of preparing these beverages affect microbial diversity, suggesting an important discussion about food security and self-sufficiency. Analyzing local knowledge of plant use can be helpful in determining how phytosanitary issues impact food security. To better understand the impact of sociocultural and agricultural practices on the occurrence of cassava bacterial blight, Pérez et al. conducted interviews with Colombian farmers. The significance of this work lies in its assessment of the potential effects of land use, phytosanitary control, and fertilizer use on the prevalence of bacteria blight in cassava and on local populations. Santos et al. investigated the environmental and social factors that drive the consumption and preferences for meat as a source of protein for indigenous populations. The authors demonstrated that deforestation, urbanization and father's occupation determine how young students consume wildlife meat which also has implications to food security.

In another group of studies, ethnobiological information is expressly used to make decisions about management and conservation strategies for biodiversity. Zarazúa-Carbajal et al. analyzed the coexistence and use of fauna by the Mexicatl (Nahua) people in Central Mexico showing that local people recognized a hundred of animal items associated to 18 use categories and three types of damage (crop loss, predation of domestic animals, and damages to health). This information is essential for establishing management plans directed toward sustainable use of wildlife. An important aspect is linked to people's perception of agroforestry systems and the motivations that lead them to carry out management actions that maintain native vegetation in agricultural areas. This is addressed in the article by Rendón-Sandoval et al. that investigates the motivations of peasants from three human groups to maintain native vegetation of Tropical Dry Forest in their agroforestry systems in Cuicatlán, Oaxaca, Mexico. The authors highlight that the motivators indicated by people involved the contributions of these areas through material, regulatory and non-material services, which favor fundamental human needs linked to subsistence, identity and protection. As a result, it reveals that conservation actions for these environments must take into account the historical interactions with human groups, in addition to their perceptions and motivations for maintaining management actions that favor biodiversity. Another aspect of traditional ecological knowledge that can guide conservation decisions is determining the spatial and temporal distribution of threatened or economically relevant species. Jesus et al. offer some guidance on how to use data from interviews with octopus fishers to identify species distribution and comprehend potential fishing pressure that could have an impact on them. The authors used the knowledge of fishers to show a wide range of information that can aid in conservation decisions, including: (i) behavioral traits that aid in differentiating between co-occurring species, (ii) spatial distribution and fishing patterns, (iii) social factors affecting fishing success, and (iv) use of octopus fishing as a secondary source of income indicating a potential weak pressure on octopus populations. Quirino-Amador et al. explicitly integrated the ecological and scientific knowledge from fishers, divers, and reef scientists to investigate temporal changes in reef landscapes. They highlighted that the complementarity of information among different stakeholders enables a better understanding of how human behavior impacts and perceives changes in natural ecosystems, which could be essential to manage reef environments, particularly those without baseline data. In a similar way, Pereyra et al. used an interdisciplinary approach combining stable isotopes analysis and fisher's knowledge to understand trophic relationships of amazonian fishes. The authors find that the two sources of knowledge were able to predict the trophic position of six fish species. Importantly, by using the local knowledge this study provided reliable information about trophic ecology of endangered species which can help fisheries management and species conservation.

The local ecological knowledge can also be valuable to track the impact of environmental changes on human health and to understand the adaptive strategies developed by them to survive in a changing environment. Magalhães et al. explored this issue and asked how do people from different human groups perceive and develop adaptive strategies to deal with diseases caused by extreme climate change? The results showed that the perceived incidence of diseases was the factor that positively explained the frequency of adaptive strategies adopted by people. This suggests that public policy efforts should be directed toward certain groups of diseases with higher incidence to favor the health of human groups in extreme climatic events. The events may also affect water availability for people, which can have social, economical and political impacts on traditional populations. For example, Fowler studied the ways water is made and unmade on Sumba Island when subjected to tensions between local indigenous populations and off-island policies. Studies of this nature are important for the equitable and sustainable management of water, the protection of water quality, and the conservation of freshwater biota.

As concluding remarks, the 12 papers in this Research Topic shed light on the great potential of including local ecological knowledge into biodiversity disciplines to help improve conservation decision and policy (see, e.g., Gurney et al., 2019; Gelcich et al., 2019; Barbosa-Filho et al., 2020). In addition, this Research Topic provides insights that we hope will stimulate further research bringing together several academic fields concerned with biodiversity conservation and human well-being.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Conflict of interest

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References

Albuquerque, U. P., Ludwig, D., Feitosa, I. S., de Moura, J. M. B., Gonçalves, P. H. S., da Silva, R. H., et al. (2021). Integrating traditional ecological knowledge into academic research at local and global scales. *Reg. Environ. Change* 21, 45. doi: 10.1007/s10113-021-01774-2

Barbosa-Filho, M. L. V., Ramires, M., Mourão, J. S., Rosa, R. S., Alves, R. R. N., and Costa-Neto, E. M. (2020). Ethnotaxonomy of sharks by expert fishers from South Bahia, Brazil: Implications for fisheries management and conservation. *Ethnobiol. Conserv.* 10, 1–12. doi: 10.15451/ec2021-08-10.02-1-12

Gelcich, S., Martínez-Harms, M. J., Tapia-Lewin, S., Vasquez-Lavin, F., and Ruano-Chamorro, C. (2019). Comanagement of small-scale fisheries and ecosystem services. *Conserv. Lett.* 12, e12637. doi: 10.1111/conl.12637

Gurney, G. G., Darling, E. S., Jupiter, S. D., Mangubhai, S., McClanahan, T. R., Lestari, P., et al. (2019). Implementing a social-ecological systems framework for conservation monitoring: lessons from a multi-country coral reef program. *Biol. Conserv.* 240, 108298. doi: 10.1016/j.biocon.2019.108298

IPBES (2018). "The IPBES regional assessment report on biodiversity and ecosystem services for the Americas," in *Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, eds J. Rice, C. S. Seixas, M. E. Zaccagnini, M. Bedoya-Gaitán, and N. Valderrama (Bonn), 656.

Jack, J. C., Gonet, J., Mease, A., and Nowak, K. (2020). Traditional knowledge underlies one health. *Science* 369, 1576–1576. doi: 10.1126/science.abe2401

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Peasants' Motivations to Maintain Vegetation of Tropical Dry Forests in Traditional Agroforestry Systems from Cuicatlán, Oaxaca, Mexico

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The ways traditional rural communities conduct activities to meet their livelihoods commonly contribute to conservation of biodiversity and ecosystem functions. Traditional agroforestry systems (TAFS) are expressions of management that deliberately retain wild vegetation coexisting with crops to obtain multiple socio-ecological contributions. However, processes enhancing productive intensification endanger their permanence. This study aimed to 1) identify the peasants' motivations to maintain the vegetation of tropical dry forest within their agricultural fields, 2) analyze the capacity of TAFS to provide contributions to people's well-being, and 3) identify factors and processes limiting conservation capacities and possible alternatives. The study was conducted in three communities of the Tehuacán-Cuicatlán Valley, Oaxaca, Mexico. We performed a qualitative analysis with information from two workshops with local people, 10 semi-structured interviews with managers of TAFS, participant observation, complementary informal talks, and fieldwork notes. For analyzing the data, we: 1) generated a list of central themes based on the data collected, 2) established preliminary categories of such themes, 3) coded all information through the Atlas. ti software, 4) adjusted the classification of categories and codes to the data, 5) grouped codes and analyzed their relationships. We found that the peasants' motivations to maintain the wild vegetation are the provision of multiple beneficial contributions: material (edible fruit, medicinal plants, fodder, firewood), regulating (shade, soil fertility, humidity keeping, rain attraction), and nonmaterial (regional flavors, ornamental, ritual), among others, which meet some of their fundamental needs (primarily subsistence, identity, and protection). The main reasons for keeping the wild vegetation were material contributions (62%). Also, we observed that TAFS safeguarding a higher forest cover and species diversity provide a broader range of socio-ecological contributions and potential to satisfy human needs than those with lower cover. Peasant agriculture may allow maintaining biodiversity while satisfying fundamental human needs. However, it needs to be revitalized, made more efficient, profitable, and dignified. The agroecological management implemented by peasants in

TAFS is crucial for ensuring the continuity of essential environmental functions and people's well-being.

Keywords: agroecological management, biocultural diversity, biodiversity conservation, fundamental human needs, nature's contributions to people, peasant agriculture, traditional ecological knowledge

INTRODUCTION

Practically all ecosystems of the planet have had human impact (Noble and Dirzo, 1997; Díaz et al., 2019). Some of them are subject to progressive higher transformation intensity, mainly due to the accelerated industrialization, which is the leading cause of the severe impact on ecosystems at a global scale (MEA, 2005; IPCC, 2013). For this reason, the study of the relationships between human societies and the natural environment urgently requires research approaches and actions towards sustainability, one possible way to guarantee the continuity of the socio-ecological systems (Berkes and Folke, 1998). To ensure the future viability of these systems, it is indispensable stopping the productive intensification that characterizes the current hegemonic trends of the global economy (Casas et al., 2014), which involves the drastic and profound transformation of nature (Rendón-Sandoval, 2020). Besides, it is necessary to design alternative production systems to provide goods while maintaining their capacity to conserve biodiversity and environmental functions.

Important examples to face the global environmental crisis can be found in some of the ways traditional rural communities live. These societies commonly meet their livelihood needs, while contributing to biodiversity conservation and maintaining key ecosystem functions (Perfecto and Vandermeer, 2008; Altieri and Toledo, 2011; Casas et al., 2014). Understanding the rationality of the cultural and ecological features of these traditional communities, their techniques, social organization, and governance, may provide important teachings for redesigning strategies of interrelationships between society and nature. One of the most notable expressions of the biocultural legacy of rural communities are the *traditional agroforestry systems* (TAFS), which are agroecosystems that integrate the deliberate retention of forest cover and wild species managed through different ways (Casas et al., 1997), which coexist with crops and domestic animals to obtain social and ecological benefits (Moreno-Calles et al., 2014; SEMARNAT, 2019).

TAFS are important reservoirs of culture, local knowledge, technical experience, and biological diversity, with a high capacity to conserve the ecosystems surrounding agricultural areas, while providing benefits to societies (Casas et al., 2014; Vallejo et al., 2016). These systems might be reminiscences of early stages of agricultural practices that were integrated into the management of forests and landscapes (Casas et al., 1997; Blancas et al., 2010). Thus, several scholars have suggested that early horticultural practices associated to forest management could be the earliest forms of food production in Mesoamerica (MacNeish, 1967; Smith, 1967; Clement et al., 2021). Current TAFS result from a long history of interactions between societies and ecosystems, that represent millenary biocultural legacies (Boege, 2008; Toledo and Barrera-Bassols, 2008). TAFS are important settings where people experiment with different management forms of their components and processes, including the domestication of plant species, which influences the adjustment of landscapes to human needs (Casas et al., 1997, Casas et al., 2007; Moreno-Calles et al., 2014). Likewise, TAFS are living laboratories of biodiversity and ecosystem management that generate agrobiodiversity.

One of the most relevant ecosystems for the study of TAFS is the tropical dry forest (TDF), a plant community formed by tropical elements dominated by species that lose their leaves during a marked and long dry season (Rzedowski, 1978). The TDF is notable for harboring high species diversity and endemism, and it is the source of origin of wild relatives of outstanding Mesoamerican crops like maize, beans and squashes (Challenger, 1998; Banda et al., 2016). Nevertheless, this ecosystem is highly threatened, and its conservation is one priority worldwide (Janzen, 1988; Olson and Dinerstein, 2002). In Mexico, it is relevant its high level of endemism (Rendón-Sandoval et al., 2020), the highest of the TDF in the Neotropical region, with 60–73% of species restricted to the Mexican territory (Rzedowski, 1991; Banda et al., 2016).

It has been documented that TAFS provide multiple benefits or contributions to societies (Moreno-Calles et al., 2010; Altieri and Toledo, 2011; Vallejo et al., 2016; Rendón-Sandoval et al., 2020). *Nature's contributions to people* are all socio-ecological contributions that humans obtain from nature, including goods and functions from ecosystems (Díaz et al., 2018). However, the concept may also include aspects of nature that may be harmful to people (e.g. pests, pathogens, predation that damage people or their assets) (IPBES, 2019). Recently, Díaz et al. (2018) categorized such contributions in three main groups: 1) *material contributions* (substances, objects, or other tangible elements from nature that directly sustain people's life); 2) *nonmaterial contributions* (nature's effects on subjective or psychological aspects underpinning people's well-being; giving the opportunity of recreation, inspiration, spiritual experiences, and social cohesion); and 3) *regulating contributions* (functional and structural aspects of organisms and ecosystems that influence environmental conditions experienced by people and/or regulate the generation of material and nonmaterial contributions).

TAFS may maintain high proportions of forest cover, and thus provide multiple beneficial contributions, like habitat maintenance, pollination, dispersal of seeds and other propagules, air quality, climate regulation, water purification, soil formation and protection, regulation of hazards and extreme events, regulation of harmful organisms and biological processes, provision of food, fodder, medicinal, learning and inspiration, physical and psychological experiences, supporting identities, and maintenance of options (Díaz et al., 2018).

Such contributions provide the satisfaction of fundamental human needs as those pointed out by Max-Neef et al. (1998), like subsistence, protection, identity, affection, understanding, creation, participation, and leisure. These authors distinguish between *fundamental human needs* (essential human requirements and potentialities, common to all cultures in all historical periods) and *satisfiers* of such needs (different ways or means, selected by each culture to satisfy needs). For instance, food and shelter should not be considered needs, but satisfiers of subsistence need.

The attributes referred to above suggest that TAFS are outstanding alternatives to recover and implement forms of management favorable for the conservation of biodiversity, and compatible with people's well-being. Peasant women and men are crucial actors since they interact closely and continually with these systems; therefore, understanding their motivations for managing them allows documenting their knowledge on biodiversity, their strategies for conservation, and conditions for the permanence of biocultural diversity (Boege, 2008; Toledo and Barrera-Bassols, 2008). The proposals from academic, governmental, civil organizations, and other social sectors, to be viable require to be compatible with the culture, values, and wishes of those that directly manage the local ecosystems.

According to Wolf (1955), peasants have in common the following features: 1) agricultural production as their main occupation, 2) effective control of land and autonomous making decisions on their crops, and 3) their activities are more oriented towards the direct satisfaction of their subsistence rather than to reinvestment. In addition, Ploeg (2010) defines the *peasant condition* considering a base of resources controlled and administered by them, from which emerges *coproduction* (or interaction and mutual transformation between humans and nature), in turn interacting with markets maintaining their autonomy and independence. Around the world, there is a marked correspondence among areas with high biodiversity (*hotspots*) and territories of peasant and indigenous communities. Such information shows that biological and cultural diversity are reciprocally dependent and geographically coexisting (Boege, 2008; Toledo and Boege, 2010).

In this context, we consider the need to implement strategies for strengthening the peasant practices to maintain the diversity of TDF compatible with people's well-being. In such task, TAFS may have substantial contributions. The purposes of this study were to 1) identify the peasants' motivations to maintain the wild vegetation in their agricultural fields, 2) analyze the capacity of TAFS to provide contributions to people's well-being, and 3) identify factors and processes limiting conservation capacities. Previous studies have documented that both maintenance and removal of forest elements from agricultural fields are regulated by needs, values, or potential damage perceived and mediated through different management practices (Moreno-Calles et al., 2010, Moreno-Calles et al., 2012; Blancas et al., 2013; Vallejo et al., 2014, Vallejo et al., 2015, Vallejo et al., 2016; Rangel-Landa et al., 2017). In particular, our team previously documented that TAFS associated with TDF can harbor –on average– 44% of forest cover, 68% of species (30% of them endemic to Mexico), and 53% of the individuals of plants from the neighboring wild vegetation; where 96 species of useful plants (73% of the total) were recorded (Rendón-Sandoval et al., 2020). Therefore, this study seeks to deepen the understanding of the most determinant motivations for maintaining vegetation in the peasants' parcels, and the contribution of their TAFS to human well-being. For such purpose, we conducted qualitative approaches, which do not aspire to represent the state of agriculture and agricultural practices in the study area, but to understand processes and interrelationships influencing the management practices for conservation of forest cover in agricultural plots. In other words, understanding the multiple phenomena operating in a complex system of processes and factors motivating management decisions that influence the ecological expression of the agroforestry systems studied.

MATERIALS AND METHODS

Study Area

The Tehuacán-Cuicatlán Valley is one of the main reservoirs of biocultural diversity of Mexico, with a cultural history of more than 10,000 years. Important archaeological studies in the region revealed early signs of domestication and forest management practiced in the area during the prehistory, which has been recognized among the earliest signs of food production in Mesoamerica (MacNeish, 1967; Smith, 1967). It is a semi-arid zone, the most biodiverse of North America, with 37 types of plant associations (Valiente-Banuet et al., 2000) and more than 3,000 plant species registered up to now (Casas et al., 2001; Lira et al., 2009). In addition, in the Tehuacán-Cuicatlán Valley live eight indigenous groups: the Chocho (called themselves *Ngiba*), the Popoloca (*Ngiwa*), Nahua (*Macehuale*), Cuicatec (*Y'an yivacu*), Mazatec (*Enna*), Chinantec (*Tsa ju jmí*), Mixtec (*Ñuu savi*), and Ixcatec (*Xwja*) people (Casas et al., 2001; Boege, 2008).

To conserve such biological and cultural richness, the region was decreed as a Biosphere Reserve in 1998, and then inscribed in the List of World Heritage (cultural and natural) of the UNESCO in 2018, due to the extraordinary values of the natural environments and cultural Mesoamerican traditions. In addition, the Tehuacán-Cuicatlán Valley has been cataloged as one of the 23 Priority Biocultural Regions for Conservation of Mexico (Boege, 2008).

Our research was conducted in three mestizo communities with Cuicatec and Mazatec origin in the "Cañada" region, belonging to the municipality of San Juan Bautista Cuicatlán, Oaxaca (**Figure 1**). This territory, located at elevations averaging 700 m, has a semi-arid dry climate with annual rainfall averaging 485 mm, with eight dry months, and 25°C of annual mean temperature (García, 2004). It is the confluence zone of several rivers that allow the presence of riparian vegetation, coexisting with different types of columnar cacti forests and TDF. Our study was conducted in the peasant communities of Santiago Quiotepec, Cuicatlán, and Santiago Dominguillo, where the land tenure is communal and ejidal (two forms of collective tenure regimes). These communities have primary activities like

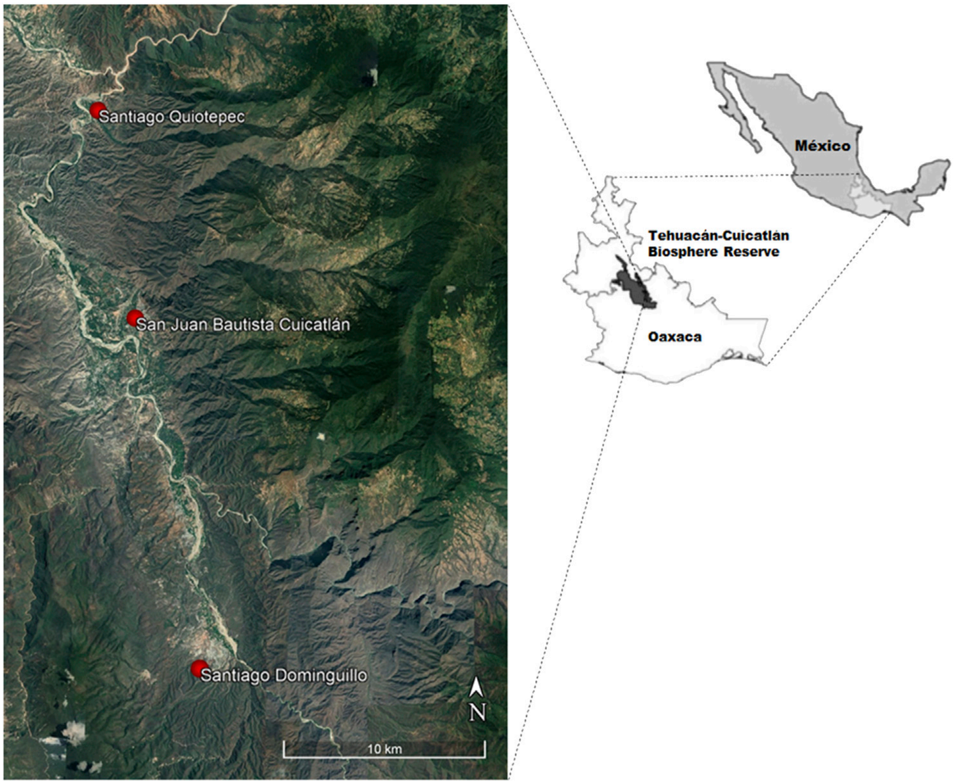

FIGURE 1 | Location of the communities where the study was conducted in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. Based on Google Earth Pro and Vallejo et al. (2015).

traditional "milpa" agriculture (a multi-crop system with maize, beans and squash), cultivation of fruit trees (lemon, mango, sapodilla, spondias plum, annona, black sapote) in irrigated areas, raising of goats, and gathering of timber and non-timber forest products (Brunel, 2008; Rendón-Sandoval et al., 2020).

Methodological Design

We carried out a qualitative analysis including as methodological referent the Grounded Theory proposed by Glaser and Strauss (1967). The Grounded Theory is a qualitative research method whose purpose is to generate theoretical explanations based on the data obtained from the specific context studied; therefore, it does not start from *a priori* selected theories. The Grounded Theory uses an inductive approach to generate theoretical concepts and identify their relationships from the analysis of the information obtained, in such a way that the explanations emerge from the data itself and is closer to reality, as it does not impose the verification of a pre-established theory (Taylor and Bogdan, 1987; Strauss and Corbin, 2002).

Qualitative analysis is supported by continual feedback from data to interpretations, a process in which: 1) the information is analyzed systematically to generate *codes* (or identifiers of particular themes), 2) these codes and their interpretations are debugged and/or nuanced through a continual contrasting with the data obtained, 3) their properties are identified, 4) codes are classified and grouped into categories, 5) their interrelationships are explored, and finally 6) these are integrated into a coherent explanation (Taylor and Bogdan, 1987).

The fieldwork started with exploratory visits to study communities, observing TAFS in their territories, and asking permission from local communitarian authorities to carry out the research. We also visited the authorities of the Tehuacán-Cuicatlán Biosphere Reserve to inform us about our research project, ask for their permit and advice.

Data Collection

For obtaining the information we carried out: 1) 10 semi-structured interviews with peasants whose agricultural fields were sampled for previous ecological studies (see Rendón-Sandoval et al., 2020). These interviews yielded results that reached the principle of information saturation, which refers to the stage in qualitative data collection when collecting more data produces little important new information or understanding relevant to the research questions (Newing et al., 2011). Semi-structured interviews allow integrating closed-ended questions (questionnaire type) as well as open-ended questions in the same tool, which makes it possible to capture specific data while delving deeper into certain topics that require more exhaustive exploration, thus providing in-

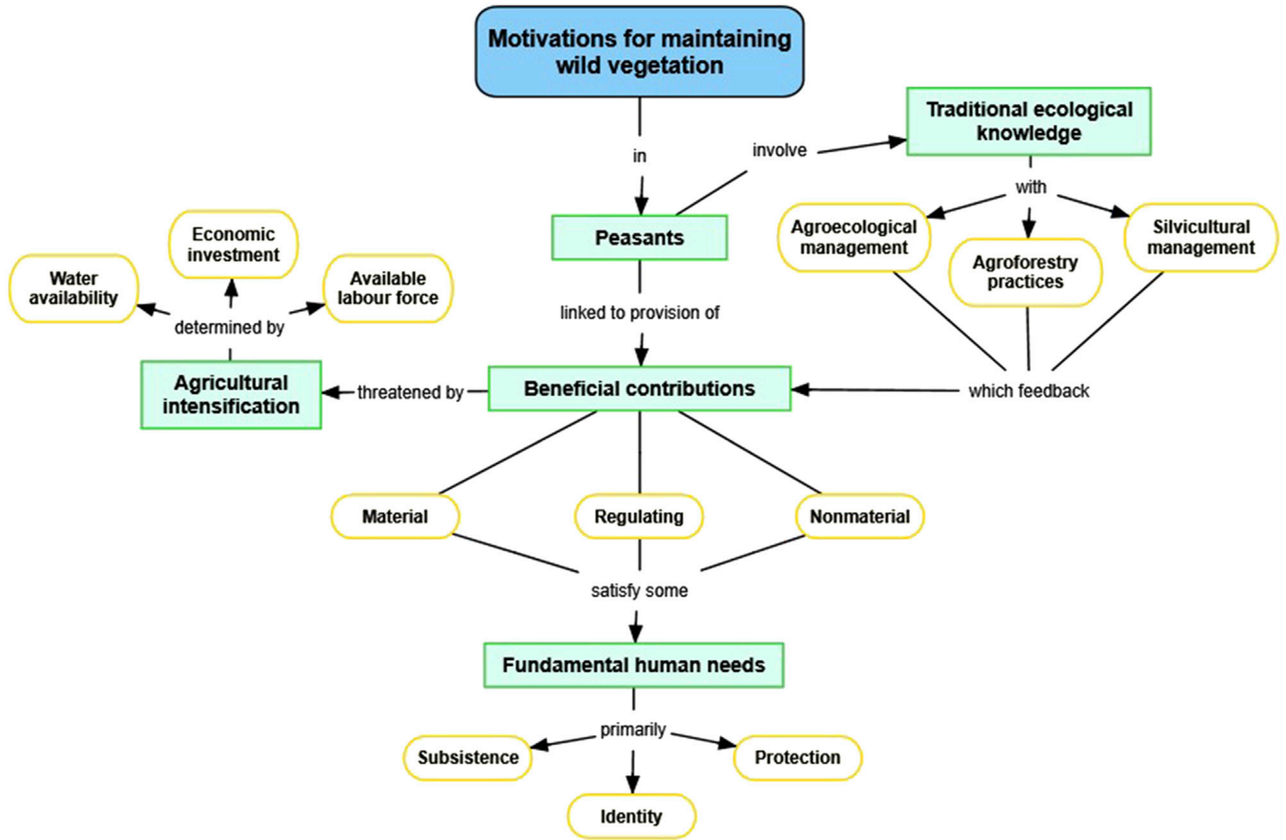

FIGURE 2 | General diagram explaining the peasants' motivations for maintaining wild vegetation within traditional agroforestry systems in the Cañada region, Oaxaca, Mexico. The blue box indicates the central research question: What motivates peasants to maintain wild vegetation within their agricultural fields? The green rectangles contain the main categories that emerged in the qualitative analysis conducted through Atlas. ti. The yellow boxes contain the main subcategories involved in, and helping to explain, the observed situation. Lines and arrows indicate relations and causative directions.

depth information. Our interview script (see **Supplementary Material**) was constructed with these characteristics (Drury et al., 2011). For the design of the interview guide we based the proposal on previous studies conducted in the region (e.g. Moreno-Calles et al., 2010, Moreno-Calles et al., 2012), incorporating relevant themes from other related studies (e. g. Pelcastre et al., 2020) to answer the research questions posed. People interviewed included two women and eight men 29–81 years old (average 60 years), from February 2018 to August 2019; 2) two workshops with local people from the community of Quiotepec (with the participation of 13 young and adult people) about "benefits of wild plants", the elaboration of free lists about nature's contributions, and the agricultural calendar followed by the community. The workshops were conducted as an additional technique to the interviews that served to complement and triangulate the information obtained through interviews. The workshops were based on guiding questions about the contributions that vegetation makes –and that motivate its conservation within the TAFS–, as well as about the seasonality of agricultural activities carried out throughout the year (e.g. planting, harvesting, seed selection and storage, fallow). People's responses were recorded on flip charts for subsequent systematization and analysis. Interviews and workshops provided more than 25 h of audio recording which were transcribed to be analyzed; 3) participant observation in communitarian activities (e.g. maize harvesting, preparation of pasture bags, goats grazing, religious ceremonies, and funerary rites); 4) informal talks with peasants during forest walks, sharing of food or resting in their homes; and 5) registering notes in a fieldwork diary.

The interviews comprised 85 questions on: 1) characteristics and history of parcels, 2) level of agricultural intensification, 3) management of vegetation, 4) contributions to human well-being, and 5) motivations for maintaining or removal of wild plant species in agricultural fields. Previously, we conducted samplings to analyze the cover and composition of forest patches in parcels of TAFS managed by people interviewed. Vegetation sampled in TAFS parcels was compared with that of native forests (see Rendón-Sandoval et al., 2020).

Data Analysis

To analyze the information, we: 1) examined the interviews to identify the most relevant elements and generate a list of central

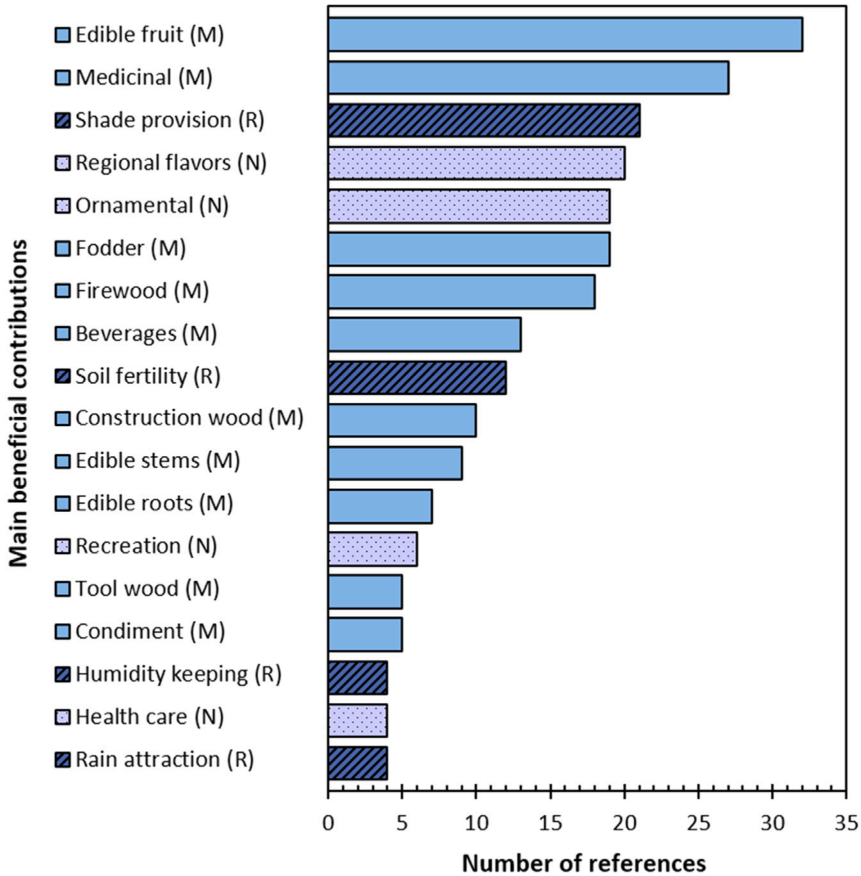

FIGURE 3 | Main beneficial contributions –motivating the maintenance of native vegetation from the tropical dry forest– referred by peasants in the Cañada region, Oaxaca, Mexico. Material contributions (M), Regulating contributions (R), Nonmaterial contributions (N).

themes, which was then complemented with information from workshops, participant observation, informal talks, and fieldwork notes; 2) classified into preliminary categories those similar themes, and identified *a priori* codes that served as the basis for an in-depth analysis of the information in a qualitative analysis software; 3) analyzed profoundly the interviews through the Atlas.ti software (version 7), which facilitated the creation of more robust codes that were grouped into more precise categories and subcategories of analysis –related to the peasant condition, traditional ecological knowledge, socio-ecological contributions, agricultural intensification, and fundamental human needs– (**Figure 2**); and 4) we analyzed the relations between codes, and between the codes and the local context, carrying out a continue observation of the coherency between data and the interpretations given, to assure the veracity of the results and explanations. The number of contributions for each TAFS was obtained from a list that condensed all the contributions registered in the three communities studied. Each contribution was contrasted with the data from the specific interviews for each TAFS, assigning values of presence-absence (0–1, respectively) for each one of them. In addition, this information was related to some ecological attributes (forest cover, and species diversity) obtained specifically for each TAFS analyzed in a previous study (see Rendón-Sandoval et al., 2020).

RESULTS

Peasants' Motivations to Maintain Vegetation

> *"What for sowing a «cucharito»* (the legume tree *Acacia cochliacantha*) *if it does not provide benefit? You have to sow a lemon tree to obtain a product . . . a mango, a chicozapote which give something"; "Herb that does not serve, why do I leave them?"; "I prefer trees that provide something –and although they do provide nothing, either way– I left them standing so that they continue living".*

The peasants' foremost motivations to maintain wild vegetation within their agricultural fields are the provision of several beneficial contributions that meet some of their fundamental needs (**Figure 2**; **Supplementary Material**). These beneficial contributions represent the most recorded contributions (83%, **Figure 3**), while 17% were detrimental

FIGURE 4 | Some outstanding material contributions that motivate the maintenance of native plants from tropical dry forests in the Cañada region, Oaxaca, Mexico. Provision of edible fruit and stems: "tunillo" *Stenocereus stellatus** **(A)**, "biznaga" *Ferocactus recurvus** **(B)**, "tempesquistle" *Sideroxylon palmeri** **(C)**, "nopal de cruz" *Acanthocereus subinermis** **(D)**. Medicinal plants: "cuachalalá" *Amphipterygium adstringens* **(E)**, "mala mujer" *Cnidoscolus tubulosus* **(F)**. *Species endemic from Mexico.

contributions. We identified that obtaining material contributions represents the peasants' main reasons to maintain plant components of TDF (62%). These were followed by regulating contributions (20%), and nonmaterial contributions (18%).

The most outstanding material contributions –which represent also the focal reasons to maintain biodiversity– include species providing edible fruit, greatly appreciated in the region (especially those of the Cactaceae family), medicinal plants, species used for live fences (with the capacity to regrowth of cuttings), fodder species, firewood for cooking, plants used for preparing beverages, those providing construction wood, edible stems and roots, condiments, materials for fabricating tools, domestic utensils and handcrafts, and edible flowers (**Figure 4**; **Table 1**).

The most relevant regulating contributions include plant species that provide shade, soil fertility, humidity keeping, rain attraction, pest control, pollinators habitat and other beneficial species, and protect soil against erosion. The nonmaterial contributions include species appreciated for special flavors conferred to regional stoves and beverages (which have high identity value), ornamental plants that are ceremonial, source of recreation, health, inspiration, as well as aromatic, ritual, and ludic plants (**Table 1**).

All these contributions of vegetation to the well-being of local people help to meet fundamental needs of subsistence, protection, and identity, but also others like affection, understanding, creation, participation, and leisure. We can visualize a direct relation between the number of contributions and the capacity to meet fundamental human needs (**Table 1**).

A few detrimental contributions of vegetation (17%), with a noteworthy importance, were referred to by peasants: 1) competence with crops for space, luminosity, humidity, and/or nutrients (primarily species with high reproductive success like "guaje" *Leucaena leucocephala*, "mantecoso" *Parkinsonia praecox*, "mezquite" *Prosopis laevigata*, "guamúchil" *Pithecellobium dulce*, and other legume trees); 2) the forest cover represents habitat of undesirable animal species since their damage to crops (e.g. birds like "chiquitón" *Melanerpes hypopolius* recognized as a seed consumer, ants *Atta mexicana* which cut flowers of some crops, or the coati *Nasua narica* which consume maize); 3) potential risk of injured due to breaking of branches and stems of giant plants (like the columnar cacti

TABLE 1 | Contributions of vegetation to local people's well-being through the satisfaction of some fundamental human needs in the Cañada region, Oaxaca, Mexico.

Contributions	Fundamental needs	Preferred plants
Material		
Edible fruit	Subsistence, identity	Cactaceae spp. ("jiotilla" or "xonostle" *Escontria chiotilla**, "garambullo" *Myrtillocactus geometrizans**, "nanabuela" or "barba de viejo" *Pilosocereus chrysacanthus**, "pitaya" *Stenocereus pruinosus**, "tunillo" *Stenocereus stellatus**), "guaje" *Leucaena leucocephala*, "tempesquistle" *Sideroxylon palmeri**
Medicinal	Protection	"Cuachalalá" *Amphipterygium adstringens* (healing), "oreganillo" *Lippia graveolens* (digestive), "mala mujer" *Cnidoscolus tubulosus* (antirheumatic)
Live fences	Protection	Cactaceae, Burseraceae, and Fabaceae spp.
Fodder	Subsistence, protection	Fabaceae spp. (immature fruits), "mantecoso" *Parkinsonia praecox* and "cardón" *Pachycereus weberi** (flowers), "caulote" *Guazuma ulmifolia*
Firewood for cooking	Subsistence	"Cucharito" *Acacia cochliacantha**, "mezquite" *Prosopis laevigata*, "oaxaqueño" *Senna atomaria*
Preparation of beverages	Identity	"chupandía" *Cyrtocarpa procera*, Cactaceae spp.
Construction wood	Protection	"Mezquite" *Prosopis laevigata*, "quebracho" *Acacia pringlei**, "cedro" *Cedrela odorata*, "caoba" *Swietenia humilis*, "cucharito" *Acacia cochliacantha**, "guajillo" *Lysiloma divaricatum*
Edible stems and leaves	Subsistence, identity	"Quelites" ("chepíl" *Crotalaria pumila*, "chepiche" *Porophyllum ruderale*, "quintonil" *Amaranthus hybridus*), "nopal de cruz" *Acanthocereus subinermis**
Edible roots	Subsistence	"Jícama de pochote" *Ceiba parvifolia**
Condiments	Identity, subsistence	"Oreganillo" *Lippia graveolens* and "aguacate" *Persea americana* (leaves)
Wood for fabricating tools and domestic utensils	Creation	"Agalán" *Karwinskia humboldtiana*, "palo prieto" *Colubrina elliptica*, "matagallina" *Quadrella incana*, "rompezallo" *Celtis pallida*
Edible flowers	Subsistence, identity	"Cacayas" of "rabo de león" *Agave quiotepecensis** and "mano de león" *Agave seemanniana**, "flor de pitayavieja" *Pilosocereus chrysacanthus**
Aphrodisiac	Affection	"Mezquite" *Prosopis laevigata*
Quench thirst	Subsistence	"Biznaga" *Ferocactus recurvus** (fruit)
Appetite stimulant	Protection, subsistence	"Chepiche" *Porophyllum ruderale* (leaves and stems)
Ferments	Identity	"Pulque rojo" of "cardón" *Pachycereus weberi**
Toys	Leisure	"Canoítas" *Amphilophium crucigerum* (fruit)
Materials for handcrafts	Creation	"Copalillo" *Bursera submoniliformis* (for fabricating sculptures of fantastic animals or "alebrijes")
Resins	Identity	"Linaloe" *Bursera linanoe**, *Bursera* spp.
Saponifiers (soap)	Protection	"Cholulo" *Ziziphus amole** (fruit)
Poisons	Protection	"Brea" *Bursera aptera** (resin)
Regulating		
Shade provision	Protection	"Mezquite" *Prosopis laevigata*, "guamúchil" *Pithecellobium dulce*, "guapinole" *Acacia coulteri**¸ "guaje" *Leucaena leucocephala*
Soil fertility	Protection	"Chimalacate" *Viguiera dentata*, Fabaceae spp.
Rain attraction	Protection, subsistence	*"All wild trees call rain"*
Humidity keeping	Protection, subsistence	"Mezquite" *Prosopis laevigata*, "higo" *Ficus cotinifolia,* "palo de agua" *Astianthus viminalis*
Pest control	Protection	"Venenillo" *Cascabela thevetia* (latex against the ant "chicatana" *Atta mexicana*)
Habitat for other species	Protection	"Mantecoso" *Parkinsonia praecox* (host of the edible mushroom "nanacate" *Schizophyllum commune*)
Prevention against soil erosion	Protection	*Agave* spp., *Hechtia* spp., *Opuntia* spp.
Nonmaterial		
Regional flavors	Identity, affection	Native (or "creole") maize *Zea mays*, "pulque rojo" of "cardón" *Pachycereus weberi**, "tesmole cuaresmeño" with "nopal de cruz" *Acanthocereus subinermis** and "tempesquistle" *Sideroxylon palmeri**, "chilhuacle" *Capsicum annuum*
Ornamental	Affection, understanding	"Roseta" *Echeveria laui**, "biznaguita" *Mammillaria huitzilopochtli**, "chilitos" or "piñitas" *Coryphantha calipensis**, "huesito" *Plocosperma buxifolium*, "solterito" *Petrea volubilis*, "cacaloxóchitl" *Plumeria rubra*, "cazahuate" *Ipomoea pauciflora*, "garañona" *Hintonia latiflora*
Source of inspiration, recreation, and health	Affection, leisure	*"Plants make feel good"*
Ceremonial or ritual	Participation, identity	"Copales" and "cuajiotes" of the genus *Bursera*, "huesito" *Plocosperma buxifolium*, "solterito" *Petrea volubilis*
Aromatic	Affection	Resins of *Bursera* spp.
Ludic	Leisure	"Canoítas" *Amphilophium crucigerum* (fruit)
"They have right to live"	Understanding	*"All wild plants"*

**Species endemics of Mexico.*

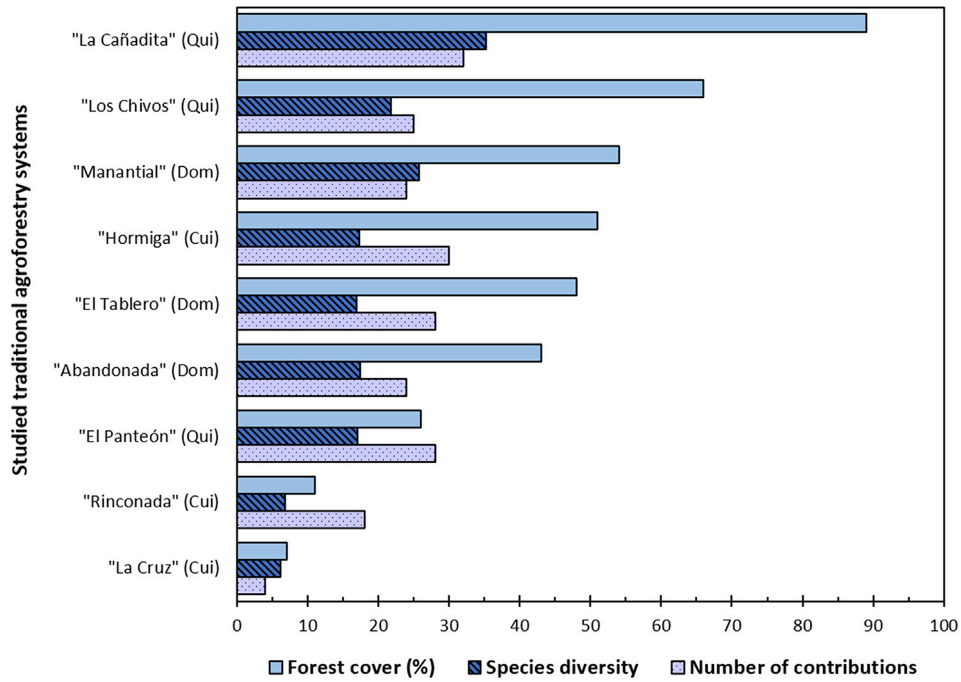

FIGURE 5 | Relation between the percentage of forest cover, species diversity, and number of contributions of vegetation to peasants managing traditional agroforestry systems –in three communities from the Cañada region, Oaxaca, Mexico–. The words in quotation marks correspond to the local names of the studied traditional agroforestry systems. Communities of Santiago Quiotepec (Qui), Santiago Dominguillo (Dom), Cuicatlán (Cui).

"cardón" *Pachycereus weberi* and "tetecho" *Neobuxbaumia tetetzo*); and 4) the presence of thorny plants hurting and making arduous agricultural labors (especially the "chile de perro" *Opuntia pubescens*, "cocoche loco" *Opuntia decumbens*, "uñas de gato" *Mimosa lactiflua*, *M. luisana* and *M. polyantha*, and the "mala mujer" *Cnidoscolus tubulosus*).

When considering some ecological parameters estimated previously by Rendón-Sandoval et al. (2020), like species diversity (average 19.38 ± 7.9 effective species per 500 m^2 sampling unit; min. 6.12, max. 35.23), and the proportion of forest cover maintained in TAFS (average 43.89% ± 26.12 min. 7%, max. 89%), we can observe that as long as these ecological attributes decline, number of contributions also decreases (average 23.67 ± 8.43 min. 4, max. 32; **Figure 5**).

Distinctive Features of the Peasant Condition

> *"The doctor does not eat his medicines, a teacher does not eat his letters, all food comes from the field, from the peasants' work who sow maize and beans..."; "Having maize and beans we are saved"; "I never added chemical, but only organic fertilizer"; "The «creole»* (native) *maize does not have chemicals, it is clean, pretty, tender, soft... and has good flavor".*

The continuity of the peasant condition documented in the Cañada region represents a form of small-scale agriculture –associated with TDF– practiced in parcels smaller than 3 ha (average 1.66 ± 0.55 ha; min. 0.69, max. 2.38) of communal or ejidal land tenure. There, peasants: 1) inherit land to successive generations, and may buy other parcels; 2) use traditional and modern tools and practices simultaneously; 3) use their own and family workforce, which represents a demanding and exhausting activity; 4) leave parcels in fallow, usually when they have more than one parcel; 5) have a communitarian organization that confers to them belonging; it is characterized by agreements in assemblies and collaboration among people of the community in non-profitable activities like "tequio" (a form of community work that is unpaid and morally obligatory only if there are no rules and sanctions for compliance) to maintain infrastructure of common use (e.g. repairing roads or irrigation systems); 6) practice a strategy of multiple use of natural components –to obtain a variety of products– (Boege, 2008; Toledo and Barrera-Bassols, 2008) which also includes the diversification of options to guarantee subsistence (e.g. a multiplicity of crops, which are spatially and temporally complementary, as well as livestock and free raising of goats in forest areas, backyard poultry, gathering of forest products, commerce, local services, and seasonal employment).

A fundamental aspect in the continuity of the peasant condition is the permanence and regeneration of the traditional ecological knowledge, which involves the set of beliefs and knowledge on relations of living beings and their environment, transmitted and recreated from generation to generation (Berkes et al., 1994). The peasant knowledge that we documented is characterized by long term planning –based on

FIGURE 6 | Traditional agroforestry systems ("milpa" and fruit plantations irrigated with "apancles") associated with tropical dry forests in the Cañada region, Oaxaca, Mexico. Communities of Santiago Quiotepec **(A,B)**, Santiago Dominguillo **(C,D)**, and Cuicatlán **(E,F)**.

careful observation and continuous interaction with the natural environment– comprising aspects mainly related to climate forecasting, ecological interactions, phenology, edaphology, taxonomy, animal behavior, germination, environmental requirements of plants, hydraulics, luminosity, morphology, territoriality, forest recovering stages, life forms, seasonality, sexual and asexual reproduction, pest control, physiology, pollination and seed dispersal syndromes. In addition, based on a complex interaction of factors and indicators they have a local precise agricultural calendar.

In the region, agriculture is characterized by the presence of TAFS which are fields irrigated through "apancles" (or irrigation channels) with water from rivers, streams, and springs that allow two cultivation cycles per year (**Figure 6**). They practice the traditional system of multi-crop "milpa" with native (or "creole") varieties of maize (white, yellow or golden, black or "negrito" or "prieto", and "pinto"), beans ("delgadito", and "mosquito"), and squashes ("támala") mainly destined to direct consumption and, sometimes, for barter, presents, or commercialization at local scale. They also cultivate fruit trees (especially lemon, sapodilla, mango, and spondias plum) destined partly for regional commercialization, and direct consumption.

People interviewed said to allow their crops coexisting with plants belonging to TDF through different forms of silvicultural management, or *in situ* management according to Casas et al. (1997): 1) *tolerance* (leave standing, selectively, some species of useful plants); 2) *promotion or enhancing* (increasing the abundance of plants valued for different purposes); 3) *protection* (eliminating competitors or herbivores, pruning, fertilizing, providing shade or light by clearing canopy of neighboring plants); and 4) *propagation* of wild plants locally appreciated through seed sowing, planting vegetative structures or transplanting entire individual plants.

All these forms of management are carried out in the following agroforestry practices: 1) *live fences*, commonly constructed with plants relocated from inside the parcels to the borders, or transplanting plants –or their parts– from forests; these fences delimit and protect the parcels; 2) *remnants of native vegetation,* which are portions of TDF with different degrees of conservation, generally associated to zones of the parcel inaccessible or difficult to use for agriculture; 3) *isolated trees*, frequently large-sized trees which are valued for providing multiple beneficial contributions; 4) *forest cover patches,* which are areas with plant species whose abundance is promoted because of their usefulness and high

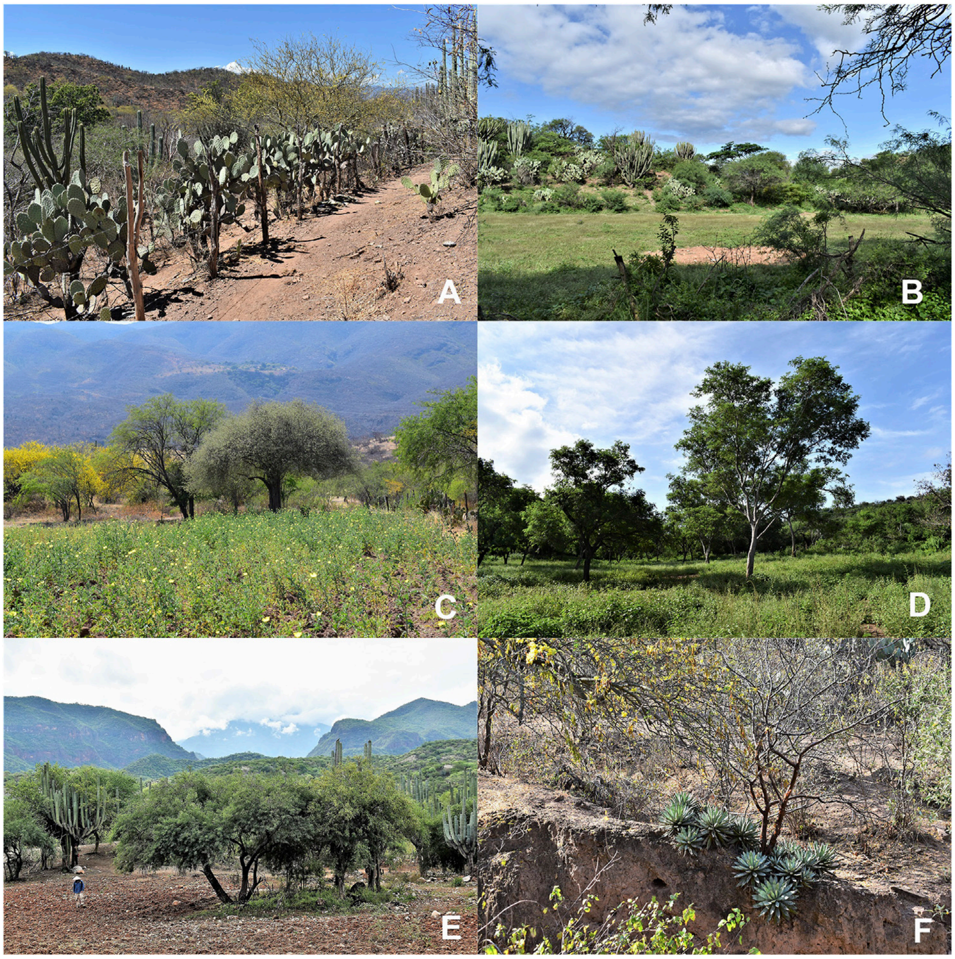

FIGURE 7 | Agroforestry practices implemented by peasants from the Cañada region, Oaxaca, Mexico. Live fences **(A)**, remnants of native vegetation **(B)**, isolated trees **(C)**, forest cover patches **(D)**, vegetation isles **(E)**, fringes against soil erosion **(F)**.

commercial value in the region; 5) *vegetation isles*, which are small patches of useful plants inside parcels; and 6) *fringes against soil erosion*, which are lines of plants arranged and maintained with the purpose of stabilizing the terrain, protecting soil against erosion, and/or maintaining humidity (**Figure 7**).

One of the attributes of the peasant condition favoring the maintenance of biocultural diversity is the agroecological management implemented, which comprise: 1) the intergenerational maintenance of agrobiodiversity through selecting and storing native seeds (a practice mainly carried out by women); 2) use of organic manures (goats and bats dung, and ash); 3) care of soil fertility by using leaf litter; 4) use of organic conservatives and repellents against pests (e.g. garlic against weevil, latex against ants); 5) the systematic experimentation of interventions on vegetation (e.g. to test less toxic pesticides on a few individuals, and to record how they respond); and 6) practice of agriculture without external inputs.

Peasants indicated some advantages of native (also called "creole") seeds over commercial varieties. According to them, native seeds have higher resistance and adaptability to the local environments, lower incidence of pests, lower cost (since after harvest these are stored for the following agricultural cycle), and lower dependence on agrochemical inputs. People consider native seeds better than the commercial ones in appearance, texture, nutritional value, performance, and, primarily, flavor (an outstanding aspect of identity and pride). It is also relevant that, according to peasants, until the mid-20th century, annual crops, and trees like avocado and papaya had good performance without using agrochemicals.

Finally, the peasant condition involves values expressed in: 1) local myths, referring to "enchanted" hills, offerings to obtain good harvests permit for using plants; 2) hope (especially to have constant rainy season); 3) gratitude (recognizing the benefits provided by nature, and the privilege to have several rivers in a semi-arid region); and 4) admiration (towards ornamental plants, natural landscapes, archaeological sites ancient, and rock paintings). It is also interesting that, in general, women frequently expressed affection and tenderness to the natural environment, while men expressed admiration and enthusiasm. Unfortunately, we also recorded cases of alcoholism, violence, abuse of authority, corruption associated with illegal traffic of species, and disputes for territories generating severe conflicts within and between communities.

Agricultural Intensification

> *"Time ago, people sowed and it was well, (I did not live that) my parents and grandparents talked to me . . . that they sowed, and they did not need neither chemical nor even plow. Plants grew big without fertilizers since the Earth was virgin, new, it had natural nutrients"; "We are finishing our lands".*

We recorded in the Cañada region some indicators of a process of agricultural intensification, which is directed to increase the total volume of agricultural production based on greater input productivity (such as labor, land, time investment, fertilizers, seeds, or cash) (FAO, 2004). In particular, we recorded the progressive replacement of native seeds –of maize and beans– by commercial varieties which causes loss of local agrobiodiversity and food autonomy. Likewise, plantations of lemon (*Citrus aurantifolia*) have increased, this represents a profitable crop that allows obtaining continuous (or at least with low uncertainty) monetary incomes throughout the year, compared with traditional "milpa". Also, local people started to practice plantations of the mezcal agave "espadín" (*Agave angustifolia*), since this profitable crop is resistant against drought. Despite these trends, we documented an active pattern of peasant diversification, with commercial crops (lemon, mango, sapodilla, spondias plum, and guaje) integrated to TAFS, coexisting with native species of TDF and traditional "milpa".

A notorious trend recorded is that in TAFS people are decreasing the forest cover inside their parcels, moving plants to the edges, in some cases even expressing disparagement for wild vegetation because they strongly competed with crops for light, water, or nutrients, which can severely limit agricultural activity. Removal of TDF occurs in the absence of communitarian agreements to protect it, since this responsibility is delegated to the Biosphere Reserve authorities.

Most people interviewed (80%) have one or two parcels relatively small (average 1.66 ha), which makes it difficult to leave resting the land. In such context, we recorded a gradient of agricultural intensification characterized by: 1) minimizing manual work and prioritizing monetary income; 2) a devaluation of the crops destined for self-consumption, where commercialization is privileged; 3) using fire to land "clearing"; 4) using tractor for soil tilling; 5) use of chemical fertilizers (nitrogenates like urea and ammonium sulfate), insecticides (malathion), herbicides (glyphosate), and fungicides (sulfured); which are expensive and unhealthy, cause a progressive resistance of pests (mainly "gusano cogollero" *Spodoptera frugiperda*, "araña roja" *Tetranychus urticae*, and "cenicilla" caused by fungi of the family Erysiphaceae), and which cause a gradual loss of peasant knowledge and agroecological management.

In contrast, there are expressions of peasant agriculture through which people: 1) give priority to native crops for direct consumption; 2) invest a high amount of familiar labor force; 3) use plow to prepare the land (since it allows precise management, where it is possible to sow "milpa" intercropped with lemons or other fruit trees); 4) employ traditional tools (mainly the "stake" for sowing, the hoe or "talacho" for weeding, and the "chicol" for collecting fruit); 5) minimizing the use of agrochemical; 6) reduce pest incidence; and 7) valuing and maintaining in TAFS some components of wild vegetation.

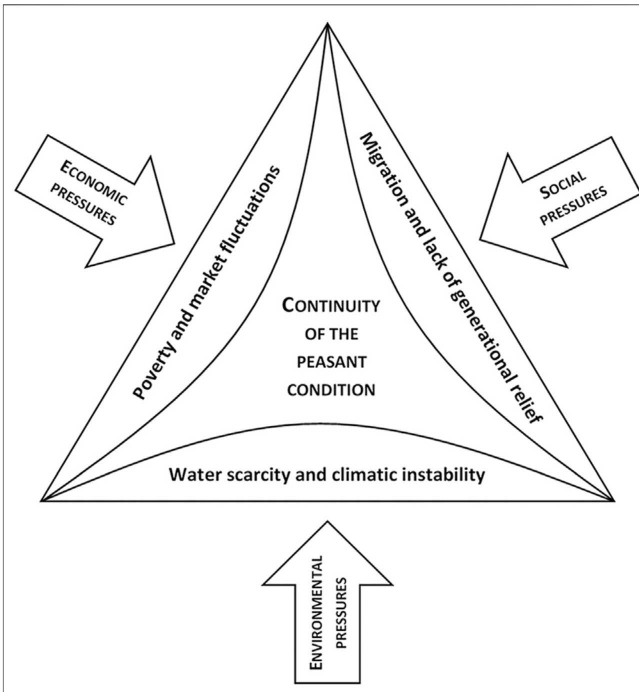

FIGURE 8 | Main environmental, economic, and social factors that weaken the continuity of the peasant condition in the Cañada region, Oaxaca, Mexico. Those attributes emerged in the qualitative analysis, and represent the most prominent factors and processes determining conservation capacities. The main economic pressure is poverty of local people and fluctuations in prices of profitable agricultural products, factors that are related to the main social pressure which is migration to cities of Mexico or the United States. These factors and the main environmental pressure which is the scarcity of water cause the eventual abandonment of agriculture and interrupt the peasant condition. Based on diagrams by Ploeg (2010).

Agricultural intensification is enhanced also by external factors like the promotion of agrochemical inputs and commercial seeds by the government and technical assistants oriented to productive intensification. Likewise, we identified other factors determining environmental, economic, and social pressures undermining the continuity of the peasant condition (**Figure 8**).

In the Cañada region, one of the most significant environmental pressures for the continuity of the peasant condition –involving the maintenance of vegetation and its provision contributions– is water scarcity, since TAFS depend directly on water from streams and springs. This condition is intimately linked to the climatic instability associated with variations in the rainy season, which is recognized by local people to have worsened since approximately 1 decade ago. Water availability represents a determinant factor favoring agricultural intensification. It was recorded that in sites irrigated throughout the year, people use to cultivate commercial varieties of "elotero" maize to be consumed as corn on the cob, which has high water requirements and agrochemical inputs. This crop is destined for commercialization in the region.

The most remarkable economic pressures are represented by the marked economic limitations of the peasants and the scarce opportunities to find salaried jobs in the communities, fluctuations in market prices, their dependence on intermediaries (or "coyotes") who hoard a considerable proportion of profits, as well as the investment in inputs and/or services like commercial seeds, agrochemicals, renting of the machinery and labor hand complementary to activities like sowing and land preparation.

The most critical social pressures are the abandonment of agriculture linked with migration to find jobs in other regions, and the weak generational relief since young people consider agriculture a demanding and tiring activity involving high uncertainty.

Other Factors Influencing Forest Conservation

> *"I hardly take them off: the «mantecoso», «mezquite», «cuachalalá», «copalillo», «tuna», «pitayas», «xoconostles», «cardón», «tetechos»...* (several species of wild plants) *all of them are in my land. I do not take them off since they have the right to live"; "Now, people of «La Biosfera»* (authorities of the Biosphere Reserve) *are who forbid to cut down trees"; "We have projects of the Biosphere Reserve to reforestation".*

During our analysis, other important elements emerged to consider the TDF conservation. These factors include: 1) the critical thinking of local people on the use of agrochemicals and health care, 2) the admiration for biodiversity and natural landscapes, the regional food, and multiple components of wild vegetation that are valued, 3) the practices directed to the restoration of biodiversity (e.g. the scattering of seeds of native trees in wild areas), 4) the respect and care of nature with ethic values and feelings of compassion towards others forms of life, 5) the restrictions from authorities of the Biosphere Reserve to use some species at risk, 6) the implementation of projects of the Biosphere Reserve like the rescue of wild plant species illegally extracted, reforestation, and environmental education, 7) the pride in biodiversity and agrobiodiversity, and 8) the inaccessibility of some areas of the territory (Trejo and Dirzo, 2000).

DISCUSSION

Peasants' Motivations to Maintain Vegetation

The peasants interviewed obtain a wide variety of socio-ecological contributions from the vegetation sheltered in the TAFS they manage. This fact shows that peasant agriculture can maintain biodiversity and provide multiple beneficial contributions that satisfy some fundamental human needs. Most of these socio-ecological contributions correspond to beneficial contributions (83%), while only 17% of the contributions we record are detrimental, which suggests that wild vegetation represents a primary source of well-being for people. This idea is supported by evidence showing that exposure to nature has a positive effect on physical and mental human health (Pretty, 2004).

The most determining motivations of peasants –to maintain components of wild vegetation within their agricultural fields– are obtaining material contributions, which help to meet subsistence, protection, and identity needs primarily. These are followed by regulating contributions which mostly provide protection, and some nonmaterial contributions that offer opportunities to meet needs for affection (through satisfiers such as admiration, care, and respect), understanding (through experimentation, rationality, and interpretation), and leisure (through tranquility, imagination, and nonchalance).

In this classification of nature's contributions to people the categories may partially overlap (Díaz et al., 2018). For instance, consuming fruits of wild cactus species helps to fulfill the need for subsistence, and simultaneously contributes to the identity of being "country people" and being able to enjoy regional flavors (that are highly valued for their ability to confer pleasure and pride). In this way, some material contributions can also have nonmaterial effects. Moreover, many contributions may be perceived as benefits or detriments depending on the cultural, socioeconomic, temporal, or spatial context (Díaz et al., 2018).

If we consider a gradient starting from material contributions (which are clearly useful, tangible, and conspicuous), through regulating contributions (which are involved in generating other contributions), these contributions could represent the *means* to realize some fundamental needs. Meanwhile, on the other side of the gradient, nonmaterial contributions (which might mistakenly be considered useless, and which are intangible, and inconspicuous) could constitute some of the ultimate *ends* of human existence, such as pleasure, inspiration, and recreation.

Remarkably, these socio-ecological contributions take shape only when there are previous valuations of natural goods in people's perceptions. Therefore, only when some values present in the natural components are known, experienced, and understood, do the contributions they make become manifest. The latter is related to the term of *resource diversity* proposed by Gerritsen (2002) to refer to the components of nature that peasants consciously identify and value, which is also recognized as a social promoter of agrobiodiversity. Thus, whereas monetary values have been broadly examined in the literature, description or measurement of symbolic, cultural, identity, and other non-economic values remain largely unexplored (Chan et al., 2012, Chan et al., 2016; Gómez-Baggethun and Barton, 2013).

The Satisfaction of Fundamental Human Needs

We distinguish the subsistence need, as a particular type of fundamental human need that is really *vital*, so it is often prioritized over other needs. However, without the satisfaction of the rest of fundamental needs, even if the human person can survive, it will be incomplete and will generate both individual and collective pathologies (Max-Neef et al., 1998).

We observed that TAFS that safeguard a greater proportion of forest cover and species diversity might provide a broader range of contributions (**Figure 5**), and thus have a greater potential to meet fundamental human needs. Is important to recognize the benefits of peasant agriculture in terms of its high capacity to provide beneficial contributions to all of humanity, compared to industrial agriculture that devastates ecosystems and eliminates ecological processes, and then seeks to replace them with commercial inputs. This acknowledgement should help overcome existing power asymmetries between western science and traditional ecological knowledge (Díaz et al., 2018).

Peasant agriculture stands out because it represents: 1) reservoirs of agrobiodiversity with thousands of edible plants strengthening food autonomy; 2) small-scale diversified systems representing a more varied diet with beneficial health implications; 3) reservoirs of local crop varieties; 4) regenerative systems that protect the soil by incorporating organic matter; 5) scenarios where local innovations, horizontal exchanges, cooperative relationships, knowledge and holistic experimentation of nature occur; and 6) a complex matrix of biological corridors at the landscape level that provide habitat for a wide variety of associated species (Perfecto and Vandermeer, 2008; Rosset and Altieri, 2019).

In addition, peasant agriculture involves some aspects that make possible the maintenance of native vegetation, with principles of respect and reciprocity towards the natural components that emanate from the traditional ecological knowledge of the peasants. However, these peasant interventions in favor of biodiversity conservation and human well-being are threatened by a prevailing model of agricultural intensification.

Finally, it would be desirable to recover, promote, and put into practice those expressions of peasant agriculture, especially the agroecological management, as well as the implementation of agroforestry practices and forms of silvicultural management, which can contribute to satisfy fundamental human needs without drastically, profoundly, and irreversibly deteriorating the natural environment.

Some Circumstances Behind the Agricultural Intensification

We identified that the principal threat affecting biodiversity conservation in TAFS is agricultural intensification. Such intensification is linked to clear environmental pressures such as water scarcity and climate instability, where increased availability of water for irrigation increases agricultural intensification.

In addition, there are economic pressures such as the poverty conditions in which many peasants live (in the face of dependence on expensive agroindustrial inputs), and fluctuations in market prices when selling their crops, which are exacerbated by the intervention of intermediaries who capture a significant share of the profits that should go to the peasants. Interestingly, some peasants expressed their willingness to increase agricultural intensification if they had the financial resources to do so, which would undoubtedly reduce the presence of native vegetation on their parcels. Serious social pressures also operate on the continuity of the peasant condition, such as migration, which causes the abandonment of agriculture and makes it difficult for the generational relief.

Furthermore, there are other structural conditions such as the historical marginalization and systematic disarticulation of the peasantry. As well as their struggle for autonomy, which takes place in a context characterized by relationships of dependence and deprivation, as Ploeg (2010) points out in his definition of the peasant condition.

The decrease in forest cover and species diversity –that commonly occur in the TAFS– also declines the number of contributions (**Figure 5**) and their potential to meet human needs. Therefore, the removal of wild vegetation from agricultural fields may represent a disadvantageous practice, but in fact, this is a trade-off since wild vegetation limits yield in agricultural production by competing with crops. This means losses for peasants, which leads most of them to use practices with varying degrees of intensification to obtain a higher yield in the shortest possible time. This is a necessity more than an option of agricultural management –if we take into account the precarious conditions peasants live–. Thus, a single detrimental contribution of wild vegetation (such as competition with crops) may outweigh the multiple beneficial contributions, and thus become a motivation to remove it.

Motivations for maintaining or removing vegetation are explained more by local contextual circumstances in multiple aspects (political, economic, environmental, cultural, historical, among others) influencing the well-being, and not only by the valuation of beneficial contributions (material, regulating, and nonmaterial). This consideration is fundamental for designing and implementing optimal strategies for both biodiversity conservation and human well-being. The underlying reasons and conditions of peasants –whose livelihoods are intrinsically linked to nature–, but whose opportunities for planned long-term agroforestry management are extremely limited for the majority must be made visible, which has to do, we reiterate, with the structural conditions of inequity and historical inequality in social sectors of the country such as the peasantry.

The Importance of Nature's Contributions for Peasants

It is essential to contemplate the importance of nature's contributions for peasants, beyond putting our valuations oriented towards biodiversity conservation (e.g. the paradox of prioritizing biodiversity conservation when the fundamental need for subsistence is not meet) because it is a fact that the exhausting peasants' work does not allow conservation to be considered as a priority.

Any hope for conserving biological diversity is predicated on a concomitant effort to appreciate and protect cultural diversity (Pretty et al., 2009). In this context, we delegate a great responsibility to peasants. When, at best, their essential labor is valued and recognized, we run the risk of idealizing their way of life, pretending that peasants renounce the comforts they could access through the capitalist commodification of their production.

We expect peasants to carry out a diversified agroecological production, nature-friendly, agrochemical-free, with community organizations linked to markets to supply the cities, etc. although they are the ones who generate and safeguard agrobiodiversity, currently produce the majority of food for human consumption (70%) –compared to industrial agriculture– (Graeub et al., 2016; Shiva, 2016; ETC Group, 2017), and have conserved biocultural diversity for thousands of years, and continue to do so today. All this in contexts of disadvantage, as mentioned above.

Finally, some relevant factors that could explain the continuity of the peasant condition, which has historically prevailed in resistance against the tide, are: 1) the cooperation (with a relative balance between individual and collective interests); 2) the relations of reciprocity and mutual aid; and 3) the dynamics where exchange-values are reinserted into peasant agriculture and converted into use-values, to produce and reproduce their base of resources (Ploeg, 2010).

Concluding Remarks

With this study we recognize the need to continue research to address the importance of the beneficial contributions of vegetation to the economy and direct subsistence of local communities. We have carried out several studies on use, extraction rates and spatial availability of plant components in forests, agricultural, and agroforestry systems of the region (e.g. Pérez-Negrón and Casas, 2007; Moreno-Calles et al., 2012). In those studies, we compared the value of forest products with that of products from agricultural systems of maize, the main crop in the area. We found that maize production in the area is, in general, insufficient to satisfy the annual local demand of households (on average, local production covers nearly 60% of the local needs). Local people, therefore, have to import most of their food and complement their economy by commercialization of fruit produced in homegardens and plantations. But importantly, they complement their diet by gathering forest products from the wild vegetation. We have estimated that, on average, the annual diet in rural communities of the Tehuacán-Cuicatlán Valley is nearly 12% formed by wild and weedy food products (Casas et al., 2008; Casas et al., 2014; Casas et al., 2016; Casas et al., 2017). In addition, Moreno-Calles et al. (2012) found that TAFS with intermediate forest cover have higher economic value than monocultures and forests.

Nevertheless, in several studies, but in this one in particular, we document that several beneficial contributions of vegetation are not marketable (e.g. shade provision, humidity keeping, or habitat for pollinators), and these are often undervalued even though they are really essential.

Small-scale peasant agriculture has some undeniable advantages over industrial agriculture. Especially when considering the social, environmental, and economic costs (or *externalities*) involved in agroindustrial production that conventional economic accounting fails to capture (Sathirathai and Barbier, 2001; Goméz-Baggethun and Martín-López, 2010; Holt-Giménez, 2017). For instance, severe environmental and social damages such as massive removal of wild vegetation and habitat destruction, biodiversity loss, demand for huge amounts of water and polluting chemical inputs, transgressing the peasant way of life, and causing disabling dependency to the detriment of local autonomies can be mentioned (Ploeg, 2010; Giraldo, 2018).

Considering the trend of productive intensification documented in this study, it would be interesting to try to predict possible scenarios of change of the TAFS in the future. Moreno-Calles et al. (2010); Moreno-Calles et al. (2012), for instance, pointed out that TAFS in the Tehuacán-Cuicatlán Valley are losing their capability to maintain forest cover, mainly because of 1) decreasing amount of land managed by households, determined by a progressive fragmentation of the land area given to new families, 2) adoption of technologies to intensify agriculture, and 3) governmental programs penalizing the presence of vegetation patches within agricultural parcels since they are considered "useless" areas.

However, a more recent study by our team (Vallejo et al., 2019) found that, despite local people and researchers perceive a progressive decline in both natural ecosystems and TAFS, agricultural areas are being abandoned, thus favoring the regeneration of wild vegetation, as well as a 9% increase of TAFS over conventional agricultural systems. Nevertheless, it should be carefully analyzed whether this "recovery" –of wild vegetation and TAFS– is being driven primarily by the abandonment of agriculture in a context of migration and/or restrictions imposed by authorities of the Biosphere Reserve and other factors determining environmental, economic, and social pressures undermining the continuity of the peasant condition (**Figure 8**).

For future research, we recommend using approaches that help to understand the complexity of TAFS. A good example could be the *Ethnoagroforestry* approach, as this perspective provides a theoretical framework that integrates socio-ecological aspects from different disciplines with traditional ecological knowledge. Ethnoagroforestry seeks to establish the basis for integrating cultural, agricultural and forest diversity –as well as the abiotic components of the system– recognizing that peasants and indigenous communities are the main drivers and planners of the use of landscape diversity. This approach also notes out that expressions of traditional agroforestry management may be able to provide the basis for food sovereignty and sustainable management of socio-ecological systems (Moreno-Calles et al., 2016).

There is an unquestionable need for complementary researches between different disciplines and worldviews, since biodiversity conservation issues cannot be addressed only by biological sciences, but must consider all the dimensions that link human societies with natural components (Alves and Albuquerque, 2012). Qualitative studies like the one we report here allow identifying processes and relationships among factors influencing management decisions and their consequence on vegetation cover, composition and potential to recover ecosystems. Pertinent questions for extensive surveys and sampling methods for rapid diagnoses of agroforestry systems at regional level may be designed based on the researches conducted until now, and that is our purpose for further studies.

The conservation and the sustainable use of nature's components is determinant for guarantee the well-being of societies. All the social-ecological systems depend on ecosystems and their components to sustain long-term conditions for life (Odum, 1989). Peasant agriculture can maintain biodiversity at the same time satisfying some fundamental human needs. However, it needs to be revitalized, made more efficient, profitable, and dignified. The agroecological management implemented by peasants –in traditional agroforestry systems– is very important for ensuring the maintenance of essential environmental functions for humanity's quality of life on the planet.

Moreover, beyond commitment and responsibility (with moral-ethical foundations), we need *affective relationships* of respect and reverence for all expressions of life and nature (including some life-sustaining components, such as water, wind, rocks), since humans and nonhuman entities are interwoven in deep relationships of kinship and reciprocal obligations (Berkes, 2017). We need an active understanding back to the relationships of reciprocity between society and nature.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

FR-S designed the study, performed fieldwork, analyzed the information, and wrote the manuscript. AC designed and advised the study, and wrote the manuscript. PS-R contributed to the methodological design, performed fieldwork, and wrote the manuscript. EG-F and AM-C designed and advised the study, and proofread the manuscript. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2021.682207/full#supplementary-material

REFERENCES

Altieri, M. A., and Toledo, V. M. (2011). The Agroecological Revolution in Latin America: Rescuing Nature, Ensuring Food Sovereignty and Empowering Peasants. *J. Peasant Stud.* 38, 587–612. doi:10.1080/03066150.2011.582947

Alves, R., and Albuquerque, U. (2012). Ethnobiology and Conservation: Why Do We Need a New Journal? *Ethnobio Conserv* 1, 2–4. doi:10.15451/ec2012-8-1.1-1-03

Banda, R. K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., et al. (2016). Plant Diversity Patterns in Neotropical Dry Forests and Their Conservation Implications. *Science* 353, 1383–1387. doi:10.1126/science.aaf5080

Berkes, F., Folke, C., and Gadgil, M. (1994). Traditional Ecological Knowledge, Biodiversity, Resilience and Sustainability. *Biodivers. Conserv.* 4, 269–287. doi:10.1007/978-94-011-0277-3_1510.1007/978-94-011-1006-8_15

Berkes, F., and Folke, C. (1998). *Linking Social and Ecological Systems. Management Practices and Social Mechanisms for Building Resilience.* Cambridge: Cambridge University Press.

Berkes, F. (2017). *Sacred Ecology*. 4th ed. New York: Routledge. doi:10.4324/9781315114644

Blancas, J., Casas, A., Pérez-Salicrup, D., Caballero, J., and Vega, E. (2013). Ecological and Socio-Cultural Factors Influencing Plant Management in Náhuatl Communities of the Tehuacán Valley, Mexico. *J. Ethnobiol. Ethnomed.* 9, 39–22. doi:10.1186/1746-4269-9-39

Blancas, J., Casas, A., Rangel-Landa, S., Moreno-Calles, A., Torres, I., Pérez-Negrón, E., et al. (2010). Plant Management in the Tehuacán-Cuicatlán Valley, Mexico1. *Econ. Bot.* 64, 287–302. doi:10.1007/s12231-010-9133-0

Boege, E. (2008). *El patrimonio biocultural de los pueblos indígenas de México. Hacia la conservación* in situ *de la biodiversidad y agrodiversidad en los territorios indígenas*. 1st ed. Ciudad de México: INAH, CDI.

Brunel, M. C. (2008). Poner la conservación al servicio de la producción campesina, reto para la construcción de un nuevo paradigma de desarrollo. *Argumentos* 57, 115–137.

Casas, A., Caballero, J., Mapes, C., and Zárate, S. (1997). Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Bot. Sci.* 61, 31–47. doi:10.17129/botsci.1537

Casas, A., Camou, A., Otero Arnaiz, A., Rangel Landa, S., Cruse-Sanders, J., Solís, L., et al. (2014). Manejo tradicional de biodiversidad y ecosistemas en Mesoamérica: el Valle de Tehuacán. *Investig. Ambient.* 6, 23–44.

Casas, A., Lira, R., Torres-García, I., Delgado-Lemus, A., Moreno-Calles, A. I., Rangel-Landa, S., et al. (2016). "Ethnobotany for Sustainable Ecosystem Management: A Regional Perspective in the Tehuacán Valley," in *Ethnobotany of Mexico. Interactions of People and Plants in Mesoamerica*. Editors R. Lira, A. Casas, and J. Blancas (Utrecht: Springer), 179–206. doi:10.1007/978-1-4614-6669-7_1

Casas, A., Otero-Arnaiz, A., Pérez-Negrón, E., and Valiente-Banuet, A. (2007). *In Situ* Management and Domestication of Plants in Mesoamerica. *Ann. Bot.* 100, 1101–1115. doi:10.1093/aob/mcm126

Casas, A., Parra-Rondinel, F. A., Aguirre-Dugua, X., Rangel-Landa, S., Blancas, J., Vallejo, M., et al. (2017). "Manejo y domesticación de plantas en Mesoamérica. Una estrategia de investigación y estado del conocimiento sobre los recursoés genéticos," in *Domesticación en el continente americano. Volumen 2. Investigación para el manejo sustentable de recursos genéticos en el Nuevo Mundo*. Editors A. Casas, J. Torres-Guevara, and F. A. Parra-Rondinel (Morelia: Editorial Morevalladolid), 69–102.

Casas, A., Rangel-Landa, S., Torres-García, I., Pérez-Negrón, E., Solís, L., Parra-Rondinel, F. A., et al. (2008). "In Situ Management and Conservation of Plant Resources in the Tehuacán-Cuicatlán Valley, Mexico: An Ethnobotanical and Ecological Approach," in *Current Topics in Ethnobotany*. Editors U. P. Albuquerque and M. Alves (Kerala: Research Signpost), 1–25.

Casas, A., Valiente-Banuet, A., Viveros, J. L., Caballero, J., Cortés, L., Dávila, P., et al. (2001). Plant Resources of the Tehuacán-Cuicatlán valley, Mexico. *Econ. Bot.* 55, 129–166. doi:10.1007/BF02864551

Challenger, A. (1998). *Utilización y conservación de los ecosistemas terrestres de México: pasado, presente y futuro*. Ciudad de México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Universidad Nacional Autónoma de México y Agrupación Sierra Madre, S.C.

Chan, K. M. A., Balvanera, P., Benessaiah, K., Chapman, M., Díaz, S., Gómez-Baggethun, E., et al. (2016). Why Protect Nature? Rethinking Values and the Environment. *Proc. Natl. Acad. Sci. USA* 113, 1462–1465. doi:10.1073/pnas.1525002113

Chan, K. M. A., Satterfield, T., and Goldstein, J. (2012). Rethinking Ecosystem Services to Better Address and Navigate Cultural Values. *Ecol. Econ.* 74, 8–18. doi:10.1016/j.ecolecon.2011.11.011

Clement, C. R., Casas, A., Parra-Rondinel, F. A., Levis, C., Peroni, N., Hanazaki, N., et al. (2021). Disentangling Domestication from Food Production Systems in the Neotropics. *Quaternary* 4, 4. doi:10.3390/quat4010004

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., et al. (2018). Assessing Nature's Contributions to People. *Science* 359, 270–272. doi:10.1126/science.aap8826

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., et al. (2019). Pervasive Human-Driven Decline of Life on Earth Points to the Need for Transformative Change. *Science* 366, eaax3100. doi:10.1126/science.aax3100

Drury, R., Homewood, K., and Randall, S. (2011). Less Is More: the Potential of Qualitative Approaches in Conservation Research. *Anim. Conserv.* 14, 18–24. doi:10.1111/j.1469-1795.2010.00375.x

ETC Group (2017). *Quién nos alimentará? La red campesina alimentaria o la cadena agroindustrial?* 3rd ed. Montreal: ETC Group.

FAO (2004). *La ética de la intensificación sostenible de la agricultura*. Roma: Food and Agriculture Organization of the United Nations (FAO).

García, E. (2004). *Modificaciones al sistema de clasificación climática de Köppen (para adaptarlo a las condiciones de la República Mexicana)*. 5th ed.. Ciudad de México: Instituto de Geografía, Universidad Nacional Autónoma de México.

Gerritsen, P. (2002). *Diversity at Stake. A Farmer's Perspective on Biodiversity and Conservation in Western Mexico*. Wageningen: Wageningen Universiteit.

Giraldo, O. F. (2018). *Ecología política de la agricultura. Agroecología y posdesarrollo*. 1st ed.. San Cristóbal de Las Casas: El Colegio de la Frontera Sur.

Glaser, B., and Strauss, A. (1967). *The Discovery of Grounded Theory*. Chicago: Aldine Press.

Gómez-Baggethun, E., and Barton, D. N. (2013). Classifying and Valuing Ecosystem Services for Urban Planning. *Ecol. Econ.* 86, 235–245. doi:10.1016/j.ecolecon.2012.08.019

Goméz-Baggethun, E., and Martín-López, B. (2010). "Los costes socioeconómicos asociados a la pérdida de biodiversidad," in *Lychnos. Consideraciones socieconómicas asociadas a la conservación* (Madrid: Fundación General CSIC), 68–74.

Graeub, B. E., Chappell, M. J., Wittman, H., Ledermann, S., Kerr, R. B., and Gemmill-Herren, B. (2016). The State of Family Farms in the World. *World Develop.* 87, 1–15. doi:10.1016/j.worlddev.2015.05.012

Holt-Giménez, E. (2017). *El capitalismo también entra por la boca: comprendamos la economía política de nuestra comida*. New York: Monthly Review Press, Food First Books.

Intergovernmental Panel for Climate Change (IPCC) (2013). *Climate Change. The Physical Science Basis*. New York: Intergovernmental Panel for Climate Change (IPCC).

IPBES (2019). *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn: IPBES secretariat.

Janzen, D. H. (1988). "Tropical Dry Forests: The Most Endangered Major Tropical Ecosystem," in *Biodiversity*. Editors E. O. Wilson and F. M. Peters (Washington, D.C.: National Academy Press), 130–137.

Lira, R., Casas, A., Rosas-López, R., Paredes-Flores, M., Pérez-Negrón, E., Rangel-Landa, S., et al. (2009). Traditional Knowledge and Useful Plant Richness in the Tehuacán-Cuicatlán Valley, Mexico. *Econ. Bot.* 63, 271–287. doi:10.1007/s12231-009-9075-6

MacNeish, R. S. (1967). "A Summary of the Subsistence,," in *The Prehistory of the Tehuacán Valley. Volume 1. Environment and Subsistence*. Editor D. S. Byers (Austin: University of Texas Press), 290–309.

Max-Neef, M., Elizalde, A., and Hopenhayn, M. (1998). *Desarrollo a Escala Humana. Conceptos, Aplicaciones Y Algunas Reflexiones*. 2nd ed.. Barcelona: Icaria Editorial.

Millennium Ecosystem Assessment (MEA) (2005). *Ecosystems and Human Well-being Biodiversity Synthesis*. Washington, D.C: Island Press.

Moreno-Calles, A., Casas, A., Blancas, J., Torres, I., Masera, O., Caballero, J., et al. (2010). Agroforestry Systems and Biodiversity Conservation in Arid Zones: the Case of the Tehuacán Valley, Central México. *Agroforest Syst.* 80, 315–331. doi:10.1007/s10457-010-9349-0

Moreno-Calles, A. I., Casas, A., García-Frapolli, E., and Torres-García, I. (2012). Traditional Agroforestry Systems of Multi-Crop "milpa" and "chichipera" Cactus forest in the Arid Tehuacán Valley, Mexico: Their Management and Role in People's Subsistence. *Agroforest Syst.* 84, 207–226. doi:10.1007/s10457-011-9460-x

Moreno-Calles, A. I., Casas, A., Rivero-Romero, A. D., Romero-Bautista, Y. A., Rangel-Landa, S., Fisher-Ortíz, R. A., et al. (2016). Ethnoagroforestry: Integration of Biocultural Diversity for Food Sovereignty in Mexico. *J. Ethnobiol. Ethnomed.* 12. doi:10.1186/s13002-016-0127-6

Moreno-Calles, A. I., Toledo, V. M., and Casas, A. (2014). "La importancia biocultural de los sistemas agroforestales tradicionales de México," in *Hacia un modelo intercultural de sociedad del conocimiento en México*. Editors L. Olive and L. Lazos-Ramírez (Ciudad de México: Universidad Nacional Autónoma de México), 35–56.

Newing, H., Eagle, C. M., Puri, R. K., and Watson, C. W. (2011). *Conducting Research in Conservation. A Social Science Perspective*. New York: Routledge.

Noble, I. R., and Dirzo, R. (1997). Forests as Human-Dominated Ecosystems. *Science* 277, 522–525. doi:10.1126/science.277.5325.522

Odum, E. P. (1989). *Ecology and Our Endangered Life-Support Systems*. Sunderland: Sinauer Associates.

Olson, D. M., and Dinerstein, E. (2002). The Global 200: Priority Ecoregions for Global Conservation. *Ann. Mo. Bot. Garden* 89, 199–224. doi:10.2307/3298564

Pelcastre, V., García-Frapolli, E., Ayala-Orozco, B., and Lazos-Chavero, E. (2020). Perspectives on Native maize Conservation in Mexico: a Public Programme Analysis. *Envir. Conserv.* 48, 33–40. doi:10.1017/S0376892920000417

Pérez-Negrón, E., and Casas, A. (2007). Use, Extraction Rates and Spatial Availability of Plant Resources in the Tehuacán-Cuicatlán Valley, Mexico: The Case of Santiago Quiotepec, Oaxaca. *J. Arid Environ.* 70, 356–379. doi:10.1016/j.jaridenv.2006.12.016

Perfecto, I., and Vandermeer, J. (2008). Biodiversity Conservation in Tropical Agroecosystems. *Ann. Acad. Sci.* 1134, 173–200. doi:10.1196/annals.1439.011

Ploeg, J. D. (2010). *Nuevos campesinos. Campesinos e imperios alimentarios*. Barcelona: Icaria.

Pretty, J., Adams, B., Berkes, F., Ferreira, S., Athayde, D., and Dudley, N. (2009). The Intersections of Biological Diversity and Cultural Diversity: Towards Integration. *Conserv. Soc.* 7, 100–112. doi:10.4103/0972-4923.58642

Pretty, J. (2004). How Nature Contributes to Mental and Physical Health. *Spirituality Health* 5, 68–78. doi:10.1002/shi.220

Rangel-Landa, S., Casas, A., García-Frapolli, E., and Lira, R. (2017). Sociocultural and Ecological Factors Influencing Management of Edible and Non-edible Plants: the Case of Ixcatlán, Mexico. *J. Ethnobiol. Ethnomed.* 13, 1–43. doi:10.1186/s13002-017-0185-4

Rendón-Sandoval, F. J., Casas, A., Moreno-Calles, A. I., Torres-García, I., and García-Frapolli, E. (2020). Traditional Agroforestry Systems and Conservation of Native Plant Diversity of Seasonally Dry Tropical Forests. *Sustainability* 12, 4600–4627. doi:10.3390/su12114600

Rendón-Sandoval, F. J. (2020). "El potencial de los sistemas agroforestales en la conservación y restauración de la vegetación nativa de la Caatinga,," in *Ecologia da Caatinga: curso de campo 2018*. Editors P. Sena, B. Pinho, D. Gomes Sousa, F. Pimentel Lopes de Melo, M. Tabarelli, and I. R. Leal (Recife: UFPE), 108–119.

Rosset, P., and Altieri, M. (2019). "Evidencias de la efectividad de la Agroecología," in *Agroecología: Ciencia Y Política*. Editors P. Rosset and M. Altieri (Zacatecas: Universidad Autónoma de Zacatecas), 87–119.

Rzedowski, J. (1991). El endemismo en la flora fanerogámica mexicana: una apreciación analítica preliminar. *Acta Bot. Mex.* 15, 47–64. doi:10.21829/abm15.1991.620

Rzedowski, J. (1978). *Vegetación de México*. Ciudad de México: Limusa.

Sathirathai, S., and Barbier, E. (2001). Valuing Mangrove Conservation in Southern Thailand. *Contemp. Econ. Pol.* 19, 109–122. doi:10.1111/j.1465-7287.2001.tb00054.x

SEMARNAT (2019). *Experiencias de Agroforestería en México*. Editor A. I. Moreno-Calles. 1st ed. (Ciudad de México: Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT).

Shiva, V. (2016). *Who Really Reeds the World? the Failures of Agribusiness and the Promise of Agroecology*. Berkeley: North Atlantic Books.

Smith, C. E. (1967). "Plant Remains," in *The Prehistory of the Tehuacán Valley. Volume 1. Environment and Subsistence*. Editor D. S. Byers (Austin: University of Texas Press), 220–255.

Strauss, A., and Corbin, J. (2002). *Basics of Qualitative Research. Techniques and Procedures for Developing Grounded Theory*. London: Sage Publications, Inc.

Taylor, S. J., and Bogdan, R. (1987). "Análisis de los datos en la investigación cualitativa," in *Introducción a los métodos cualitativos de investigación. La búsqueda de significados* (Barcelona: Paidós), 152–176.

Toledo, V. M., and Barrera-Bassols, N. (2008). *La memoria biocultural. La importancia ecológica de las sabidurías tradicionales*. Barcelona: Icaria Editorial.

Toledo, V. M., and Boege, E. (2010). "La biodiversidad, las culturas y los pueblos indígenas," in *La biodiversidad de México*. Editor V. M. Toledo (Ciudad de México: FCE-CONACULTA), 160–192.

Trejo, I., and Dirzo, R. (2000). Deforestation of Seasonally Dry Tropical forest. *Biol. Conser.* 94, 133–142. doi:10.1016/S0006-3207(99)00188-3

Valiente-Banuet, A., Casas, A., Alcántara, A., Dávila, P., Flores-Hernández, N., Arizmendi, M. d. C., et al. (2000). La vegetación del Valle de Tehuacán-Cuicatlán. *Bot. Sci.* 67, 25–74. doi:10.17129/botsci.1625

Vallejo, M., Casas, A., Blancas, J., Moreno-Calles, A. I., Solís, L., Rangel-Landa, S., et al. (2014). Agroforestry Systems in the highlands of the Tehuacán Valley, Mexico: Indigenous Cultures and Biodiversity Conservation. *Agroforest Syst.* 88, 125–140. doi:10.1007/s10457-013-9660-7

Vallejo, M., Casas, A., Pérez-Negrón, E., Moreno-Calles, A. I., Hernández-Ordoñez, O., Tellez, O., et al. (2015). Agroforestry Systems of the lowland Alluvial Valleys of the Tehuacán-Cuicatlán Biosphere Reserve: an Evaluation of Their Biocultural Capacity. *J. Ethnobiol. Ethnomed.* 11, 8. doi:10.1186/1746-4269-11-8

Vallejo, M., Moreno-Calles, A. I., and Casas, A. (2016). TEK and Biodiversity Management in Agroforestry Systems of Different Sociocological Contexts of the Tehuacán Valley. *J. Ethnobiol. Ethnomed.* 12, 31. doi:10.1186/s13002-016-0102-2

Vallejo, M., Ramírez, M. I., Reyes-González, A., López-Sánchez, J., and Casas, A. (2019). Agroforestry Systems of the Tehuacán-Cuicatlán Valley: Land Use for Biocultural Diversity Conservation. *Land* 8, 24. doi:10.3390/LAND8020024

Wolf, E. R. (1955). Types of Latin American Peasantry: A Preliminary Discussion. *Am. Anthropol.* 57, 452–471. doi:10.1525/aa.1955.57.3.02a00050

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‘Taking Fishers’ Knowledge to the Lab’: An Interdisciplinary Approach to Understand Fish Trophic Relationships in the Brazilian Amazon

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Trophic levels can be applied to describe the ecological role of organisms in food webs and assess changes in ecosystems. Stable isotopes analysis can assist in the understanding of trophic interactions and use of food resources by aquatic organisms. The local ecological knowledge (LEK) of fishers can be an alternative to advance understanding about fish trophic interactions and to construct aquatic food webs, especially in regions lacking research capacity. The objectives of this study are: to calculate the trophic levels of six fish species important to fishing by combining data from stable isotopes analysis and fishers’ LEK in two clear water rivers (Tapajós and Tocantins) in the Brazilian Amazon; to compare the trophic levels of these fish between the two methods (stable isotopes analysis and LEK) and the two rivers; and to develop diagrams representing the trophic webs of the main fish prey and predators based on fisher’s LEK. The fish species studied were Pescada (*Plagioscion squamosissimus*), Tucunaré (*Cichla pinima*), Piranha (*Serrasalmus rhombeus*), Aracu (*Leporinus fasciatus*), Charuto (*Hemiodus unimaculatus*), and Jaraqui (*Semaprochilodus* spp.). A total of 98 interviews and 63 samples for stable isotopes analysis were carried out in both rivers. The average fish trophic levels did not differ between the stable isotopes analysis and the LEK in the Tapajós, nor in the Tocantins Rivers. The overall trophic level of the studied fish species obtained through the LEK did not differ from data obtained through the stable isotopes analysis in both rivers, except for the Aracu in the Tapajós River. The main food items consumed by the fish according to fishers’ LEK did agree with fish diets as described in the biological literature. Fishers provided useful information on fish predators and feeding habits of endangered species, such as river dolphin and river otter. Collaboration with fishers through LEK studies can be a viable approach to produce reliable data on fish trophic ecology to improve fisheries management and species conservation in tropical freshwater environments and other regions with data limitations.

Keywords: fish ecology, food webs, local ecological knowledge, stable isotopes, Tapajós River, Tocantins River

INTRODUCTION

Freshwater environments can be considered the most altered and threatened in the world (Geist, 2011; Reid et al., 2019; Albert et al., 2020). Due to the human interaction and dependence on riverine environments, populations of aquatic organisms are vulnerable to the effects of increasing environmental and anthropogenic changes, such as long and unusual periods of drought (climate change), dams, mining, habitat change (deforestation), and overfishing (Castilhos et al., 1998; Junk et al., 2007; Malhi et al., 2008; Latrubesse et al., 2017; Arantes et al., 2019a). The lack of available data, combined with scarce financial and human resources, are among the main current problems affecting the management of freshwater ecosystems (Castello et al., 2013; Cavole et al., 2015). Therefore, research on the ecology of freshwater environments is essential for the conservation of these aquatic ecosystems and the maintenance of their ecosystem services (Barletta et al., 2010).

One way to monitor and to evaluate environmental changes, both natural and anthropogenic, consists of studies on ecosystems' trophic structure (Newsome et al., 2010; Andrade et al., 2019; Melo et al., 2019). The trophic level consists on the position occupied by the organism in the food web (Lindeman, 1942). In this sense, the ecological role of organisms can be described through the calculation of their trophic level (Post, 2002; Quezada-Romegialli et al., 2018). The trophic level also allows for the assessment of ecological effects of fishing, to the extent that some organisms, such as top predators (large fish), are selectively removed from the aquatic food webs (Pauly et al., 1998; Shin et al., 2005). These selective removals can alter the structure of the food webs, thus affecting the flow of matter and energy in the environments (Andersen and Pedersen, 2010; Loh et al., 2015). Some effects of these removals may be the trophic cascades (Scheffer et al., 2005; Myers et al., 2007), on which a consumer-resource interaction indirectly influences the other trophic levels (Paine, 1980; Estes et al., 2011). Another possible effect is the simplification of food webs, on which there is a decline in species with higher trophic levels (Estes et al., 2011). These effects (trophic cascades, simplification of food webs) can have consequences even for non-exploited species (Pauly et al., 1998; Estes et al., 2011).

A method that has been used to study aquatic food webs consists on the stable isotopes analysis, which can assist in the understanding of trophic interactions and use of food resources by organisms (Fry, 2006; Pereyra et al., 2016; Arantes et al., 2019b). The stable isotopes analysis allows a determination of the part of the diet that was consumed and assimilated by the organisms (De Niro and Epstein, 1978; Newsome et al., 2009; Carvalho et al., 2018). The carbon isotope allows to trace the main basal energy sources assimilated by the organisms (Fry, 2006; Correa and Winemiller, 2018; Costa et al., 2020). Conversely, nitrogen values predictably increase from prey to predator (Minagawa and Wada, 1984), being thus used to calculate the trophic position along the food chain, or the trophic level (Post, 2002; Olivar et al., 2018; Chiang et al., 2020).

However, the technique of stable isotopes analysis requires specialized machinery, detailed protocols and a considerably amount of processing time. Therefore, the local ecological knowledge (LEK) of fishers can be a reliable and alternative approach to advance understanding about fish trophic interactions and to construct aquatic food webs (Silvano and Begossi, 2002; Gerhardinger et al., 2006; Batista and Lima, 2010; Nunes et al., 2011; Ramires et al., 2015; Souza et al., 2020). Fishers' LEK, which can be propagated over time by cultural transmission (Berkes, 1999; Diamond, 2001), can provide useful information about aquatic animals and their behaviors (Huntington, 2000; Johannes et al., 2008; Herbst and Hanazaki, 2014). Such information from fishers' LEK, which can be mixed or incorporated into conventional research data, can be an important source for creating new ecological hypotheses (Silvano and Valbo-Jørgensen, 2008; Turvey et al., 2010). Among its many applications, fishers' LEK can contribute to identify environmental changes and assess impacts from development projects on fisheries resources (Hallwass et al., 2013; Baird et al., 2020; Runde et al., 2020; Santos et al., 2020), to calculate fish trophic level and to indicate patterns of mercury bioaccumulation in fish (Silvano and Begossi, 2016), besides providing needed data on the abundance patterns, occurrence and distribution of threatened species (Bender et al., 2014; Zapelini et al., 2017; Lopes et al., 2018; Freitas et al., 2020; Hallwass et al., 2020b; Ribeiro et al., 2021).

In the Amazon region, studies applying stable isotopes analysis to analyze trophic relationships have been conducted mainly in white and black water rivers (Araujo-Lima et al., 1986; Oliveira et al., 2006; Mortillaro et al., 2015; Aguiar-Santos et al., 2018; Carvalho et al., 2018), whereas fewer studies have been conducted in clear water rivers (Zuluaga-Gómez et al., 2016; Andrade et al., 2019). Clear water basins covering 27.3% of the total area of the Amazon basin and are the most impacted basins of the Amazon (Goulding et al., 2003). In the Brazilian Amazon, there are two large protected areas, besides indigenous lands, in the region of the Lower Tapajós, which is a clear water river (Keppeler et al., 2017). However, dams and other projects are planned in the upstream region of the Tapajós River and its tributaries, including some projects already approved and built, which represent a challenge for the conservation of aquatic biodiversity (Fearnside, 2015; Winemiller et al., 2016; Athayde et al., 2019; Runde et al., 2020). The Tocantins River, which is another clear water river, can be considered one of the most impacted sub-basins in the Brazilian Amazon (Barthem et al., 2005), mainly due to the high rates of deforestation and the construction of highways and dams, which have caused several environmental and social impacts affecting both fish and riverine people (Fearnside, 1999, 2001; Hallwass et al., 2013). The installation of several hydroelectric projects in the Tocantins-Araguaia river basin since the 1980s, associated with high rates of deforestation for agricultural expansion, can have numerous effects on the trophic ecology of animals, such as disruption of food webs, alterations on the abundance of prey and predators, altering the functional diversity of fish (Mérona et al., 2001; Arantes et al., 2019a; Melo et al., 2019).

The main objectives of this study are to investigate the trophic structure of the ichthyofauna by calculating the trophic level of six fish species relevant for small scale fisheries, to compare fish trophic level data obtained from different methods, stable isotopes analysis and fisher's LEK, and to compare fish trophic level values and trophic structure between two clear water rivers in the Brazilian Amazon (Tapajós and Tocantins) that differ on environmental integrity and history of environmental impacts. Another objective is to construct diagrams representing the trophic webs of the main prey and predators of fish based on the fisher's LEK and to compare these LEK data with the literature, in the two studied rivers. We tested the following hypotheses: (1) the trophic level of the fish obtained through the LEK will be consistent with the data obtained in the stable isotopes analysis. A previous study indicates that the trophic levels of fish species, including Amazonian fish, calculated through the fishers' LEK are consistent with the trophic levels recorded in the literature (Silvano and Begossi, 2016). In the present study, we will use an approach that considers what was assimilated by the organisms through the stable isotopes analysis (Newsome et al., 2009), thus calculating the trophic level based on nutrients assimilated to support the consumer fish (Fry, 2006), but from the same species in the same sites where we conducted the fishers' LEK survey; (2) Due to a more accentuated history of environmental impacts in the Tocantins river basin, we expect that fishers would mention less food items and predators for the studied fish in the Tocantins than in the Tapajós River.

MATERIALS AND METHODS

Study Area

The clear water rivers Tapajós and Tocantins have transparent and greenish waters with low amounts of sediments and dissolved solids (Junk and Piedade, 2010). The acidity of the waters in clear water rivers can vary between pH 5 and 6 depending on the river stretch (Sioli, 1984; Junk et al., 2007). Both the basins of the Tapajós River (490.000 km^2) and the Tocantins-Araguaia River (757.000 km^2) are entirely located within the Brazilian territory (Latrubesse et al., 2005). Both rivers originate in the central Brazilian plateau (Cerrado biome) and have their mouth and most of their course running through the Amazon Forest (Scoles, 2014). In the areas of flooded vegetation of these rivers there is a highly specialized flora with two types of vegetation: flooded rain forest (Salomão et al., 2007) and alluvial riparian vegetation (Veloso et al., 1991).

Study Population

The population that was studied in both rivers belongs to the "caboclos" cultural group, who are also called "ribeirinhos" (riverine people). These people are descendants of indigenous Brazilians and Portuguese colonizers, but more recently there has been an immigration of people from the northeast of Brazil (Begossi, 1998). The small-scale fisheries are predominant in these tropical rivers in the Brazilian Amazon (Bayley and Petrere, 1989; Hallwass et al., 2011, 2020a), where fishing is considered to be amongst the most important economic activities, both for subsistence and for commercialization, in addition to small-scale agriculture and livestock (McGrath et al., 2008; Runde et al., 2020). The level of formal education of fishers limits their reallocation to other economic activities not directly related to the use of natural resources (Lima et al., 2012).

Interviews

The interviews were conducted in eight fishing communities in the Tapajós River and five in the Tocantins River (13 communities in total, **Figure 1**), respectively in September and October, 2018. The communities that were selected to be included in the study were located at least 5 km apart from each other and following a distance gradient from the largest cities: Itaituba (PA) in the Tapajós river and Marabá (PA) in the Tocantins river. When arriving in the communities, community leaders were initially contacted, the objectives of the work were explained to them, and agreement and permission to conduct our research in the community were requested. After agreeing with the research, the community leader indicated the first fishers to be interviewed, according to the minimum criteria for inclusion in the study: fishing as a main activity, being older than 18 years of age, and living in the region for at least 10 years. Fishers were interviewed individually, usually in their homes and before each interview the research was explained and consent was requested from the fisher to participate in the interview. After the interview, the interviewed fisher was solicited to indicate another fisher in the community who would fits the same criteria, through the snowball method, which has been successfully applied in previous studies on fisher's LEK in the Brazilian Amazon (Hallwass et al., 2013, 2020b; Runde et al., 2020). The interviews were based on a semi-structured questionnaire (**Supplementary Material 3**), in which photos of the fish were shown, always in the same order, following previous methods of ethnoecological studies (Silvano and Begossi, 2002, Begossi, 2012). The questions asked addressed the fisher's socioeconomic profile and the questions about fish analyzed in this study were: (a) What is the name of this fish? (b) What does this fish eat? (c) Who eats this fish? Six species, or groups of species that receive the same popular name, were chosen, which occur both in the Tapajós river and in the Tocantins river, because these fish belong to different trophic level (according to the literature) and because they are important for fishing (trade or consumption) (Hallwass et al., 2011, 2013, 2020a; Runde et al., 2020). The fish species chosen were Pescada (*Plagioscion squamosissimus*), Tucunaré (*Cichla pinima*), Piranha (*Serrasalmus rhombeus*), Aracu (*Leporinus fasciatus*), Charuto (*Hemiodus unimaculatus*), and Jaraqui (*Semaprochilodus* spp.). The species Jaraqui (*Semaprochilodus* spp.) was not collected in the Tocantins river, hence it was not included in the stable isotopes analysis comparison. This study was approved by the ethics' committees for studies with people (CONEP/CAAE: 82355618.0.0000.5347) and animals (CEUA: 34186) at the Federal University of Rio Grande do Sul.

Fish Sampling

The fish were collected from lakes or river stretches close to the communities where interviews were conducted (**Figure 1**). The fish sampling was performed using two sets of fishing nets (420 m^2 each), each set with different mesh sizes (ranging from 15 to 80 mm between adjacent nodes), over 24 h. The specimens were identified at the species level and the standard

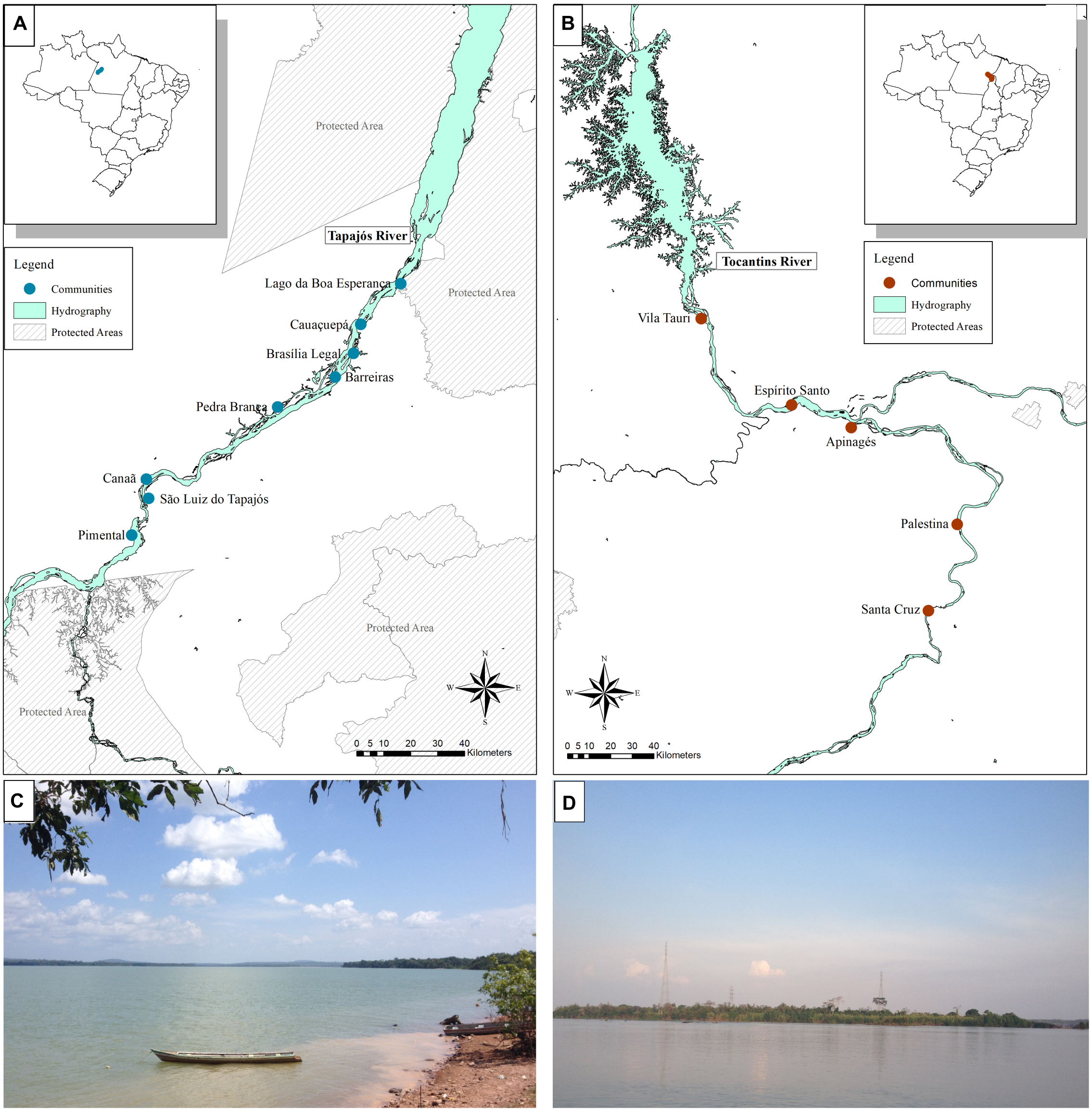

FIGURE 1 | Location of rivers, communities and sampling sites of interviews and fish samples for stable isotopes analysis in the Tapajós **(A,C)** and Tocantins **(B,D)** rivers, in the Brazilian Amazon.

length (SL-cm) and weight (g) were measured. In addition to fish, samples from the benthic macrofauna (mollusks) were manually collected, to be used as a baseline in isotopic models. All samples were stored in plastic bags and preserved on ice until processed.

Processing

After collection, samples of antero-dorsal muscle tissue from fish and of adductor muscle from mollusks were removed for stable isotopes analysis. In the laboratory, these samples were washed with distilled water and inspected to remove only the tissue of interest. Afterward, each sample was placed in a Petri dish, which was pre-sterilized in a hydrochloric acid bath for 24 h, and then placed in the oven at 60° for 48 h. After that, the samples were transformed into fine powder with a mortar and pestle and sub-samples (approximately 1 mg) were weighed on a precision scale (∼ 1 mg) and stored in ultrapure tin capsules (Elemental-D-1008). Sample readings were performed with the Thermo iCAP6300 Duo isotope ratio mass spectrometer (Cambridge, United Kingdom) at the University of Alberta, Canada. The results were expressed in delta notation: $\delta^{13}C$ or $\delta^{15}N$ = [(Ramostra/Standard) -1] * 1000, where R = $^{12}C/^{13}C$/ or $^{14}N/^{15}N$. The values obtained were compared with reference standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric air) and their isotopic ratios ($\delta^{13}C$, $\delta\ ^{15}N$) expressed in per mil (‰) (Fry, 2006). The internal standard of known carbon and nitrogen composition was analyzed with each sequence to assess the accuracy of the instrument. The standard deviation was $\delta^{13}C$ = 0.05 ‰ and $\delta^{15}N$ = 0.19 ‰.

In some cases, samples may have a high lipid content, which can influence $\delta^{13}C$ values (De Niro and Epstein, 1978; Logan et al., 2008). There are two approaches to increase the accuracy of $\delta^{13}C$ measurements: lipids can be removed chemically (Mintenbeck et al., 2008), or mathematical corrections based on empirical equations can be used (Post et al., 2007). Lipid extraction can affect $\delta^{15}N$ values, as other non-lipid materials can be removed (Pinnegar and Polunin, 1999; Sweeting et al., 2006; Mintenbeck et al., 2008). This method is also time-consuming and requires the use of hazardous materials, such as chloroform (Elliott et al., 2014). Due to these limitations, mathematical corrections have been quite effective and used for different types of animals (Post et al., 2007; Ehrich et al., 2011; Elliott et al., 2014; Olivar et al., 2018; Clark et al., 2019). Based on this, as all fish samples showed a C: N ratio equal to or greater than 3.5 a mathematical normalization was applied to correct the carbon values, by using the equation $\Delta\delta^{13}C = -3.32 + 0.99 \times C : N$ (Post et al., 2007).

Data Analysis

The fish trophic level was calculated based on the fisher's LEK obtained through interviews by following the methodology adopted in a previous study (Silvano and Begossi, 2016). According to this methodology, food items were grouped into main categories and a trophic level value was assigned to each category: fruits and seeds (Trophic level = 2), other plants and flowers (aquatic plants, leaves, and other plant parts, Trophic level = 2), detritus (including mud and algae, Trophic level = 2), terrestrial invertebrates (insects, spiders, earthworms, Trophic level = 3), aquatic invertebrates (crustaceans, mainly shrimp, Trophic level = 3), terrestrial vertebrates (birds, frogs, and others, Trophic level = 4) and fish that could not be identified (Trophic level = 4). First, the trophic level of each food item was multiplied by the percentage of fishers who cited that item and the trophic level of all items were summed. This sum was then divided by the sum of the percentages of fisher who cited each item. For example, fishers on the Tapajós river cited that the fish Charuto (*H. unimaculatus*) eats vegetables (Trophic level = 2 cited by 13.65% of fishers), detritus (Trophic level = 2, 92.43% of fishers), invertebrates (Trophic level = 3, 9.09% of fishers) and Piaba (a general name for small fish) (Trophic level = 3.8, 1.52% of fishers). Therefore, the Charuto trophic level was estimated as: $(2 * 13.65) + (2 * 92.43) + (3 * 9.09) + (3.8 * 1.52) = 245.26$, then $245.26/116.69 = 2.10$. Considering that the basal food items (plants) will have the value of 1, the lowest value of calculated trophic level of the studied fish would be 2 (for a strictly herbivorous fish) and the highest value would be 4 for a piscivorous fish. Whenever possible to identify the species of fish that were mentioned by fishers as prey, we calculated the trophic position of these prey fish considering the food items mentioned in the literature.

Fish trophic position value were also estimated through stable isotope data using the "tRophicPosition" package in R (Quezada-Romegialli et al., 2018). This method incorporates Bayesian inference to calculate the trophic level of consumers at the population level, considering the individual variability in the data of stable isotopes. The trophic level of each species was modeled using Monte Carlo via Markov chains (MCMC) with 20,000 interactions and 20,000 adaptive samples in JAGS 4.3.0, using both isotopes of carbon and nitrogen. Two baselines were used: the scraper mollusk of the genus *Doryssa* spp. was chosen to represent the benthic baseline and the herbivorous fish *Hemiodus unimaculatus* was chosen to be the baseline referring to the pelagic pathway. The isotopic fractionation values used for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were 0.39 ± 1.3 and 3.4 ± 0.98, respectively (Post, 2002).

The paired *t*-test was calculated to determine if the average trophic level values for all fish species analyzed were significantly different between the fishers' LEK data and the data generated in the models by stable isotopes analysis, in both rivers. This analysis has already been used in a previous study comparing fish trophic level between fishers' LEK data and the biological literature (Silvano and Begossi, 2016). The *t*-test was performed to compare the average number of prey and fish predators cited by fishers between the two studied rivers. Before running *t*-tests, the Shapiro–Wilk and the Levene tests both based on residuals were performed to check normality and variance homogeneity of data, respectively. All residuals' tests indicated normality and homogeneity of variances. All statistical analyzes were performed using the R 4.0.3 software (R Development Core Team, 2021).

Diagrams were constructed to represent the trophic webs of the main fish prey and predators based on the fisher's LEK and these data were compared with prey and predators of fish according to the biological literature (Silvano and Begossi, 2002, Begossi, 2012). These trophic webs included all fish prey cited by fishers, whereas only those fish predators cited by more than 10% of fishers were included. This criterion was adopted to better visualize the relationships between predators and prey, given the higher variability of cited predators. The sum of cited prey or predators may exceed 100%, as fishers could cite more than one food item or predator for each fish species studied.

RESULTS

A total of 98 fishers were interviewed, 65 in the Tapajós river and 33 in the Tocantins river, including 61 men and four women in Tapajós and 30 men and three women in the Tocantins. The average age of the fishers interviewed in the Tapajós River was 47.2 years (±11.4 years), the average fishing experience (time since started fishing) was 25.5 years (±11.9 years) and the time residing in the region was 36.8 years (±15.3 years). The average age of the fishers interviewed in the Tocantins River was 56.5 years (±14 years), the average fishing experience was 34.8 years (±17.6 years) and the time residing in the region was 41.5 years (±16.3 years).

A total of 63 samples of fish and mollusks were analyzed through stable isotopes analysis, including 40 samples from the Tapajós river (34 fish and six mollusks) and 23 samples from the Tocantins river (20 fish and three mollusks) (**Table 1**). The mean trophic level considering all studied fish species did not differ ($t = -0.58$, df = 5, $p = 0.96$) between data from stable isotopes analysis (2.84 ± 0.52) and fishers' LEK (2.83 ± 0.86) in the Tapajós river (**Figure 2A**). Similarly, the mean trophic

TABLE 1 | Mean and standard deviation (SD) of size (total length), number of samples (n) and values of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of fish and mollusks sampled in the Tapajós and Tocantins rivers.

			Tapajós						Tocantins					
Fish (species)	**Common name**	**Ecological guild**	***n***	**Size (+SD)**	**$\delta^{13}C$**	***SD***	**$\delta^{15}N$**	***SD***	***n***	**size (+SD)**	**$\delta^{13}C$**	***SD***	**$\delta^{15}N$**	***SD***
Cichla pinima	Tucunaré	Piscivorous	5	13.40 ± 0.54	–29.94	1.32	13.02	0.73	3	10.53 ± 0.06	–20.57	0.20	12.10	0.07
Hemiodus unimaculatus	Charuto, Piau	Herbivore	6	13.77 ± 0.86	–31.72	3.38	9.77	1.46	4	12.65 ± 1.05	–23.36	2.00	10.18	1.63
Leporinus fasciatus	Aracu	Omnivorous	3	14.83 ± 1.19	–31.56	1.08	11.71	0.23	4	16.09 ± 2.82	–27.77	2.17	11.62	0.32
Plagioscion squamosissimus	Pescada	Piscivorous	6	23.62 ± 1.97	–29.33	0.91	13.79	0.72	4	24.65 ± 2.13	–28.75	1.76	13.27	1.77
Semaprochilodus spp.	Jaraqui	Detritivores	9	20.81 ± 3.19	–30.32	1.64	10.18	0.66						
Serrasalmus rhombeus	Piranha preta	Piscivorous	5	11.58 ± 1.96	–27.40	1.49	14.03	0.24	5	10.46 ± 2.84	–26.00	2.40	13.15	1.45
Mollusk (species)														
Doryssa spp.			6		–21.59	2.61	7.91	0.83	3		–26.33	0.09	8.05	0.07
Total			40						23					

level did not differ (t = 0.48, df = 4, p = 0.66) between stable isotopes analysis (2.96 ± 0.33) and LEK (3.10 ± 0.88) in the Tocantins river (**Figure 2B**). The trophic level values obtained through the LEK did not differ from those obtained through the stable isotopes analysis for all species in the Tocantins river and nearly all species in the Tapajós river, except for Aracu *L. fasciatus*, which had a lower trophic level according to LEK (**Table 2**).

The interviewed fishers cited 57 prey items and 22 fish predators in the Tapajós River and 27 prey items and 18 fish predators in the Tocantins river (**Supplementary Tables 1**, **2**). The average number of prey cited for the studied fish species differed (t = 4.96, df = 97, $p < 0.01$) between fishers interviewed in the Tapajós (1.97 ± 0.46) and Tocantins (1.47 ± 0.45) rivers (**Figure 3A**). Conversely, the average number of predators cited did not differ (t = 0.88, df = 97, p = 0.38) between fishers interviewed in the Tapajós (1.82 ± 0.68) and Tocantins (1.69 ± 0.65) rivers (**Figure 3B**).

Simplified food webs were built based on fishers' citations on fish prey (**Figure 4**) and predators (**Figure 5**) in the Tapajós (**Figures 4A, 5A**) and Tocantins (**Figures 4B, 5B**) rivers. According to the fisher's LEK, fish species such as Pescada (*P. squamosissimus*), Tucunaré (*C. pinima*) and Piranha (*S. rhombeus*) can be considered mainly piscivorous in both rivers (**Figure 4**). According to most fishers interviewed in the Tapajós (**Figure 4A**) and in the Tocantins (**Figure 4B**) Rivers, detritus was the main food for the fishes Charuto (*H. unimaculatus*) and Jaraqui (*Semaprochilodus* spp.). The fish Aracu (*L. fasciatus*) can be considered as herbivorous or omnivorous species according to the fishers' LEK in both rivers, as this fish can feed on different items, but it eats mainly fruits (**Figure 4**).

One of the fish predators most cited by fishers in both rivers was the red dolphin *Inia* spp. (**Figure 5**). In both rivers, the piranha (*Serrasalmus* spp.) was the main predatory fish mentioned by the interviewed fishers (**Figure 5**). Other fish identified as fish predators by the interviewed fishers were the Pirarara (*Phractocephalus hemioliopterus*), Pirarucu (*Arapaima gigas*) and Surubim (*Pseudoplatystoma* spp.) in the Tapajós river (**Figure 5A**), as well as the Jaú (Pimelodidae) and peixe-cachorro (*Acestrorhynchus* spp., *Raphiodon vulpinus,* and *Hydrolicus* spp.) in the Tocantins River (**Figure 5B**).

DISCUSSION

Fishers' LEK was a robust estimator of trophic level in relation to stable isotopes analysis in both rivers. Ten of a total of the 11 trophic levels estimated based on LEK were within the credibility interval of estimates of trophic levels through the stable isotopes analysis. This result further demonstrates that fisher's LEK can be a promising rapid and low cost alternative to obtain reliable data for studies on fish trophic ecology, as observed in previous studies (Ramires et al., 2015; Silvano and Begossi, 2016).

Fishers can acquire knowledge about fish diets by observing fish stomach contents while manipulating and gutting fish (Silvano and Begossi, 2002). Furthermore, fishers constantly manipulate food items to be used as baits, thus gaining knowledge about food preferences of fish, considering that those food items cited as part of fish diets are also commonly used as baits (Silvano and Begossi, 2005; Baird, 2007; Ramires et al., 2015). On the other hand, fish predators preying fish on gill nets may be commonly observed by fishers, thus fishing activity can be an important source of knowledge about the feeding behavior of fish and other animals (Silvano and Begossi, 2002; Ramires et al., 2015).

Despite an overall agreement, there were small differences between the trophic level estimates based on LEK and stable isotopes analysis: the trophic level based on the LEK of the fish Aracu fell outside the credibility interval and was thus lower than the trophic level of this fish estimated through the stable isotopes analysis model in the Tapajós river. This and other slight differences between LEK and stable isotopes analysis regarding the estimated trophic levels can be explained by the fact that fishers make their inferences about fish diets through observation of fish stomach contents, besides direct observation of fish behavior. Therefore, LEK is mostly based on what was ingested by fish, not on what was actually assimilated in fish tissues, as measured by stable isotopes analysis. Indeed, some of the food items present in fish stomachs may be refractory to digestion (e.g., vegetation, fruits, shells) and may not be digested nor assimilated by the consumer. Furthermore, the differences in trophic levels between the LEK and stable isotopes analysis observed in the present study can be at least partially attributed to the temporal differences in the methods being compared. The data from the

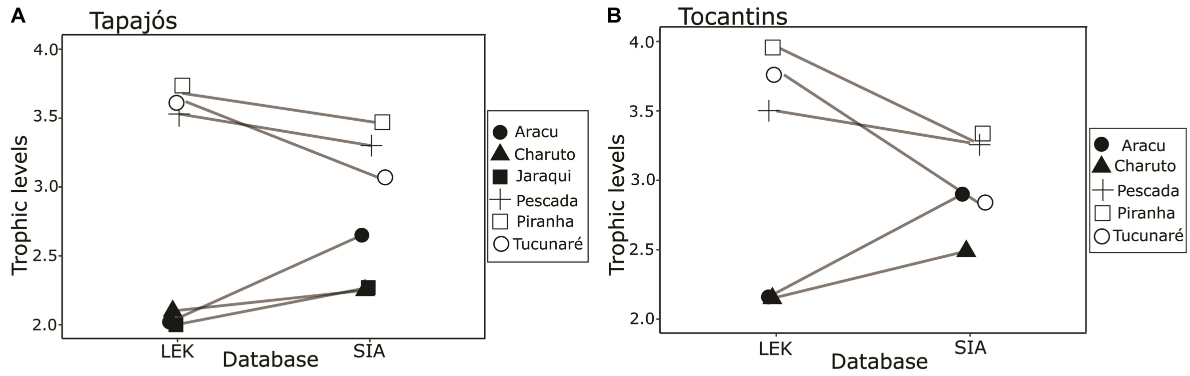

FIGURE 2 | Paired comparison between trophic levels of fish species based on fisher's knowledge (LEK) and stable isotope analysis (SIA) in the **(A)** Tapajós river (t = –0.58, df = 5, p = 0.96) and **(B)** Tocantins river (t = 0.48, df = 4, p = 0.66). The fish species analyzed were Aracu (*Leporinus fasciatus*), Charuto (*Hemiodus unimaculatus*), Jaraqui (*Semaprochilodus* spp.) except in the Tocantins river, Pescada (*Plagioscion squamosissimus*), Piranha (*Serrasalmus rhombeus*), and Tucunaré (*Cichla pinima*).

stable isotopes analysis indicate what has been assimilated and transformed into tissues by the consumer fish, considering a time span of approximately 90 days from consumption (Mont'Alverne et al., 2016). On the other hand, data obtained through the fishers' LEK may include a much longer time window on fish diets, as fishers can acquire this knowledge through the accumulation of observations over several years of fishing activity, along their experience in contact with the environment (Silvano and Begossi, 2002), besides the transmission of knowledge among fishers (Johnson, 2006). Therefore, these two methods or approaches can be used concurrently in studies of trophic ecology. For example, the simultaneous use of LEK and stable isotopes analysis has been successfully applied to assess habitat use by turtles in estuarine environments (Wedemeyer-Strombel, 2019).

Considering the diversity of species in the Brazilian Amazon basin (Dagosta and de Pinna, 2019), detailed information on fish feeding habits may be relatively scarce (Mérona et al., 2001; Mérona and Rankin-de-Mérona, 2004; Silvano and Begossi, 2016; Dary et al., 2017). Moreover, studies on fish trophic ecology may show some limitations, such as small sample sizes, geographically restricted sampling and not including seasonal variation. Conventional studies based on the method of stomach content analysis may have, among their main limitations, a large number of empty stomachs of piscivorous fish (Vinson and Angradi, 2011) and the difficulty to identify certain items, which may be very digested and are often only bones, not allowing identification at the species level. These limitations can complicate the identification of the diets of piscivores, such as piranhas (Prudente et al., 2016) and alligators (Magnusson et al., 1987). However, in the present study, fishers cited potential fish prey of these two species of predators, in some cases identifying even more refined taxonomic levels than those generally described in the biological literature. Another advantage of including fishers' LEK in studies on trophic ecology is the possibility of building conceptual models of food interactions, which can be used in different environments, such as freshwater and marine (Silvano and Begossi, 2002, Begossi, 2012; Le Fur et al., 2011). Furthermore, the LEK based data can be also applied in ecosystem modeling studies, aiming to improve management of fisheries resources in environments that need management, but lack data (Ainsworth and Pitcher, 2005; Bevilacqua et al., 2016; Bentley et al., 2019).

TABLE 2 | Trophic levels calculated from the local ecological knowledge (LEK) of fishers and posterior trophic level estimates originated from Bayesian models (mean values and 95% credibility interval) based on stable isotopes analysis for the fish species studied in the Tapajós and Tocantins rivers.

River	Specie	LEK	Stable isotopes analysis
Tapajós	*Cichla pinima*	**3.62**	3.07 (2.48–3.65)
	Hemiodus unimaculatus	**2.10**	2.25 (2.00–2.75)
	Leporinus fasciatus	2.02	2.65 (2.09–3.11)
	Plagioscion squamosissimus	**3.53**	3.30 (2.77–3.82)
	Semaprochilodus spp.	**2.00**	2.27 (2.00–2.64)
	Serrasalmus rhombeus	**3.68**	3.47 (2.98–3.90)
Tocantins	*Cichla pinima*	**3.76**	2.84 (2.00–4.03)
	Hemiodus unimaculatus	**2.15**	2.49 (2.00–3.79)
	Leporinus fasciatus	**2.16**	2.90 (2.14–3.30)
	Plagioscion squamosissimus	**3.50**	3.27 (2.04–4.24)
	Serrasalmus rhombeus	**3.95**	3.28 (2.30–4.08)

Values of trophic levels calculated from LEK in bold are those within the credibility range of the values calculated trough the stable isotopes analysis.

The results of this and previous studies provide evidence that fisher's LEK has clear potential to "fit the pieces" and fill knowledge gaps regarding ecosystem function of fish, especially in remote tropical regions where scientific knowledge is still incipient. Moreover, information about the diet of fish and large predatory species is usually scarce in the scientific literature, as well as studies addressing the interactions between trophic ecology and fishing resources. In the present study, all food items most mentioned by fishers as being important to the diet of the studied fish corroborated with data from the literature. In both rivers, the general food items mentioned for piscivorous fish, such as Pescada and Tucunaré, were fish and crustaceans, whereas fishers mentioned fish being eaten by Piranha, fruits and plants as food of the Aracu and detritus as the main food item of

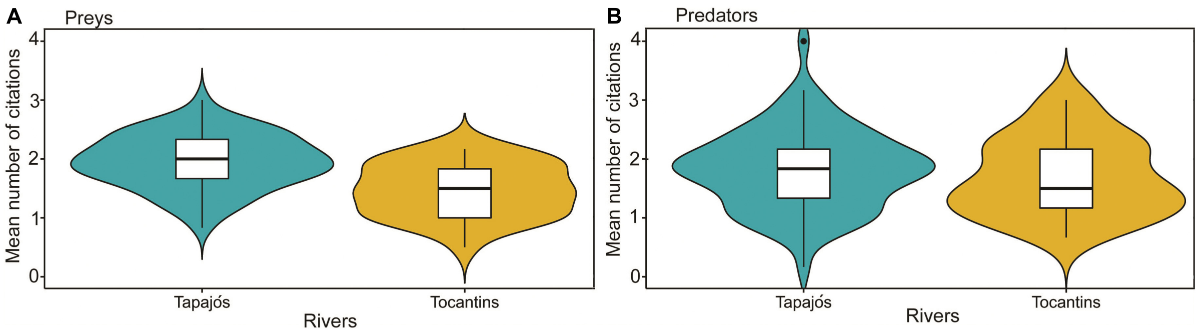

FIGURE 3 | Comparison of the average number of fishers' citations between the Tapajós and Tocantins rivers regarding the number of **(A)** fish prey (t = 4.96, df = 97, $p < 0.01$) and **(B)** fish predators (t = 0.88, df = 97, p = 0.38). Boxplot indicates the median (dark line inside box) and quartiles (25 and 75%, outer lines of the box). Data distribution is indicated by violin-colored area.

Jaraqui. Therefore, fishers' LEK can help to better understand the trophic ecology of fish that may receive a higher fishing pressure and thus more urgently demand management and conservation actions, such as some large piscivorous and herbivorous fishes in the Brazilian Amazon and elsewhere (Pauly et al., 1998; Welcomme, 1999; Hallwass et al., 2020b). Furthermore, the detailed information revealed by fishers' LEK regarding the diet and trophic interactions of freshwater fishes can be useful to identify, and hence to maintain, some of the important ecosystem services provided by fish, such as seed dispersal (Lucas, 2008; Anderson et al., 2009; Horn et al., 2011), nutrient cycling (Flecker, 1996; Winemiller et al., 2006) and the food security of riverine populations (Isaac and Almeida, 2011; Begossi et al., 2019).

The fishers' LEK can assist in understanding ecological aspects of emblematic species, such as the endangered red dolphin or boto, *Inia* spp. (Silva et al., 2018; Vidal et al., 2019; Campbell et al., 2020). In this study, fishers reported that the boto consumes the fish Tucunaré, Pescada, Aracu, and Charuto, all of which corroborate with a study on the boto diet carried out in the 1980s, through stomach content analysis (Best, 1984). However, the Jaraqui fish was also mentioned as being consumed by the boto by 73% of the interviewed fishers in both rivers, but this fish has not been mentioned in the literature as being part of the boto diet. Similarly, a previous study also shows that fishers mention the river dolphin as important predators of the fish Jaraqui in the Central Amazon (Batista and Lima, 2010). This hypothesis of Jaraqui predation by botos or other freshwater dolphins can be investigated in more detail in the future, given the importance of Jaraqui for small-scale fisheries throughout the Brazilian Amazon (Hallwass and Silvano, 2015; Hallwass et al., 2020a,b; Runde et al., 2020). Therefore, the potential predation of Jaraqui by the boto, as evidenced by the interviewed fishers, indicates a possible overlap between the resources used by this river dolphin and humans (fishers), which can become a source of conservation related conflicts (Loch et al., 2009; Kelkar et al., 2010). The interviewed fishers mentioned some fish, such as Aracu, Jaraqui, and Tucunaré, as being consumed by the river otter, and these same fish have been described as being part of the river otter diet through the analysis of fecal samples in the Negro River Basin, in the Brazilian Amazon (Silva et al., 2013).

Some discrepancies between fishers' LEK and the biological literature were recorded in relation to fish predators. Fishers indicated Pescada and Piranha as being consumed by the Pirarucu, however, these species have not yet been recorded in studies on the feeding of Pirarucu. These differences between the two knowledge bases (LEK and biological) may occur due to the natural variation in the availability and occurrence of food items throughout the aquatic ecosystems in the Amazon, since the existing studies on trophic ecology of Pirarucu have not been conducted in the same rivers addressed in this study (Tapajós and Tocantins).

Studies on trophic ecology are even more relevant in the context of the Amazon biome, which is highly dynamic and which has undergone numerous changes during the last few years (Dagosta et al., 2020; Latrubesse et al., 2020). The Tocantins-Araguaia river basin is considered as an important and priority area for conservation, due both to the high presence of endemic species and the high number of dams (Dagosta et al., 2020). Dams can alter the abundance of prey and predators in the environment (Mérona et al., 2001), besides influencing and modifying fish feeding habits due to lack of food (Melo et al., 2019). The impacts and changes to fish and fisheries already observed in the Tocantins River (Mérona et al., 2001; Hallwass et al., 2013) can be repeated in the Tapajós river in the near future, as this river is targeted for development projects directed to energy production and enhancing navigation for the export of soy and meat (Fearnside, 2015; Latrubesse et al., 2020). Even considering that the Tapajós River basin has a high diversity of species (Dagosta and de Pinna, 2019) and several protected areas, there is a rapid loss in the forest area, especially in the region of the Lower Tapajós River (Dagosta et al., 2020), that may affect all food web of the river, mainly the large-bodied fish species as the top predators (Capitani et al., 2021). Besides these potential future impacts, there have been mining activities in the middle and upper Tapajós River since the mid-1980s, thus affecting both human populations and aquatic organisms due to mercury contamination, including contamination of fish consumed by people (Harada et al., 2001; Faial et al., 2015; Vasconcellos et al., 2021). A previous study demonstrates that fish trophic levels estimated by LEK, which are equivalent to trophic levels

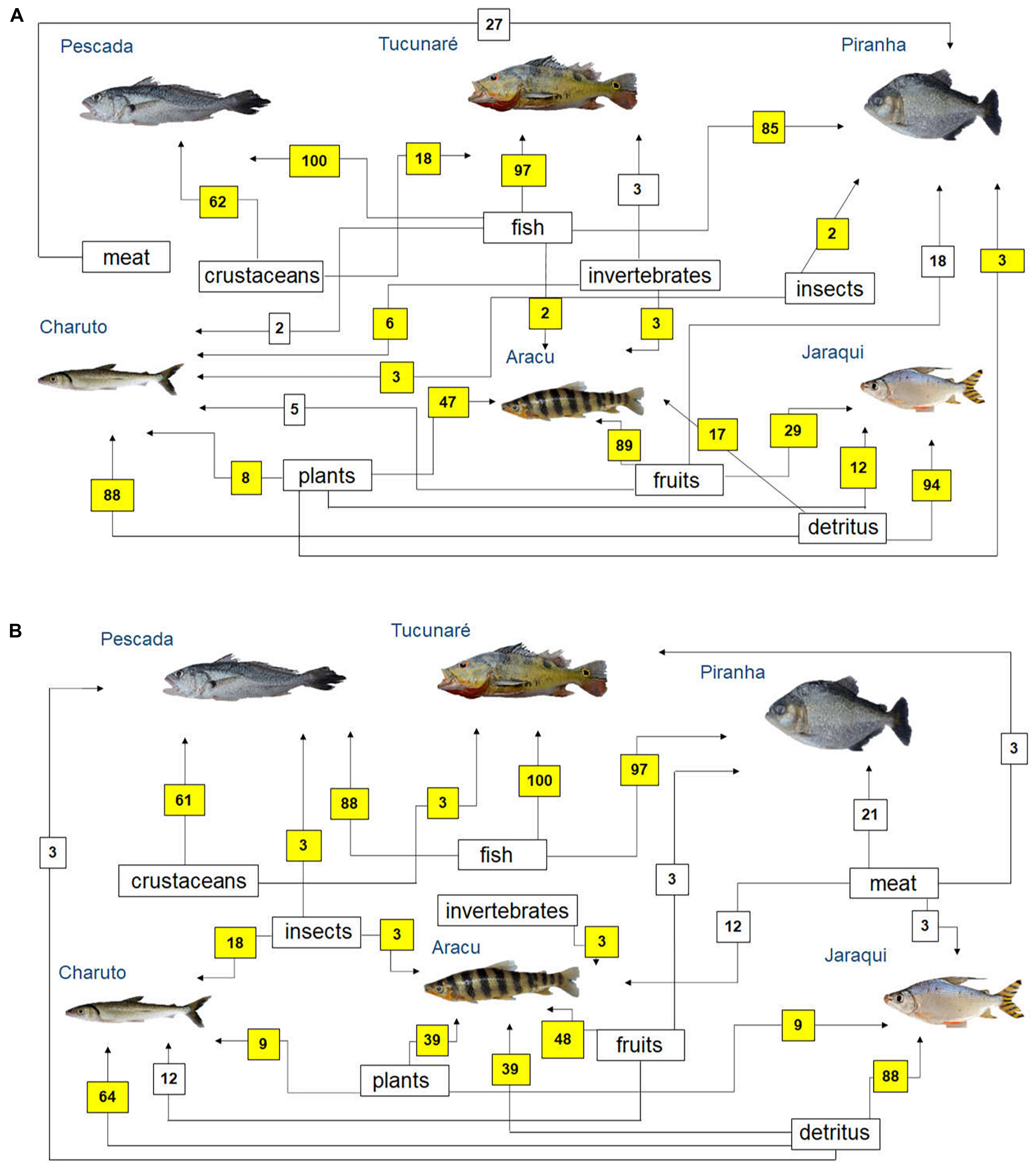

FIGURE 4 | Diagram representing fish feeding relationships (simplified food web) of the studied fish species, based on fishers' local ecological knowledge about fish prey (question: What this fish eats?) in the rivers **(A)** Tapajós (*n* = 65 fishers) and **(B)** Tocantins (*n* = 33 fishers), in the Brazilian Amazon. The numbers are the percentage of interviewed fishers who mentioned each feeding interaction. The sum may be greater than 100%, as fishers could cite more than one food item for each studied fish species. Those food interactions that agree with fish feeding relationships reported in the biological literature (Mérona et al., 2001; Mérona and Rankin-de-Mérona, 2004; Dary et al., 2017) are marked in yellow.

according to literature data, are also related to mercury content on fish, thus showing the potential of fishers' LEK as an indicator of fish trophic level in bioaccumulation studies (Silvano and Begossi, 2016). The present study corroborated and advance these previous findings on the potential value of fishers' LEK to indicate fish trophic levels and associated ecological properties (Silvano and Begossi, 2016). The previous study compared trophic levels estimated through the LEK with those from biological literature (Silvano and Begossi, 2016), whereas this study compared trophic levels estimated by LEK with data showing what was indeed assimilated by the organisms through the use of stable isotopes analysis (Newsome et al., 2009) for the same fish species and in the same sites where the interviews with fishers were conducted. Therefore, by adopting a more refined and accurate comparison, this study showed a very close agreement between fishers' LEK and biological data on fish trophic levels, paving the way for a collaboration between fishers and scientists to develop ecological and ecotoxicological indicators.

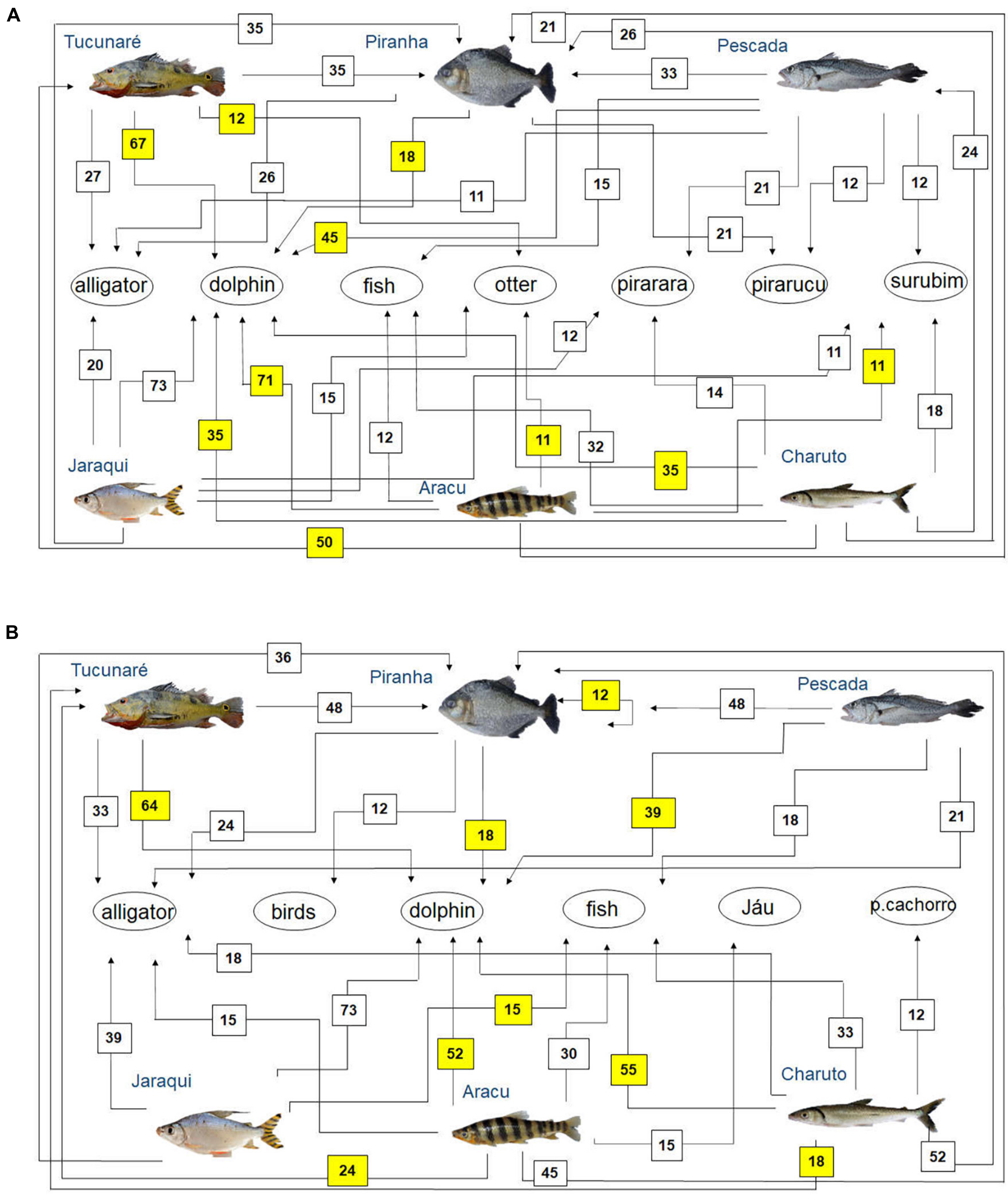

FIGURE 5 | Diagram representing fish feeding relationships (simplified food web) of the studied fish species, based on fishers' local ecological knowledge about fish predators (question: Who eats this fish?) in the rivers **(A)** Tapajós (*n* = 65 fishers) and **(B)** Tocantins (*n* = 33 fishers), in the Brazilian Amazon. The numbers are the percentage of interviewed fishers who mentioned each feeding interaction. The sum may be greater than 100%, as fishers could cite more than one food item for each studied fish species. Those food interactions that agree with fish feeding relationships reported in the biological literature (Best, 1984; Silva et al., 2013; Dary et al., 2017; Jacobi et al., 2020) are marked in yellow.

Contrary to the initial hypothesis, the overall fishers' LEK about the trophic levels and feeding interactions of fish did not differ between the two studied rivers, even though they have a distinct history and intensity of environmental impacts. For example, there were no differences on the number of fish predators cited by fishers between the Tapajós (22 predators) and the Tocantins (18 predators) rivers. This may be partially due to some degree of plasticity in the feeding behavior of at least some aquatic species, which may adapt to environmental changes that are occurring over time. Alternatively, it may be that fish and aquatic predators had not changed their feeding habits yet in the more altered Tocantins River, so impacts had not lead to perceived modifications in the diet of these organisms. These suggestions or hypotheses need to be checked in future studies aimed to understand the influences of river modification on fish diets and trophic ecology. However, as expected according to the proposed hypothesis, a greater number of food items was cited by fishers in the Tapajós river (57 items) when compared to the Tocantins river (27 items). This difference may be possibly due to the lower availability of some food items, such as fruits, in the Tocantins River, as a consequence of a more intense deforestation in this river basin. The results provided from fishers' LEK thus reinforce the need to prioritize conservation and restoration strategies for aquatic environments in the Tocantins-Araguaia river basin.

The combination of both approaches (LEK and stable isotopes analysis) can advance the knowledge base on diet and trophic interactions of fish species with greater reliability, by producing accurate data, in a fast and effective way. Although such combination is desirable whenever possible, the stable isotopes analysis technique requires financial resources, specialized machinery, and considerable processing time, which may be beyond the reach of many researchers and communities in tropical developing countries. In such a context, this study adds to previous research to show that fishers' LEK can provide useful information on fish trophic ecology and that such information based on LEK is closely related to biological data. The fishers' LEK can thus be reliably applied to improve fisheries management and species conservation in those regions of the world that have data limitations but need urgent management.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Federal University of Rio Grande do Sul (CONEP/CAAE: 82355618.0.0000.5347). The ethics committee waived the requirement of written informed consent for participation. The animal study was reviewed and approved by Federal University of Rio Grande do Sul, (CEUA: 34186).

AUTHOR CONTRIBUTIONS

PP and RS conceived and designed the experiment. PP, GH, and RS conducted the field work. PP conduced the lab work, processed the stable isotope samples, performed all the statistical analyses, and wrote the first draft of the manuscript. MP contributed to reading of isotope samples. All authors contributed to subsequent versions and revisions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.723026/full#supplementary-material

REFERENCES

Aguiar-Santos, J., deHart, P. A. P., Pouilly, M., Freitas, C. E. C., and Siqueira-Souza, F. K. (2018). Trophic ecology of speckled peacock bass *Cichla temensis* Humboldt 1821 in the middle Negro River, Amazon, Brazil. *Ecol. Freshw. Fish* 27, 1076–1086. doi: 10.1111/eff.12416

Ainsworth, C. H., and Pitcher, T. J. (2005). "Using local ecological knowledge in ecosystem models," in *Fisheries Assessment and Management in Data-Limited*, eds G. H. Kruse, V. F. Gallucci, D. E. Hay, R. I. Perry, R. M. Peterman, T. C. Shirley, et al. (Fairbanks, AK: Alaska Sea Grant College Program, University of Alaska), 289–304. doi: 10.4027/famdis.2005.17

Albert, J. S., Destouni, G., Duke-Sylvester, S. M., Magurran, A. E., Oberdorff, T., Reis, R. E., et al. (2020). Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* 50, 85–94. doi: 10.1007/s13280-020-01318-8

Andersen, K. H., and Pedersen, M. (2010). Damped trophic cascades driven by fishing in model marine ecosystems. *Proc. R. Soc. Lond. B Biol. Sci.* 277, 795–802. doi: 10.1098/rspb.2009.1512

Anderson, J. T., Rojas, S. J., and Flecker, A. S. (2009). High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia* 161, 279–290. doi: 10.1007/s00442-009-1371-4

Andrade, M. C., Fitzgerald, D. B., Winemiller, K. O., Barbosa, P. S., and Giarrizzo, T. (2019). Trophic niche segregation among herbivorous serrasalmids from rapids of the lower Xingu River, Brazilian Amazon. *Hydrobiologia* 829, 265–280. doi: 10.1007/s10750-018-3838-y

Arantes, C. C., Winemiller, K. O., Asher, A., Castello, L., Hess, L. L., Petrere, M., et al. (2019a). Floodplain land cover affects biomass distribution of fish functional diversity in the Amazon River. *Sci. Rep.* 9:16684. doi: 10.1038/s41598-019-52243-0

Arantes, C. C., Winemiller, K. O., Petrere, M., and Freitas, C. E. C. (2019b). Spatial variation in aquatic food webs in the Amazon River floodplain. *Freshw. Sci.* 38, 213–228. doi: 10.1086/701841

Araujo-Lima, C. A. R. M., Forsberg, B. R., Victoria, R., and Martinelli, L. (1986). Energy sources for detritivorous fishes in the Amazon. *Science* 234, 1256–1258. doi: 10.1126/science.234.4781.1256

Athayde, S., Duarte, C. G., Gallardo, A. L. C. F., Moretto, E. M., Sangoi, L. A., Dibo, A. P. A., et al. (2019). Improving policies and instruments to address cumulative impacts of small hydropower in the Amazon. *Energy Policy* 132, 265–271. doi: 10.1016/j.enpol.2019.05.003

Baird, I. G. (2007). Fishes and forests: the importance of seasonally flooded riverine habitat for Mekong River fish feeding. *Nat. Hist. Bull. Siam Soc.* 55, 121–148.

Baird, I. G., Manorom, K., Phenow, A., and Gaja-Svasti, S. (2020). What about the tributaries of the tributaries? Fish migrations, fisheries, dams and fishers' knowledge in North-Eastern Thailand. *Int. J. Water Resour. Dev.* 36, 170–199. doi: 10.1080/07900627.2019.1611549

Barletta, M., Jaureguizar, A. J., Baigun, C., Fontoura, N. F., Agostinho, A. A., Almeida-Val, V. M. F., et al. (2010). Fish and aquatic habitat conservation in South America: a continental overview with emphasis on neotropical systems. *J. Fish Biol.* 76, 2118–2176. doi: 10.1111/j.1095-8649.2010.02684.x

Barthem, R., Marques, M., Charvet-Almeida, P., and Montag, L. F. A. (2005). Amazon River Basin: I – characterization and environmental impacts due to deforestation. *Ecosyst. Sustain. Dev. V* 81, 615–625.

Batista, V. S., and Lima, L. G. (2010). In search of traditional bio-ecological knowledge useful for fisheries co-management: the case of jaraquis *Semaprochilodus* spp. (Characiformes, Prochilodontidae) in Central Amazon, Brazil. *J. Ethnobiol. Ethnomed.* 6:15. doi: 10.1186/1746-4269-6-15

Bayley, P. B., and Petrere, M. J. (1989). "Amazon fisheries: assessment methods, current status and management points," in *Proceedings of the International Large River Symposium*, ed. D. P. Dodge (Ottawa, ON: Canadian Special Publication of Fisheries and Aquatic Sciences), 385–398.

Begossi, A. (1998). "Cultural and ecological resilience among caiçaras of the Atlantic Forest and caboclos of the Amazon, Brazil," in *Linking Social and Cultural Systems for Resilience*, eds C. Folke and F. Berkes (Cambridge: Cambridge U. Press), 129–157.

Begossi, A., Salivonchyk, S. V., Hallwass, G., Hanazaki, N., Lopes, P. F. M., Silvano, R. A. M., et al. (2019). Fish consumption on the Amazon: a review of biodiversity, hydropower and food security issues. *Braz. J. Biol.* 79, 345–357.

Bender, M. G., Machado, G. R., De Azevedo Silva, P. J., Floeter, S. R., Monteiro-Netto, C., Luiz, O. J., et al. (2014). Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. *PLoS One* 9:e110332. doi: 10.1371/journal.pone.0110332

Bentley, J. W., Hines, D. E., Borrett, S. R., Serpetti, N., Hernandez-Milian, G., Fox, C., et al. (2019). Combining scientific and fishers' knowledge to co-create indicators of food web structure and function. *ICES J. Mar. Sci.* 76, 2218–2234. doi: 10.1093/icesjms/fsz121

Berkes, F. (1999). *Sacred Ecology: Traditional Ecological Knowledge and Resource Management*. Philadelphia, PA: Taylor and Francis.

Best, R. C. (1984). *The Aquatic Mammals and Reptiles of the Amazon*. Dordrecht: Dr. W. Junk Publishers, 371–412. doi: 10.1007/978-94-009-6542-3_15

Bevilacqua, A. H. V., Carvalho, A. R., Angelini, R., and Christensen, V. (2016). More than anecdotes: fishers' ecological knowledge can fill gaps for ecosystem modeling. *PLoS One* 11:e0155655. doi: 10.1371/journal.pone.0155655

Campbell, E., Mangel, J. C., Alfaro-Shigueto, J., Mena, J. L., Thurstan, R. H., and Godley, B. J. (2020). Coexisting in the Peruvian Amazon: interactions between fisheries and river dolphins. *J. Nat. Conserv.* 56:125859. doi: 10.1016/j.jnc.2020.125859

Capitani, L., Angelini, R., Keppeler, F. W., Hallwass, G., Azevedo, R., and Silvano, M. (2021). Food web modeling indicates the potential impacts of increasing deforestation and fishing pressure in the Tapajós River, Brazilian Amazon. *Reg. Environ. Change* 21:42.

Carvalho, F., Power, M., Forsberg, B. R., Castello, L., Martins, E. G., and Freitas, C. E. C. (2018). Trophic ecology of *Arapaima* sp. in a ria lake—river–floodplain transition zone of the Amazon. *Ecol. Freshw. Fish* 27, 237–246. doi: 10.1111/eff.12341

Castello, L., Mcgrath, D. G., Hess, L. L., Coe, M. T., Lefebvre, P. A., Petry, P., et al. (2013). The vulnerability of Amazon freshwater ecosystems. *Conserv. Lett.* 6, 217–229. doi: 10.1111/conl.12008

Castilhos, Z. C., Bidone, E. D., and Lacerda, L. D. (1998). Increase of the background human exposure to mercury through fish consumption due to gold mining at the Tapajos river region, Para State, Amazon. *Bull. Environ. Contam. Toxicol.* 61, 202–209. doi: 10.1007/s001289900749

Cavole, L. M., Arantes, C. C., and Castello, L. (2015). How illegal are tropical small-scale fisheries? An estimate for arapaima in the Amazon. *Fish. Res.* 168, 1–5. doi: 10.1016/j.fishres.2015.03.012

Chiang, W. C., Chang, C. T., Madigan, D. J., Carlisle, A. B., Musyl, M. K., Chang, Y. C., et al. (2020). Stable isotope analysis reveals feeding ecology and trophic position of black marlin off eastern Taiwan. *Deep. Res. Part II Top. Stud. Oceanogr.* 175:104821. doi: 10.1016/j.dsr2.2020.104821

Clark, C. T., Horstmann, L., and Misarti, N. (2019). Lipid normalization and stable isotope discrimination in Pacific walrus tissues. *Sci. Rep.* 9:5843. doi: 10.1038/s41598-019-42095-z

Correa, S. B., and Winemiller, K. (2018). Terrestrial–aquatic trophic linkages support fish production in a tropical oligotrophic river. *Oecologia* 186, 1069–1078. doi: 10.1007/s00442-018-4093-7

Costa, A. F., Botta, S., Siciliano, S., and Giarrizzo, T. (2020). Resource partitioning among stranded aquatic mammals from Amazon and Northeastern coast of Brazil revealed through carbon and nitrogen stable isotopes. *Sci. Rep.* 10:12897. doi: 10.1038/s41598-020-69516-8

Dagosta, F. C. P., and de Pinna, M. (2019). The fishes of the Amazon: distribution and biogeographical patterns, with a compreehensive list of species. *Bull. Am. Museum. Nat. Hist.* 2019:163.

Dagosta, F. C. P., de Pinna, M., Peres, C. A., and Tagliacollo, V. A. (2020). Existing protected areas provide a poor safety-net for threatened Amazonian fish species. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 31, 1167–1189. doi: 10.1002/aqc.3461

Dary, E. P., Ferreira, E., Zuanon, J., and Röpke, C. P. (2017). Diet and trophic structure of the fish assemblage in the mid-course of the Teles Pires river, Tapajós river basin, Brazil. *Neotrop. Ichthyol.* 15, 1–14. doi: 10.1590/1982-0224-20160173

De Niro, M. J., and Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochxm. Cosmochim. Acta* 42, 495–506.

Diamond, J. (2001). Unwritten knowledge. *Nature* 410:90095.

Ehrich, D., Tarroux, A., and Killengreen, S. T. (2011). Stable isotope analysis: modelling lipid normalization for muscle and eggs from arctic mammals and birds. *Methods Ecol. Evol.* 2, 66–76. doi: 10.1111/j.2041-210X.2010.00047.x

Elliott, K. H., Davis, M., and Elliott, J. E. (2014). Equations for lipid normalization of carbon stable isotope ratios in aquatic bird eggs. *PLoS One* 9:e83597. doi: 10.1371/journal.pone.0083597

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., et al. (2011). Trophic downgrading of planet earth. *Science* 333, 301–306. doi: 10.1126/science.1205106

Faial, K., Deus, R., Deus, S., Neves, R., Jesus, I., Santos, E., et al. (2015). Mercury levels assessment in hair of riverside inhabitants of the Tapajós River, Pará State, Amazon, Brazil: fish consumption as a possible route of exposure. *J. Trace Elem. Med. Biol.* 30, 66–76. doi: 10.1016/j.jtemb.2014.10.009

Fearnside, P. M. (1999). Social impacts of Brazil's Tucuruí Dam. *Environ. Manage.* 24, 483–495.

Fearnside, P. M. (2001). Environmental impacts of Brazil's Tucuruí Dam: unlearned lessons for hydroelectric development in amazonia. *Environ. Manage.* 27, 377–396. doi: 10.1007/s002670010156

Fearnside, P. M. (2015). Amazon dams and waterways: Brazil's Tapajós Basin plans. *Ambio* 44, 426–439. doi: 10.1007/s13280-015-0642-z

Flecker, A. S. (1996). Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* 77, 1845–1854. doi: 10.2307/2265788

Freitas, C. T., Espírito-Santo, H. M. V., Campos-Silva, J. V., Peres, C. A., and Lopes, P. F. M. (2020). Resource co-management as a step towards gender equity in fisheries. *Ecol. Econ.* 176:106709. doi: 10.1016/j.ecolecon.2020.106709

Fry, B. (2006). *Stable Isotope Ecology*. New York, NY: Springer-Verlag. doi: 10.1007/0-387-33745-8

Geist, J. (2011). Integrative freshwater ecology and biodiversity conservation. *Ecol. Indic.* 11, 1507–1516. doi: 10.1016/j.ecolind.2011.04.002

Gerhardinger, L. C., Freitas, M. O., Bertoncini, ÁA., Borgonha, M., and Hostim-Silva, M. (2006). Collaborative approach in the study of the reproductive biology of the dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Perciformes: Serranidae). *Acta Sci. Biol. Sci.* 28, 219–226.

Goulding, M., Barthem, R., and Ferreira, E. J. G. (2003). *The Smithsonian Atlas of the Amazon*. Washington, D.C: Smithsonian Books. doi: 10.4324/9780203028049

Hallwass, G., and Silvano, R. A. M. (2015). Patterns of selectiveness in the Amazonian freshwater fisheries: implications for management. *J. Environ. Plan. Manag.* 59, 1537–1559. doi: 10.1080/09640568.2015.1081587

Hallwass, G., da Silva, L. H., Nagl, P., Clauzet, M., and Begossi, A. (2020a). "Small-scale fisheries, livelihoods and food security of riverine people," in *Fish and Fisheries in the Brazilian Amazon: People, Ecology and Conservation in Black and Clear Water Rivers*, (São Paulo: Springer International Publishing).

Hallwass, G., Lopes, P. F., Juras, A. A., and Silvano, R. A. M. (2011). Fishing effort and catch composition of Urban market and rural villages in Brazilian Amazon. *Environ. Manage.* 47, 188–200. doi: 10.1007/s00267-010-9584-1

Hallwass, G., Lopes, P. F., Juras, A. A., and Silvano, R. A. M. (2013). Fishers' knowledge identifies environmental changes and fish abundance trends in impounded tropical rivers. *Ecol. Appl.* 23, 392–407. doi: 10.1890/12-0429.1

Hallwass, G., Schiavetti, A., and Silvano, R. A. M. (2020b). Fishers' knowledge indicates temporal changes in composition and abundance of fishing resources in Amazon protected areas. *Anim. Conserv.* 23, 36–47. doi: 10.1111/acv.12504

Harada, M., Nakanishi, J., Yasoda, E., Pinheiro, M. D. C. N., Oikawa, T., De Assis Guimarães, G., et al. (2001). Mercury pollution in the Tapajos River basin, Amazon mercury level of head hair and health effects. *Environ. Int.* 27, 285–290. doi: 10.1016/S0160-4120(01)00059-9

Herbst, D. F., and Hanazaki, N. (2014). Local ecological knowledge of fishers about the life cycle and temporal patterns in the migration of mullet (*Mugil liza*) in Southern Brazil. *Neotrop. Ichthyol.* 12, 879–890. doi: 10.1590/1982-0224-20130156

Horn, M. H., Correa, S. B., Parolin, P., Pollux, B. J. A., Anderson, J. T., Lucas, C., et al. (2011). Seed dispersal by fishes in tropical and temperate fresh waters: the growing evidence. *Acta Oecol.* 37, 561–577. doi: 10.1016/j.actao.2011.06.004

Huntington, H. P. (2000). Using traditional ecological knowledge in science: methods and applications. *Ecol. Appl.* 10, 1270–1274.

Isaac, V. J., and Almeida, M. C. (2011). *El Consumo de Pescado en la Amazonía Brasileña. COPESCAALC Documento Ocasional. No 13*. Available online at: www.fao.org/icatalog/inter-e.htm (accessed July 8, 2021).

Jacobi, C. M., Villamarín, F., Campos-Silva, J. V., Jardine, T., and Magnusson, W. E. (2020). Feeding of *Arapaima* sp.: integrating stomach contents and local ecological knowledge. *J. Fish Biol.* 97, 265–272. doi: 10.1111/jfb.14372

Johannes, R. E., Freeman, M. M. R., and Hamilton, R. J. (2008). Ignore fishers' knowledge and miss the boat. *Fish Fish.* 1, 257–271. doi: 10.1111/j.1467-2979.2000.00019.x

Johnson, D. S. (2006). Category, narrative, and value in the governance of small-scale fisheries. *Marine Policy* 30, 747–756. doi: 10.1016/j.marpol.2006.01.002

Junk, W. J., and Piedade, M. T. F. (2010). "An introduction to South American wetland forests: distribution, definitions and general characterization," in *Amazonian Floodplain Forests. Ecological Studies (Analysis and Synthesis)*, Vol. 210, eds W. Junk, M. Piedade, F. Wittmann, J. Schöngart, and P. Parolin (Dordrecht: Springer), 3–25. doi: 10.1007/978-90-481-8725-6_1

Junk, W. J., Soares, M. G. M., and Bayley, P. B. (2007). Freshwater fishes of the Amazon River basin: their biodiversity, fisheries, and habitats. *Aquat. Ecosyst. Heal. Manag.* 10, 153–173. doi: 10.1080/14634980701351023

Kelkar, N., Krishnaswamy, J., and Choudhary, S. (2010). Coexistence of fisheries with River Dolphin. *Conserv. Biol.* 24, 1130–1140. doi: 10.1111/j.1523-1739.2010.01467.x

Keppeler, F. W., Hallwass, G., and Silvano, R. A. M. (2017). Influence of protected areas on fish assemblages and fisheries in a large tropical river. *Oryx* 51, 268–279. doi: 10.1017/S0030605316000247

Latrubesse, E. M., Arima, E. Y., Dunne, T., Park, E., Baker, V. R., D'Horta, F. M., et al. (2017). Damming the rivers of the Amazon basin. *Nature* 546, 363–369. doi: 10.1038/nature22333

Latrubesse, E. M., d'Horta, F. M., Ribas, C. C., Wittmann, F., Zuanon, J., Park, E., et al. (2020). Vulnerability of the biota in riverine and seasonally flooded habitats to damming of Amazonian rivers. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 31, 1136–1149. doi: 10.1002/aqc.3424

Latrubesse, E. M., Stevaux, J. C., and Sinha, R. (2005). Tropical rivers. *Geomorphology* 70, 187–206. doi: 10.1016/j.geomorph.2005.02.005

Le Fur, J., Guilavogui, A., and Teitelbaum, A. (2011). Contribution of local fishermen to improving knowledge of the marine ecosystem and resources in the Republic of Guinea, West Africa. *Can. J. Fish. Aquat. Sci.* 68, 1454–1469. doi: 10.1139/f2011-061

Lima, M. A. L., Doria, C. R. D. C., and Freitas, C. E. D. C. (2012). Pescarias artesanais em comunidades ribeirinhas na amazônia brasileira: perfil socioeconômico, conflitos e cenário da atividade. *Ambient. Soc.* 15, 73–90. doi: 10.1590/S1414-753X2012000200005

Lindeman, R. L. (1942). The trophic-dinamic aspect of ecology. *Ecology* 23, 399–417.

Loch, C., Marmontel, M., and Simões-Lopes, P. C. (2009). Conflicts with fisheries and intentional killing of freshwater dolphins (Cetacea: Odontoceti) in the Western Brazilian Amazon. *Biodivers. Conserv.* 18, 3979–3988. doi: 10.1007/s10531-009-9693-4

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A., and Lutcavage, M. E. (2008). Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J. Anim. Ecol.* 77, 838–846. doi: 10.1111/j.1365-2656.2008.01394.x

Loh, T. L., McMurray, S. E., Henkel, T. P., Vicente, J., and Pawlik, J. R. (2015). Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. *PeerJ* 2015:e901. doi: 10.7717/peerj.901

Lopes, P. F. M., Verba, J. T., Begossi, A., and Pennino, M. G. (2018). Predicting species distribution from fishers' local ecological knowledge: a new alternative for data-poor management. *Can. J. Fish. Aquat. Sci.* 76, 1423–1431. doi: 10.1139/cjfas-2018-0148

Lucas, C. M. (2008). Within flood season variation in fruit consumption and seed dispersal by two Characin fishes of the Amazon. *Biotropica* 40, 581–589.

Magnusson, W. E., Vieira Da Silva, E., and Lima, A. P. (1987). Diets of Amazonian crocodilians. *J. Herpetol.* 21, 85–95. doi: 10.2307/1564468

Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J., Li, W., and Nobre, C. A. (2008). Climate change, deforestation, and the fate of the Amazon. *Science* 319, 169–172. doi: 10.1126/science.1146961

McGrath, D. G., Cardoso, A., Almeida, O. T., and Pezzuti, J. (2008). Constructing a policy and institutional framework for an ecosystem-based approach to managing the Lower Amazon floodplain. *Environ. Dev. Sustain.* 10, 677–695. doi: 10.1007/s10668-008-9154-3

Melo, T., Torrente-Vilara, G., and Röpke, C. P. (2019). Flipped reducetarianism: a vegan fish subordinated to carnivory by suppression of the flooded forest in the Amazon. *For. Ecol. Manage.* 435, 138–143. doi: 10.1016/j.foreco.2018.12.050

Mérona, B., and Rankin-de-Mérona, J. (2004). Food resource partitioning in a fish community of the central Amazon floodplain. *Neotrop. Ichthyol.* 2, 75–84.

Mérona, B., Mendes dos Santos, G., and Gonçalves de Almeida, R. (2001). Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. *Environ. Biol. Fishes* 60, 375–392. doi: 10.1023/A:1011033025706

Minagawa, M., and Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. *Geochim. Cosmochim. Acta* 48, 1135–1140. doi: 10.1016/0016-7037(84)90204-7

Mintenbeck, K., Brey, T., Jacob, U., Knust, R., and Struck, U. (2008). How to account for the lipid effect on carbon stable-isotope ratio (δ^{13}C): sample treatment effects and model bias. *J. Fish Biol.* 72, 815–830. doi: 10.1111/j.1095-8649.2007.01754.x

Mont'Alverne, R., Jardine, T. D., Pereyra, P. E. R., Oliveira, M. C. L. M., Medeiros, R. S., Sampaio, L. A., et al. (2016). Elemental turnover rates and isotopic discrimination in a euryhaline fish reared under different salinities: implications for movement studies. *J. Exp. Mar. Bio. Ecol.* 480, 36–44. doi: 10.1016/j.jembe.2016.03.021

Mortillaro, J. M., Pouilly, M., Wach, M., Freitas, C. E. C., Abril, G., and Meziane, T. (2015). Trophic opportunism of central Amazon floodplain fish. *Freshw. Biol.* 60, 1659–1670. doi: 10.1111/fwb.12598

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., and Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846–1850. doi: 10.1126/science.1138657

Newsome, S. D., Ralls, K., Van Horn Job, C., Fogel, M. L., and Cypher, B. L. (2010). Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). *J. Mammal.* 91, 1313–1321. doi: 10.1644/09-MAMM-A-362.1

Newsome, S. D., Tinker, M. T., Monson, D. H., Oftedal, O. T., Ralls, K., Staedler, M. M., et al. (2009). Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90, 961–974.

Nunes, D. M., Hartz, S. M., and Silvano, R. A. M. (2011). Conhecimento ecológico local e científico sobre os peixes na pesca artesanal no sul do Brasil. *Bol. Inst. Pesca* 37, 209–223.

Olivar, M. P., Bode, A., Lo, C., and Hulley, P. A. (2018). Trophic position of lanternfishes (Pisces: Myctophidae) of the tropical and equatorial Atlantic estimated using stable isotopes. *ICES J. Mar. Sci.* 76, 649–661. doi: 10.1093/icesjms/fsx243

Oliveira, A. C. B., Soares, M. G. M., Martinelli, L. A., and Moreira, M. Z. (2006). Carbon sources of fish in an Amazonian floodplain lake. *Aquat. Sci.* 68, 229–238. doi: 10.1007/s00027-006-0808-7

Paine, R. T. (1980). Food webs: linkage, interaction strenght and community infrastructure. *J. Anim. Ecol.* 49, 666–685.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing down marine food webs. *Science* 279, 860–863. doi: 10.1126/science.279.5352.860

Pereyra, P. E. R., Mont'Alverne, R., and Garcia, A. M. (2016). Carbon primary sources and estuarine habitat use by two congeneric ariid catfishes in a subtropical coastal lagoon. *Zoologia* 33, 1–7. doi: 10.1590/S1984-4689zool-20150075

Pinnegar, J. K., and Polunin, N. V. C. (1999). Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. *Funct. Ecol.* 13, 225–231. doi: 10.1046/j.1365-2435.1999.00301.x

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., and Montaña, C. G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152, 179–189. doi: 10.1007/s00442-006-0630-x

Prudente, B., da, S., Carneiro-Marinho, P., Valente, R., de, M., Montag, L. F., et al. (2016). Feeding ecology of *Serrasalmus gouldingi* (Characiformes: Serrasalmidae) in the lower Anapu River region, Eastern Amazon, Brazil. *Acta Amaz.* 46, 259–270. doi: 10.1590/1809-43922016 00123

Quezada-Romegialli, C., Jackson, A. L., Hayden, B., Kahilainen, K. K., Lopes, C., and Harrod, C. (2018). tRophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Methods Ecol. Evol.* 9, 1592–1599. doi: 10.1111/2041-210X.13009

R Development Core Team. (2021). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramires, M., Clauzet, M., Barrella, W., Rotundo, M. M., Silvano, R. A. M., and Begossi, A. (2015). Fishers' knowledge about fish trophic interactions in the southeastern Brazilian coast. *J. Ethnobiol. Ethnomed.* 11:19. doi: 10.1186/s13002-015-0012-8

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873. doi: 10.1111/brv.1 2480

Ribeiro, A. R., Damasio, L. M. A., and Silvano, R. A. M. (2021). Fishers' ecological knowledge to support conservation of reef fish (groupers) in the tropical Atlantic. *Ocean Coast. Manag.* 204:105543. doi: 10.1016/j.ocecoaman.2021. 105543

Runde, A., Hallwass, G., and Silvano, R. A. M. (2020). Fishers' knowledge indicates extensive socioecological impacts downstream of proposed dams in a Tropical River. *One Earth* 2, 255–268. doi: 10.1016/j.oneear.2020. 02.012

Salomão, R. D. P., Vieira, I. C. G., Suemitsu, C., Rosa, N., de, A., de Almeida, S. S., et al. (2007). As florestas de Belo Monte na grande curva do Xingu, Amazônia Oriental. *Bol. Mus. Para. Emilio Goeldi Cienc. Nat.* 2, 57–153.

Santos, R. E., Pinto-Coelho, R. M., Drumond, M. A., Fonseca, R., and Zanchi, F. B. (2020). Damming Amazon Rivers: environmental impacts of hydroelectric dams on Brazil's Madeira River according to local fishers' perception. *Ambio* 49, 1612–1628. doi: 10.1007/s13280-020-01316-w

Scheffer, M., Carpenter, S., and De Young, B. (2005). Cascading effects of overfishing marine systems. *Trends Ecol. Evol.* 20, 579–581. doi: 10.1016/j.tree. 2005.08.018

Scoles, R. (2014). Caracterização ambiental da bacia do Tapajós. *Environ. Int.* 36, 593–608.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396. doi: 10.1016/j.icesjms.2005.01.004

Silva, R. E., Rosas, F. C. W., and Zuanon, J. (2013). Feeding ecology of the giant otter (*Pteronura brasiliensis*) and the Neotropical otter (*Lontra longicaudis*) in Jaú National Park, Amazon, Brazil. *J. Nat. Hist.* 48, 465–479. doi: 10.1080/00222933.2013.800607

Silva, V. M. F., Freitas, C. E. C., Dias, R. L., and Martin, A. R. (2018). Both cetaceans in the Brazilian Amazon show sustained, profound population declines over two decades. *PLoS One* 13:e0191304. doi: 10.1371/journal.pone.019 1304

Silvano, R. A. M., and Begossi, A. (2002). Ethnoichthyology and fish conservation in the Piracicaba River (Brazil). *J. Ethnobiol.* 22, 285–306.

Silvano, R. A. M., and Begossi, A. (2005). Local knowledge on a cosmopolitan fish: Local knowledge on a cosmopolitan fish Ethnoecology of *Pomatomus saltatrix* (Pomatomidae) in Brazil and Australia ethnoecology of *Pomatomus saltatrix* (Pomatomidae) in Brazil and Australia. *Fish. Res.* 71, 43–59. doi: 10.1016/j.fishres.2004.07.007

Silvano, R. A. M., and Begossi, A. (2012). Fishermen's local ecological knowledge on southeastern Brazilian coastal fishes: contributions to research, conservation, and management. *Neotrop. Ichthyol.* 10, 133–147. doi: 10.1590/S1679-62252012000100013

Silvano, R. A. M., and Begossi, A. (2016). From ethnobiology to ecotoxicology: fishers' knowledge on trophic levels as indicator of bioaccumulation in tropical marine and freshwater fishes. *Ecosystems* 19, 1310–1324. doi: 10.1007/s10021-016-0002-2

Silvano, R. A. M., and Valbo-Jørgensen, J. (2008). Beyond fishermen's tales: contributions of fishers' local ecological knowledge to fish ecology and fisheries management. *Environ. Dev. Sustain.* 10, 657–675. doi: 10.1007/s10668-008-9149-0

Sioli, H. (1984). *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin*. Dordrecht: Springer. doi: 10.1007/978-94-009-6542-3

Souza, O. G. Jr., Nunes, J. L. G., and Silvano, R. A. M. (2020). Biology, ecology and behavior of the acoupa weakfish *Cynoscion acoupa* (Lacepède, 1801) according to the local knowledge of fishermen in the northern coast of Brazil. *Mar. Policy* 115:103870. doi: 10.1016/j.marpol.2020.103870

Sweeting, C. J., Polunin, N. V. C., and Jennings, S. (2006). Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. *Rapid Commun. Mass Spectrom.* 20, 595–601. doi: 10.1002/rcm. 2347

Turvey, S. T., Barrett, L. A., Yujiang, H., Lei, Z., Xinqiao, Z., Xianyan, W., et al. (2010). Cambios rápidos en las directrices en comunidades de pescadores de yangtze y en la memoria local de especies extintas. *Conserv. Biol.* 24, 778–787. doi: 10.1111/j.1523-1739.2009.01395.x

Vasconcellos, A., Hallwass, G., Bezerra, J., Serrão, A., Meneses, H., Lima, M., et al. (2021). Health risk assessment from consumption of mercury-contaminated fish in Munduruku Indigenous Communities in Amazon. *Int. J. Environ. Res. Public Heal.* 18, 1–16.

Veloso, H. P., Rangel Filho, A. L. R., and Lima, J. C. A. L. (1991). *Classificação da Vegetação Brasileira, Adaptada a um Sistema Universal*. Rio de Janeiro: IBGE.

Vidal, M. D., de Moura, M. F., and Muniz, G. P. S. (2019). Conhecimentos e crenças de pescadores artesanais sobre os golfinhos fluviais do Médio Rio Tapajós, Pará. *Rev. Bras. Biociências* 17, 53–60.

Vinson, M. R., and Angradi, T. R. (2011). Stomach emptiness in fishes: sources of variation and study design implications. *Rev. Fish. Sci.* 19, 63–73. doi: 10.1080/10641262.2010.536856

Wedemeyer-Strombel, K. R. (2019). *Fishers' Ecological Knowledge and Stable Isotope Analysis: A Social-Ecological Systems Approach to Endangered Species Conservation*. Available online at: https://scholarworks.utep.edu/open_etd/185 (accessed July 8, 2021).

Welcomme, R. L. (1999). A review of a model for qualitative evaluation of exploitation levels in multi-species fisheries. *Fish. Manag. Ecol.* 6, 1–19.

Winemiller, K. O., Montoya, J. V., Roelke, D. L., Layman, C. A., and Cotner, J. B. (2006). Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. *J. North Am. Benthol. Soc.* 25, 250–262.

Winemiller, K. O., Nam, S., Baird, I. G., Darwall, W., Lujan, N. K., Harrison, I., et al. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351, 128–129.

Zapelini, C., Giglio, V. J., Carvalho, R. C., Bender, M. G., and Gerhardinger, L. C. (2017). Assessing fishing experts' knowledge to improve conservation strategies for an endangered grouper in the Southwestern Atlantic. *J. Ethnobiol.* 37, 478–493. doi: 10.2993/0278-0771-37.3.478

Zuluaga-Gómez, M. A., Fitzgerald, D. B., Giarrizzo, T., and Winemiller, K. O. (2016). Morphologic and trophic diversity of fish assemblages in rapids of the Xingu River, a major Amazon tributary and region of endemism. *Environ. Biol. Fishes* 99, 647–658. doi: 10.1007/s10641-016-0506-9

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Integrating Different Types of Knowledge to Understand Temporal Changes in Reef Landscapes

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Reefs are highly diverse ecosystems threatened by anthropogenic actions that change their structure and dynamics. Many of these changes have been witnessed by different reef users who hold specific knowledge about the reefscape according to their experiences and uses. We aimed to understand whether fishers, divers, and reef scientists have different perceptions of general changes that have occurred in reefs and whether their knowledge converge, diverge or are complementary. We conducted 172 semi-structured interviews with stakeholders from Northeast and Southeast Brazil where either coral or rocky reefs occur, comprising most reefs occurring in the Southwestern Atlantic Ocean. Reef scientists and divers perceived corals have undergone the sharpest declines among reef species and indicate pollution and tourism as the major negative impacts on reefs. On the contrary, fishers noticed greater declines in fishing targets (i.e., groupers) and have hardly noticed differences in coral abundance or diversity over time. Divers had a broader view of changes in reef organisms, with some level of convergence with both reef scientists and fishers, while reef scientists and fishers provided information on more specific groups and economically relevant resources, respectively. The different stakeholders generally agree that reefscapes have undergone negative changes including diversity loss and abundance declines of reef organisms. The complementarity of information among different stakeholders enables a better understanding of how human behavior impact and perceive changes in natural ecosystems, which could be essential to manage reef environments, particularly those without baseline data.

Keywords: stakeholder perceptions, Brazilian reefs, environmental perception, random forest, Southwestern Atlantic reefs, recreational divers, artisanal fishers, marine scientists

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INTRODUCTION

Humans have depended on coastal reef resources for millennia (Cinner et al., 2018). The dependency and interactions between people and reefs (i.e., economic and cultural) may vary greatly over time, within and among social groups. Certain groups of people may be more dependent on reefs than others, which may also vary through time or seasonally (Costanza, 1999).

The interactions between human populations and reefscapes happen through different stakeholders (Marshall et al., 2018), for example, institutional agents responsible for ordering reef use, non-governmental organizations that focus on reef conservation, reef scientists interested in understanding how reefs work, and people that make direct use (extractive or not) of reefs, such as fishers, tourism operators, diving companies, and tourists.

These stakeholders may have different and/or complementary perceptions of the reefs depending on the type and frequency of their use (Eddy et al., 2018). Regular users can pay attention to different characteristics of these environments depending on how they use and access them, which would explain why people have contrasting memories of changes in natural environments (Hicks et al., 2013). For example, there is strong evidence that fishers have detailed knowledge about temporal changes in their target species (Johannes et al., 2000) but do not notice declines in species with less or none economic importance (Damasio et al., 2015). Divers may perceive differences in biological attributes such as fish richness and coral cover, as well as in the structural complexity of coral reefs (Uyarra et al., 2009) and scientists may restrict their perceptions to their particular study target (e.g., fishes or corals).

Reconciling knowledge from different stakeholders, of variable age groups and experiences is an alternative to reconstruct the process of change that a particular species or environment gone through (Hansen et al., 2006). This could be an important tool to reconstruct sensitive reefscapes in areas that lack baseline data and struggle with research funding, management, and enforcement. This is the case of Southwestern Atlantic reefs, most of which are within Brazilian territory, occurring between the latitudes ~5°N and 27°S and are marked by high species endemism of corals and fishes (Leão et al., 2016; Francini-Filho et al., 2018). These reefs are not homogeneous (Aued et al., 2018), while some of them are similar to typical coral reefs (Northeast region), others consist of rocky reefs that can support coral assemblages (Southeast and South regions; Leão et al., 2003). Brazilian reefs are found in shallow margins close to the coast, island edges and isolated banks (Leão et al., 2003; Kikuchi et al., 2010), many of them are close to densely populated areas where they are more subjected to direct anthropogenic impacts (Moura, 2000; Magris et al., 2021). Brazilian reefs are generally used for both extractive (i.e., fishing) and non-extractive activities (i.e., tourism, recreational diving, and scientific research), and these uses are often more intense when reefs are closer to the shore. Fishing, climate changes and pollution are among the main threats to Brazilian marine biodiversity (Magris et al., 2021), which combined may have caused severe changes in reef biodiversity.

We aimed to understand whether fishers, recreational divers, and reef scientists who use Brazilian reefs have a different perception about potential changes these reefs have undergone and whether they tend to converge or diverge on specific aspects of change. By unraveling, recognizing and connecting these perceptions we may be able to produce a more accurate historical reconstruction of changes and their magnitude in these ecosystems.

MATERIALS AND METHODS

This study was conducted between June 2018 and October 2019 in seven states along 3,133 km of the Brazilian coast (**Figure 1**), an area that comprises more than 50% of the distribution of reefs and diverse reef structures in Northeast and Southeast Brazil (Leão et al., 2016; Aued et al., 2018). The interview procedures were approved by the Ethics Committee at the Federal University of Rio Grande do Norte (CAAE: 73739917.3.0000.5537) and, in the case of protected areas, by the Brazilian System for Authorization and Information on Biodiversity (SISBIO: 65379).

Interviewed Stakeholders

We interviewed the stakeholders who make direct and constant use of reefs, namely fishers, recreational divers, and reef scientists. Among fishers, we focused on those who practice spearfishing to ensure a closer contact with the reefs, although we eventually included some fishers who use gillnets and hook-and-line, provided they were specialists in reef fishing. Despite not having a daily contact with reefs, recreational divers tend to have a unique and contemplative view of reefscapes because of the cultural values attributed to this leisure activity (Arin and Kramer, 2002), therefore we interviewed recreational divers and diving instructors. Among reef scientists, we focused on those whose research is focused on understanding reef ecological processes as we were interested in observable changes in living organisms. Despite our effort to find individuals within each of these groups of stakeholders (fishers, divers, and scientists) in every state we visited, we were unable to include representatives from all three categories in all states, either for logistical reasons and/or ease of access to certain groups. For example, in the state of Paraíba, we were only able to interview divers (**Figure 1**).

Data Collection

First, we identified key informants as leaders of fishing organizations, diving companies and recreational divers, and acquainted professors at universities known to at least one of the authors. From this initial list, we used the "snowball" technique, in which the key informants indicated people who they deemed relevant to contribute with the requested information (Goodman, 1961). These new informants named successive ones until we exhausted names or our capacity to reach them. Opportunistic interviews were also conducted with stakeholders who fit the criteria to answer the questionnaire. All interviewees exclusively answered about the reefs locations they had experience with throughout their lives. The interviews were conducted in two ways: in-person and using online forms. The online form was mainly used to reach divers, although some reef scientists also used this platform due to the difficulty of arranging face-to-face meetings.

The questionnaire was divided in three sessions (**Table 1**): "Personal data and impressions" in which we collected information on stakeholders' age, experience, reef region, among others; "Historical knowledge" in which we were interested in identifying the stakeholders' perception of organisms that decreased or increased in reef landscapes; and "Abiotic environment and threats" in which we asked

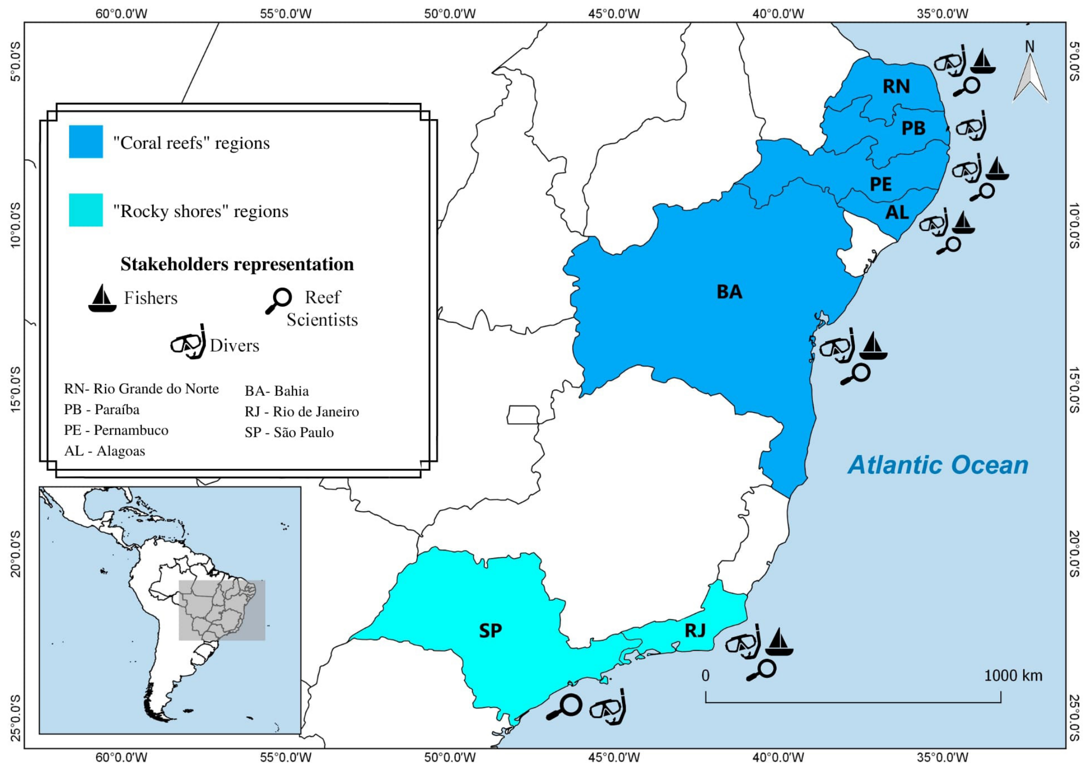

FIGURE 1 | States, where stakeholders were interviewed, are highlighted and divided between the region where coral reefs (states in darker blue) and rocky reefs (states in light blue) are found. It is shown which stakeholders were interviewed in each state: fishers with a sailboat, divers represented with a snorkel, and reef scientists symbolized with a hand glass. The map on the bottom left showing South America, localizing Brazil.

interviewees about changes in water and climate, how they perceived the pollution, and impacts in reef landscapes. We included in the questionnaires organisms that are conspicuous to the benthic (Aued et al., 2018) and fish communities (Morais et al., 2017), and that are perceived to be more subject to changes (**Supplementary Table 1**). We presented photographs of these organisms to the interviewees so that they could inform whether they knew the species and whether they had noticed changes in their abundance. Respondents were also free to list other species or groups of organisms for which they noticed changes in abundance. All data will be available upon reasonable request to the authors.

Data Analysis

In order to assess the agreement between and within the groups of stakeholders we combined three analytical methods: Random Forest (RF), Permutational Analysis of Variance (PERMANOVA) and Non-metric Multidimensional Scaling (NMDS). The RF is a supervised learning algorithm (James et al., 2013) that randomly creates a forest, combining decision trees to obtain predictions with greater accuracy and stability (James et al., 2013). The RF was used herein for two main purposes: (1) to understand how the different variables contribute to define a group of stakeholders (i.e., perceiving changes in abundance in a specific group) through the accuracy and Gini value; and (2) to assess how cohesive each stakeholder group is in their perceptions through a confusion matrix. The accuracy and Gini indicators designate which variables define the groups (fishers, divers, and reef scientists). The confusion matrix is obtained using the "out-of-bag" forecast for each observation in the training set of trees (Cutler et al., 2012). The variables with the highest number of mentions by stakeholders in each category (two models: decrease and increase) were chosen to compose the RF model (**Table 1**). All variables contained in the "Abiotic environment and threats" component and the "Environmental health" variable were used for the characteristics of the "Abiotic environment and impressions" block (**Table 1**). PERMANOVA and nMDS were used to test and visualize the groups formed by organisms which have decreased and organisms that have increased (**Table 1**). The PERMANOVA was used to assess if the dispersion of the stakeholders' responses is different among the three groups (Anderson, 2017). The nMDS based on Jaccard distances was used to visualize the outputs of the RF allowing to assess the qualitative interrelationships between the variables and to define which variables were most related to each stakeholder group. The number of axes in the nMDS was chosen to maintain the stress value below 0.15 and ensure that any existing patterns in the data would be captured by the multidimensional ordination space. All analyzes were performed using the RStudio v interface 1.2.5033, an integrated development environment for R program (R Core Team, 2019), using the "randomForest" (Liaw and Wiener, 2002), "factoextra" (Kassambara and Mundt, 2017),

TABLE 1 | Variables used in the study organized into three different components with their description, types, and analyses performed.

Components	Groups and variables	Description	Variables types	Analysis
Personal data and impressions	Stakeholder	Type of stakeholder. "Fisher"; "Diver," and "Reef scientists"	Nominal	Descriptive
	Age	Stakeholder's age (years)	Discrete	Descriptive
	Experience	How long the stakeholders have been engaged in research, fishing, or diving (years)	Discrete	Descriptive
	Initial and final contact	Years of initial and final contact with the chosen reef environment (year)	Discrete	Descriptive
	Environmental health	Regards the first and last contact with the environment, evaluated in the following categories: excellent; good; median; bad; and terrible. Divided into two categories: "initial health" and "recent health"	Ordinal	Random Forest
Historical knowledge	Organism decrease	Species the stakeholders noticed which have decreased in the reef environment	Nominal	Descriptive
	Organism decrease groups	Number of mentions per stakeholder for each category of organisms that have decreased It includes the following variables: "Massive corals," "Branched corals," "Echinoderm," "Cartilaginous fish," "Epinephelidae fish" (groupers), "Labridae fish: Scarinae" (parrotfish), "Other reef groups," "Mollusks," and "Crustaceans"	Discrete	Random Forest and NMDS PERMANOVA
	Organism increase	Species that the stakeholders noticed that have increased in the reef environment	Nominal	Descriptive
	Organism increase groups	Number of mentions per stakeholder for each category of organisms that have increased Includes the following: "other reef groups," "Invasive," "Zoanthids," "Echinoderm," "Pomacentridae Fish" (damselfish), and "Algae"	Discrete	Random Forest, NMDS, and PERMANOVA
	New organisms	Exotic and invasive species	Nominal	Descriptive
Abiotic environment and threats	Water	Assessment of reef water turbidity: "More turbid"; "Less turbid"; and "The same"	Ordinal	Random Forest
	Climate	Changes that have occurred in the regional climate (open response)	Nominal	Random Forest
	Pollution	Perception of pollution of the reef environment: "More polluted"; "Less polluted"; and "The same"	Ordinal	Random Forest
	Impacts	The three main threats to reef landscapes in order of importance	Nominal	Random Forest

"FactoMineR" (Lê et al., 2008), "vegan" (Oksanen et al., 2019), "ggplot2" (Wickham, 2016), "grid" (R Core Team, 2019), and "ggrepel" packages (Slowikowski, 2019).

RESULTS

Stakeholders' Profile

Fishers

Fishers formed the oldest (average = 49 yo) and most experienced group of respondents (~33 years of career; **Table 2**), providing approximately six decades of perceptions about the changes in Brazilian reefs. Most of them were spearfishers (71.0%), although some fished with gillnets (20.2%), and hook-and-line (8.7%). Fishers made 297 citations of organisms that they perceived as having declined (**Table 2**), but 29 of them were disregarded as they did not refer to species necessarily dependent on reefs (i.e., manatees). Likewise, six mentions of organisms that fishers perceived as having increased were disregarded for referring to cetaceans.

Among the organisms perceived by fishers to have decreased, the most cited groups were parrotfish ("Labridae: Scarinae," 36.1% of the fishers citations), followed by groupers ("Epinephelinae," 52.1%), sharks and rays ("Cartilaginous," 55.95% of fishers citations; **Figure 2A**). Among the organisms perceived to have increased, sea turtles stood out with 64.6% of the citations (**Figure 2B**). Only nine fishers mentioned the presence of new organisms, which exclusively referred to the sun coral (*Tubastraea* spp.). Most fishers said they believe reefs became more polluted (56.5%) and more turbid (68.1%) in comparison to the beginning of their career. About 55% also noticed changes in the local climate over their years of experience. Fishers also indicate industrial fishing as the main threat to reefs.

TABLE 2 | Main qualitative results according to the interviewed stakeholders (fishers, reef scientists, and divers).

	Fishers	Divers	Reef scientists
No. of interviews	69	60	43
Age (with standard deviation)	49 years (mean) 25 to 75 years (± 10.2)	35 years (mean) 21 to 54 (± 8.6)	45 years (mean) 24 to 80 years (± 13.0)
Experience (with standard deviation)	33 years (mean) 10 to 63 years (± 12.2)	15 years (mean) 1 to 42 years (± 11.08)	20 years (mean) 4 to 48 years (± 12.01)
Organisms that decreased (citations)	297 (4.3 per person)	336 (5.6 per person)	213 (5 per person)
Organisms that increased (citations)	126 (1.8 per person)	78 (1.3 per person)	107 (2.8 per person)
Reef threats (main answers %)	Industrial fishing (44.9) Tourism (17.4) Divines reasons (14.5)	Climate change (55.9) Pollution (48.3) Tourism (33.3)	Fishing (27.5) Tourism (27.5) Pollution (22.5)
Pollution % (more polluted)	56.5	68.3	74.4
Water % (more turbid)	68.1	35	37.2
Climate change % (noticed any change)	33.3	43.7	20.9
Environmental health – beginning (main answers %)	Great (72.5) Good (11.6)	Great (45) Good (38.3)	Intermediate (51.2) Good (30.2)
Environmental health – currently (main answers %)	Bad (46.4) Horrible (43.5)	Intermediate (38.3) Bad (35)	Intermediate (53.4) Bad (27.9)

Divers

Divers formed the youngest and least experienced group (35 years old, 15 years of experience, on average), but even so, they were the ones who cited the highest number of organisms that have declined (N = 336; **Table 2**). Similar to other stakeholders, divers highlighted the decline of "Massive corals" (55.31% of divers' citations) followed by parrotfish ("Labridae: Scarinae"; 42.6%), (**Figure 2A**). On the other hand, divers also noticed an increase in damselfish ("Pomacentridae"; 37.9% of divers' citations), "Zoanthids" (34.8%) and "Algae" (27.2%) (**Figure 2B**). Divers also indicated the appearance of new organisms, with 11 mentions of the sun coral (*Tubastraea* spp.) and six mentions of other organisms including algae, mollusks, and the lionfish (*Pterois volitans*). Most divers believe that water turbidity (65%) and climate (56.3%) have not changed since the beginning of their experiences in the past decades. On the other hand, most divers suggested that the reef environment became more polluted, sustain an intermediate health status (**Table 2**), and indicate climate change as the major threat to reefs.

Reef Scientists

Reef scientists were on average 45 years old and a maximum of 20 years of experience (**Table 2**). Similar to fishers, reef scientists also noticed declines of parrotfish ("Labridae: Scarinae"; 21.3% of the reef scientists' citations), and "Massive corals" (42.5%) (**Figure 2A**). They also noticed an increase in "Sea turtles" (24.4% of citations) and "Zoanthids" (46.5%) (**Figure 2B**). Ten reef scientists (23.2%) also noticed the presence of new organisms in the reef landscapes, especially the sun coral (*Tubastraea* spp.; 10 mentions). The other new organisms mentioned (N = 14) included octocoral species, ascidians, lionfish (*P. volitans*), sponges, the polychaeta *Branchioma* spp. and the ophiuroid *Ophiothela* spp. Most reef scientists (74.4%) suggested that reefs are now more polluted and some of them (37.2%) indicated that the water is more turbid in comparison the beginning of their careers. Most of them also chose not to give their opinion on the impact of climate changes on reefscapes. Reef scientists see fishing as the main threat to reefs and have more conservative opinions on general reef health classifying it as intermediate but stable since the beginning of their careers (**Table 2**).

Agreement Among Stakeholders

The three groups of stakeholders share a general perception that the reef health has deteriorated over time. About 46% of fishers classified the current reef health as "bad," 53.4% of reef scientists and 38.3% of divers classified as "intermediate" (**Table 2**). Regarding the general and abiotic aspects of perception (first random forest analysis), the three groups of stakeholders differ in how they evaluate the "Initial health," "Recent health," and the "Impacts" sources (Random Forest: accuracy 63.4%) (**Figure 3A**). Divers and reef scientists showed less homogeneous responses within each group, with 50% and 34% being mistakenly classified as belonging to another group of stakeholders, respectively (**Supplementary Table 2**). Most fishers were recognized as such

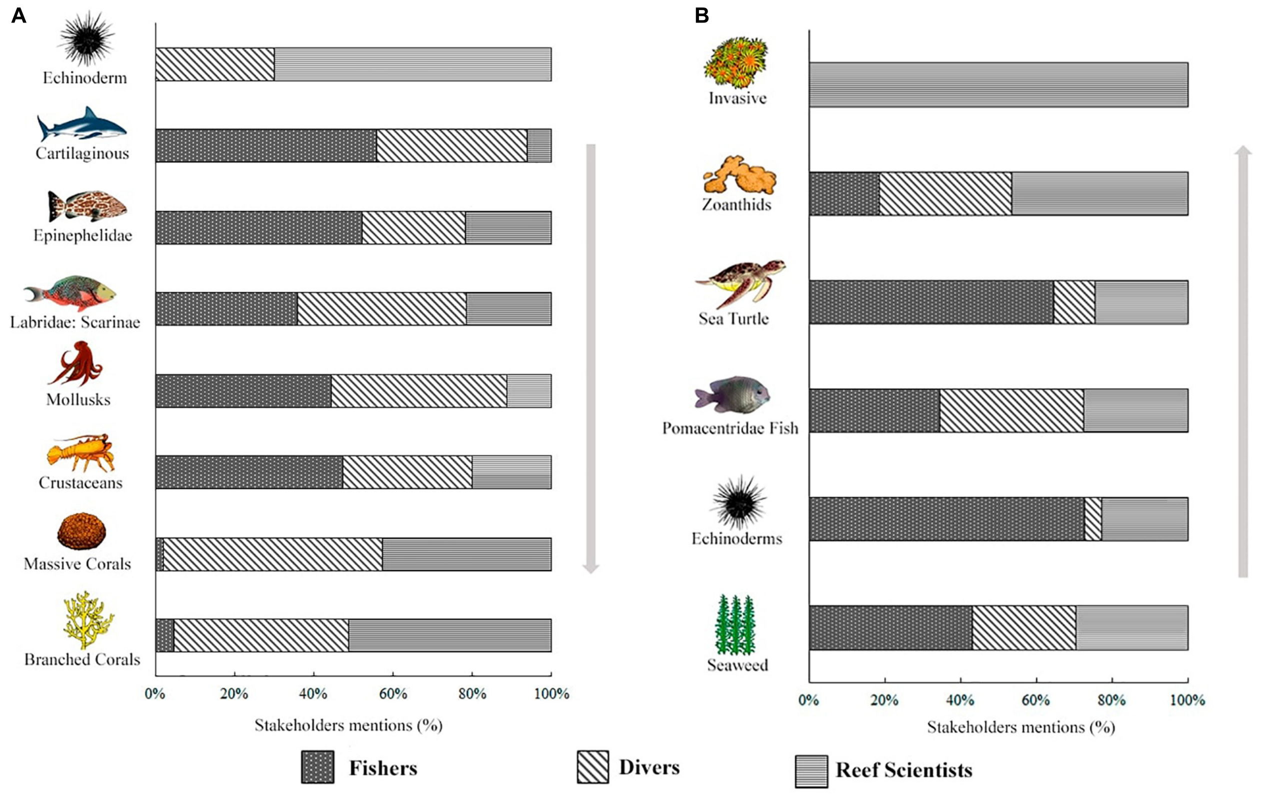

FIGURE 2 | Main organisms mentioned by fishers, divers, and reef scientists as having decreased **(A)** or increased **(B)** in the Brazilian reef landscapes in the last six decades. Only organisms that had a minimum of 5% in each group of citations were included among the total citations of increase and decrease, respectively. The down arrow on the left represents the organisms that declined, and the up arrow on the right represents the organisms that increased in reef landscapes.

(74%), 21.7% were recognized as divers, and 4.3% as reef scientists. About 50% of the divers were recognized as such, 26.6% as fishers and 23.3% as reef scientists. Among the reef scientists, 65.1% were recognized as such and 27.9% as divers (**Supplementary Table 2**).

Regarding the species that stakeholders perceive to have declined (second random forest analysis), their main differences were on the groups "Massive Corals" and "Epinephelidae Fish" (Random Forest: 63.4% accuracy; **Figure 3B**). The fact that fishers mostly perceive decreases in fish-related organisms, such as parrotfishes and groupers made them significantly different from the other stakeholders (PERMANOVA p-adjusted (0.003; **Supplementary Table 3**), who tended to mention massive corals more often (**Supplementary Tables 2**, **3**). Reef scientists were highly mixed with the other stakeholders in the Random Forest: 53.5% were identified as divers and 13.9% as fishers. Specifically, most fishers were recognized as such, but 18.8% were recognized as divers. Most divers were also identified as belonging to their own group, however, 18.3% were recognized as fishers and 15% as reef scientists (**Supplementary Table 2**). These trends were confirmed by the nMDS analysis, which showed that fishers tended to mention more "Cartilaginous Fish" and "Epinephelidae Fish" compared to the other stakeholders (**Figure 4A**). In turn, reef scientists and divers tended to mention "Massive corals," "Echinoderm," and "Branched corals" (**Figure 4A**).

The most important factors separating the stakeholders for species which were perceived as having increased are "other reef groups," "Invasive" and "Echinoderm" groups (Random Forest: accuracy 59.9%) (**Figure 3C**). In this case, all groups of stakeholders were significantly different from each other (**Supplementary Table 3**). Again, reef scientists were the least recognized stakeholders by the model: only 39.5% were recognized as such, 46.5% were characterized as divers, and 13.9% as fishers, reinforcing the dispersion of information among these stakeholders (**Supplementary Table 2**). Most fishers and divers were identified as such, except for 37.7% of the fishers who were recognized as divers, and 25% of the divers who were characterized as fishers. In this specific nMDS, fishers were more associated through citations of "Sea turtle" groups, while reef scientists and divers were more associated to the citation of "Zoanthids" and "Invasive" groups (**Figure 4B**).

DISCUSSION

The three groups of stakeholders perceived changes in reef health and pollution, generally agreeing that many species declined in abundance. Because these groups had different perceptions regarding which species have declined or increased, combining their knowledge can help create a more comprehensive

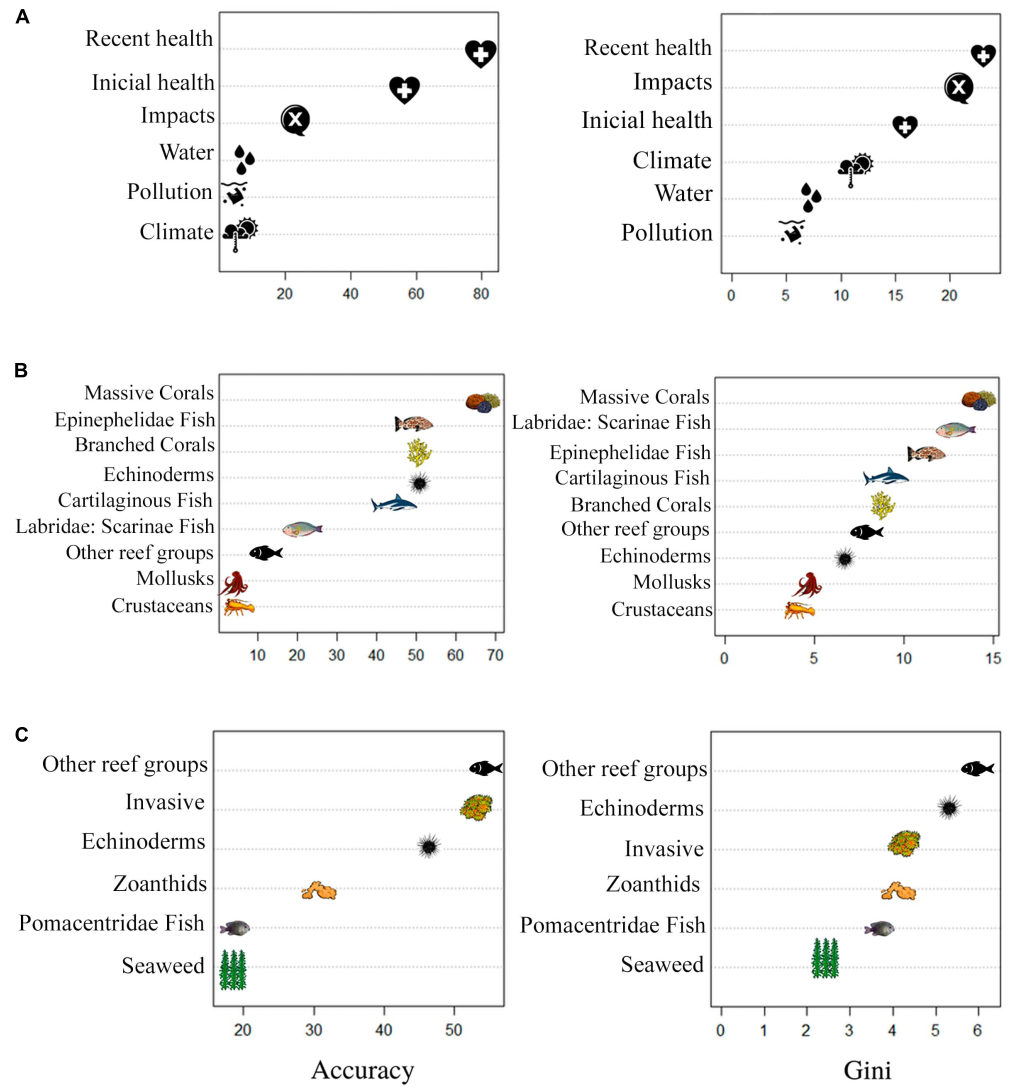

FIGURE 3 | Random Forest accuracy and Gini values showing the main variables responsible for the differences in stakeholder perception on. **(A)** Changes in abiotic reef environment. **(B)** Organisms that have decreased. **(C)** Organisms that have increased in reef landscapes. Notice that the higher the accuracy or the Gini value, the more likely it is that that variable contributed to separating the stakeholders according to their perceptions.

understanding of past changes in Southwestern Atlantic reefs. Stakeholders noticed changes in organisms related to their occupations. For instance, fishers mentioned decreases in targeted fishes, such as parrotfish, groupers, sharks and rays, including multiple species that have been overfished and in dire need of management (Giglio et al., 2014; Lessa et al., 2016; Roos et al., 2020). They also indicated a great decrease in shark species within the genus *Sphyrna* spp. and particularly the species *Ginglymostoma cirratum* between the 1980s and 1990s (Leduc et al., 2021), and in the locally important black grouper *Mycteroperca bonaci* (Bender et al., 2014). Parrotfish decline have started in the 1990s, although the exploitation of some species, such as *Scarus trispinosus*, may have started in the mid-1980s in some parts of the country (Bender et al., 2014). Divers and reef scientists noticed coral declines more frequently than fishers probably because they are more likely to pay attention to the reef substrate and sessile invertebrates due to their recreational and scientific interest, respectively (Giglio et al., 2015). This perception is corroborated by the increase in coral mortality due to more frequent and intense thermal anomalies in addition to land-based stressors in Brazil (Teixeira et al., 2021). Reef scientists were also the only stakeholder group to notice a decline in sea urchin populations. Interestingly, fishers reported an increase in the abundance of black urchins. Sea urchin declines were largely documented in the Atlantic Ocean, such as the emblematic case of *Diadema antillarum* that almost disappeared after a massive die-off caused by a disease in 1983–1984, which is linked to increased algal abundance in many Caribbean reefs (Hughes, 1994; Tuya et al., 2005). However, such decline noticed by scientists in Brazil probably had little to know effect on sea urchin

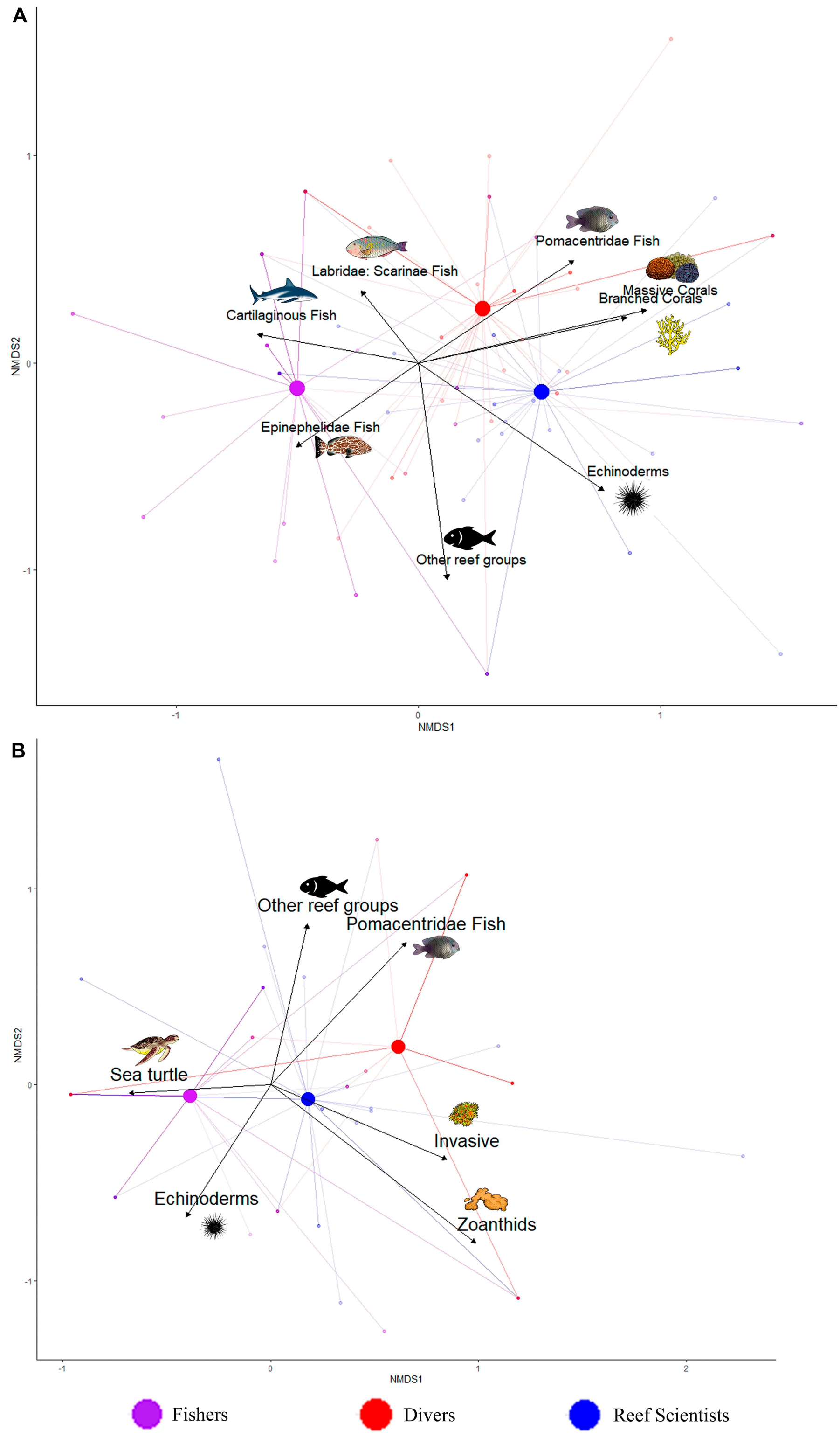

FIGURE 4 | Non-metric multidimensional scaling (NMDS) for organisms that have change in reef landscapes comparing the perception of the three types of stakeholders in the study: fishers, divers, and reef scientists. **(A)** Organisms that have declined ("stress value" = 0.12). **(B)** Organisms that have increased ("stress value" = 0.07). The stakeholders are represented through the colorful vectors, purple for fishers, red for divers, and blue for reef scientists. The black vectors represented the trend data for three types of stakeholders.

herbivory since current abundances seem to be enough to control macroalgal in shallow zones of subtropical reefs (Cordeiro et al., 2020). Stakeholders also have different perceptions on which organisms have increased in Southwestern Atlantic reefs. Divers mentioned the increase of organisms in shallow coastal reefs (i.e., Pomacentridae fish, zoanthids, and algae), an area often used by diving companies. Illegal feeding to attract fish and entertain tourists in some of these areas (Silva et al., 2020) may also have affected their perception of increase in abundance. Reef scientists mentioned reef organisms that increased but that were not on the original list (e.g., sponges) and were the only stakeholder group to spontaneously classify a species as invasive. Fishers mentioned an increase in sea turtle abundance more often than any other group of stakeholders, which may be directly related to a fishing ban established in the early 1990's (Marcovaldi and Marcovaldi, 1999) and to the numerous reports of bycatch in gillnets (Marcovaldi et al., 2006), increasing the contact between fishers and sea turtles. The recovery in sea turtle populations can also be attributed to a massive protection of sea turtle nests in Brazil for over 30 years (Marcovaldi and Chaloupka, 2007). Mentions of new organisms was rare regardless of the stakeholder group, but when it occurred the sun coral *Tubastraea* spp. was the most cited organism. There is evidence that *Tubastraea* spp. have been spreading throughout Brazilian reefs, from the states of Ceará (3°S) to Santa Catarina ($\sim$27°S), being a major problem in rocky reefs of Southeastern Brazil (Riul et al., 2013; Capel et al., 2019). Indeed, the sun coral may significantly change the reef community, since experimental competitive interactions between the invasive *Tubastraea tagusensis* and the native coral *Siderastrea stellata* caused significant damaged and mortality in the native species (Miranda et al., 2016).

Fishers were generally more pessimistic about the current health state of reefs, which may be related to the decline in stocks of their fishing targets, but also to the fact that they use reefs and the oceans more often than any other user. Divers also classified the current reef health as "bad," which is likely due to their greater contact with touristic sites, which tend to be more degraded compared to those far from the coast (Hannak et al., 2011). Reef scientists were relatively more optimistic classifying reef health as "intermediate" or "bad." Although it is not possible to state the reason for this difference in perception among stakeholders, reef scientists use external references from the literature in addition to personal experiences to assess the health status of Brazilian reefs. Therefore, these unified opinions of reef health among scientists may exist because of their education and experience, that could even compensate the shifting baseline because of their formal knowledge (Muldrow et al., 2020). In addition, reef scientists are divers with scientific training and experience, and often interact with fishers or assess information provided by fishers (Bender et al., 2013), which could explain why their perception was mixed with those groups of stakeholder.

Different stakeholders also attributed different threats to the reefs that would help explain their current health status. We only interviewed artisanal fishers and they cited industrial fishing as an important impact on reefs. However, reefs are mainly fished by artisanal fishing, and some of its gear can indeed damage corals (Link et al., 2019) and cause significant impact to fish stocks (Bender et al., 2014). Denying that artisanal fishing activities can have negative consequences to reefs can hinder decision-making (Vaclavikova et al., 2011). For example, fishers may resist management measures, even those aimed at protecting endangered species, if they do not feel at least partially responsible for current reef health. Some fishers also highlighted that impacts on reefs happen for divine reasons, which suggests the difficulty and need to bring scientific information to these groups (Hilborn, 2007). Reef scientists also highlighted the negative impacts of fishing activity on reefs, specifically causing overfishing. Part of these reef scientists may be more aware of the impact of fisheries for being part of groups that assist the government in designing fishing regulations, so they may have access to more detailed fisheries information on a national level. These scientists are invited to these groups exactly for their expertise on the species and awareness of the stock status, these groups facilitate the exchange of information increasing their understanding of fishing impacts.

All groups perceived some level of negative impact of tourism on reefs, which is widely recognized in the literature (Giglio et al., 2017, 2020). Reef scientists are likely to deal with or be aware of impacts caused by tourism such as fish feeding, coral removal, and over-visitation (Liu et al., 2012). Fishers may have a conflict with tourism activities, including competition over space use (Outeiro et al., 2019). Divers may be especially aware of the impact of tourism because they are directly related to this activity (Neto et al., 2017), some of them are tour guides in reef environments and/or have great contact with tourism companies that often give or receive instructions to avoid their impacts on reefs. The fact that some divers understand the impacts of tourism, despite working in or promoting the sector, possibly suggests that they have been following reef degradation in areas increasingly subjected to visitation (Dearden et al., 2007). Conversely, divers can also be critical allies of science and conservation through their involvement in citizen-science programs that suggest divers without previous scientific training can provide reliable estimates of fish abundance (Vieira et al., 2020).

The increase in pollution was also perceived by most stakeholders, although especially by reef scientists and divers, who are more likely to visually notice it in reefs (Costa, 2007). Only divers rated climate change as the most important factor among reef threats. Perhaps divers are more exposed to this type of information through the media and social media than fishers, who tend to have low education levels and poor access to other social services. Divers are also possibly less afraid of expressing an unsupported opinion than reef scientists who do not work on climate-related issues. Scientists are experts in their specialism and expect to be recognized for it, which is probably why scientists do not want to express opinions about subjects outside their expertise (Myers, 2003). In fact, not even the consecutive cases of bleaching observed on the Brazilian coast (Dias and Gondim, 2016; Leão et al., 2019; Ferreira et al., 2021) seem to have been enough to make climate change an important issue to be raised here by reef scientists. A possible factor for this is the lower frequency of thermal anomalies in South Atlantic and particularly low post-bleaching mortality ($<$5%) when compared to the Pacific and Caribbean until recently (Mies et al., 2020). Climate change may also be difficult to be perceived on its own, especially when it is not easily associated to local climate events (Spence et al., 2011).

Overall, fishers provided more consistent responses. The interviewed fishers were precisely those who target species similar to the fish presented in the questionnaire. Fishers may also be immersed in a more culturally homogeneous world in small coastal communities than that shared by reef scientists and divers from different regions of the country (Reis and D'Incao, 2000). Unlike fishers, reef scientists have their specific interests diffused over a large set of reef species. Compared to the other stakeholder groups, reef scientists provided the least homogeneous responses, sometimes confused with those of fishers, but mainly with those of divers. Although many reef scientists are attentive to interspecific relationships, most are focused on particular groups of organisms and their opinions may only lean toward their research object.

Different stakeholder groups agreed with the changes in reef landscapes, but also share conflicting notions on specific subjects. This disagreement can represent an obstacle to governance and the management of natural resources (Yandle, 2003; Suárez de Vivero et al., 2008), but can also be a source of complementarity as each group perceive unique aspects of changes on ecosystems. Converging information reinforces the idea that some species or certain abiotic characteristics have undergone significant changes that are noticeable by all. By combining these perceptions, we gathered strong evidence that parrotfishes, groupers, sharks, and corals have undergone significant declines, whereas seaweeds, zoanthids and damselfishes have increased in Brazilian reefs. Pollution and fishing are major problems and reef health has suffered and overall decline. Such a scenario may jeopardize not only reef biodiversity but the benefit it provides to many people that depend on it for multiple uses. Combining different knowledge is an important step toward understanding the history of human-caused impacts on ecosystems, mitigating impacts, restoring key ecosystem functions, and preparing for the future.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethics Committee at the Federal University of Rio Grande do Norte (CAAE: 73739917.3.0000.5537) and Brazilian System for Authorization and Information on Biodiversity (SISBIO: 65379), with the latter specifically for research done in protected areas. Written informed consent for participation was not required for this study in accordance with the National Legislation and the Institutional Requirements.

AUTHOR CONTRIBUTIONS

MQ-A and GL conceived the idea and developed it with PL. MQ-A collected all the data. PL and GL contacted key participants for the interviews. MQ-A and FF performed the statistical analyses. MQ-A and PL wrote the manuscript with inputs from all co-authors and also designed the figures. All authors contributed with text revision and the final format of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.709414/full#supplementary-material

REFERENCES

Anderson, M. J. (2017). Permutational multivariate analysis of variance (Permanova). *Wiley Stat. Ref. Online* 2017:7841. doi: 10.1002/9781118445112.stat07841

Arin, T., and Kramer, R. A. (2002). Divers willingness to pay to visit marine sanctuaries: an exploratory study. *Ocean Coast Manag.* 45, 171–183. doi: 10.1016/s0964-5691(02)00049-2

Aued, A., Smith, F., Quimbayo, J. P., Candido, D. V., Longo, O., Ferreira, E. L. C., et al. (2018). Large-scale patterns of benthic marine communities in the Brazilian Province. *PLoS One* 13:90. doi: 10.5061/dryad.f5s90

Bender, M. G., Floeter, S. R., and Hanazaki, N. (2013). Do traditional fishers recognise reef fish species declines? Shifting environmental baselines in Eastern Brazil. *Fish. Manag. Ecol.* 20, 58–67. doi: 10.1111/fme.12006

Bender, M. G., Machado, G. R., Silva, P. J., de, A., Floeter, S. R., Monteiro-Netto, C., et al. (2014). Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the southwestern atlantic. *PLoS One* 9:332. doi: 10.1371/journal.pone.0110332

Capel, K. C. C., Creed, J., Kitahara, M. V., Chen, C. A., and Zilberberg, C. (2019). Multiple introductions and secondary dispersion of *Tubastraea* spp. in the Southwestern Atlantic. *Sci. Rep.* 9, 1–11. doi: 10.1038/s41598-019-50442-3

Cinner, J. E., Maire, E., Huchery, C., Aaron MacNeil, M., Graham, N. A. J., Mora, C., et al. (2018). Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl. Acad. Sci. USA*. 115, E6116–E6125. doi: 10.1073/pnas.1708001115

Cordeiro, C. A. M. M., Harborne, A. R., and Ferreira, C. E. L. (2020). The biophysical controls of macroalgal growth on subtropical reefs. *Front. Mar. Sci.* 7:488. doi: 10.3389/fmars.2020.00488

Costa, O. S. Jr. (2007). Anthropogenic nutrient pollution of coral reefs in southern bahia, brazil. *Brazil. J. Oceanogr.* 55, 265–279. doi: 10.1590/s1679-87592007000400004

Costanza, R. (1999). The ecological, economic, and social importance of the oceans. *Ecol. Econ.* 31, 199–213. doi: 10.1016/s0921-8009(99)00079-8

Cutler, A., Cutler, D. R., and Stevens, J. R. (2012). Random Forests. *Ensemb. Mach. Learn.* 2012, 157–175. doi: 10.1007/978-1-4419-9326-7

Damasio, L., de, M. A., Lopes, P. F. M., Guariento, R. D., and Carvalho, A. R. (2015). Matching Fishers' knowledge and landing data to overcome data missing in small-scale fisheries. *PLoS One* 10:133122. doi: 10.1371/journal.pone.0133122

Dearden, P., Bennett, M., Rollins, R., Dearden, P., Bennett, M., Rollins, R., et al. (2007). Perceptions of diving impacts and implications for reef conservation perceptions of diving impacts and implications. *Coast. Manag.* 35, 305–317. doi: 10.1080/08920750601169584

Dias, T. L. P., and Gondim, A. I. (2016). Bleaching in scleractinians, hydrocorals, and octocorals during thermal stress in a northeastern Brazilian reef. *Mar. Biodivers.* 46, 303–307. doi: 10.1007/s12526-015-0342-8

Eddy, T. D., Cheung, W. W. L., and Bruno, J. F. (2018). Historical baselines of coral cover on tropical reefs as estimated by expert opinion. *PeerJ* 2018, 1–16. doi: 10.7717/peerj.4308

Ferreira, L. C. L., Grillo, A. C., Repinaldo Filho, F. P. M., Souza, F. N. R., and Longo, G. O. (2021). Different responses of massive and branching corals to a major heatwave at the largest and richest reef complex in South Atlantic. *Mar. Biol.* 168, 1–8. doi: 10.1007/s00227-021-03863-6

Francini-Filho, R. B., Asp, N. E., Siegle, E., Hocevar, J., Lowyck, K., D'Avila, N., et al. (2018). Perspectives on the Great Amazon Reef: Extension, biodiversity, and threats. *Front. Mar. Sci.* 5:142. doi: 10.3389/fmars.2018.00142

Giglio, V. J., Bertoncini, A. A., Ferreira, B. P., Hostim-Silva, M., and Freitas, M. O. (2014). Landings of goliath grouper, *Epinephelus itajara*, in Brazil: Despite prohibited over ten years, fishing continues. *Nat. Conserv.* 12, 118–123. doi: 10.1016/j.ncon.2014.09.004

Giglio, V. J., Luiz, O. J., and Ferreira, C. E. L. (2020). Ecological impacts and management strategies for recreational diving: A review. *J. Environ. Manage.* 256:109949. doi: 10.1016/j.jenvman.2019.109949

Giglio, V. J., Luiz, O. J., and Schiavetti, A. (2015). Marine life preferences and perceptions among recreational divers in Brazilian coral reefs. *Tour. Manag.* 51, 49–57. doi: 10.1016/j.tourman.2015.04.006

Giglio, V. J., Ternes, M. L. F., Mendes, T. C., Cordeiro, C. A. M. M., and Ferreira, C. E. L. (2017). Anchoring damages to benthic organisms in a subtropical scuba dive hotspot. *J. Coast. Conserv.* 21, 311–316. doi: 10.1007/s11852-017-0507-7

Goodman, L. A. (1961). Snowball Sampling. *Ann. Math. Stat.* 32, 148–170.

Hannak, J. S., Kompatscher, S., Stachowitsch, M., and Herler, J. (2011). Snorkelling and trampling in shallow-water fringing reefs: Risk assessment and proposed management strategy. *J. Environ. Manage.* 92, 2723–2733. doi: 10.1016/j.jenvman.2011.06.012

Hansen, L., Noe, E., and Højring, K. (2006). Nature and nature values in organic agriculture. An analysis of contested concepts and values among different actors in organic farming. *J. Agric. Environ. Ethics* 19, 147–168. doi: 10.1007/s10806-005-1804-y

Hicks, C. C., Graham, N. A. J., and Cinner, J. E. (2013). Synergies and tradeoffs in how managers, scientists, and fishers value coral reef ecosystem services. *Glob. Environ. Chang.* 23, 1444–1453. doi: 10.1016/j.gloenvcha.2013.07.028

Hilborn, R. (2007). Defining success in fisheries and conflicts in objectives. *Mar. Policy* 31, 153–158. doi: 10.1016/j.marpol.2006.05.014

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551. doi: 10.1126/science.265.5178.1547

James, G., Witten, D., Hastie, T., and Tibshirani, R. (2013). *An Introduction to Statistical Learning with Applications in R*. New York, NY: Springer.

Johannes, R. E., Freeman, M. M. R., and Hamilton, R. J. (2000). Ignore fishers' knowledge and miss the boat. *Fish Fish.* 1, 257–271. doi: 10.1111/j.1467-2979.2000.00019.x

Kassambara, A., and Mundt, F. (2017). *Factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. Available online at: https://cran.r-project.org/package=factoextra (accessed April 1, 2020).

Kikuchi, R. K. P., Leão, Z. M. D. A. N., and Oliveira, M. D. M. (2010). Conservation status and spatial patterns of AGRRA vitality indices. *Rev. Biol. Trop.* 58, 1–31. doi: 10.1016/j.visres.2006.04.012

Lê, S., Josse, J., and Husson, F. (2008). FactoMineR: A Package for Multivariate Analysis. *J. Stat. Softw.* 25, 1–18. doi: 10.18637/jss.v025.i01

Leão, Z. M. A. N., Kikuchi, R. K. P., Ferreira, B. P., Neves, E. G., Sovierzoski, H. H., Oliveira, M. D. M., et al. (2016). Brazilian coral reefs in a period of global change: A synthesis. *Brazil. J. Oceanogr.* 64, 97–116. doi: 10.1590/S1679-875920160916064sp2

Leão, Z. M. A. N., Kikuchi, R. K. P., and Oliveira, M. D. M. (2019). *The coral reef province of Brazil*. Second Edi. Amsterdam: Elsevier Ltd. doi: 10.1016/B978-0-12-805068-2.00048-6

Leão, Z. M. A. N., Kikuchi, R. K. P., and Testa, V. (2003). *Corals and coral reefs of Brazil*. Amsterdam: Elsevier Ltd. doi: 10.1016/B978-044451388-5/50003-5

Leduc, A. O. H. C., De Carvalho, F. H. D., Hussey, N. E., Reis-Filho, J. A., Longo, G. O., and Lopes, P. F. M. (2021). Local ecological knowledge to assist conservation status assessments in data poor contexts: a case study with the threatened sharks of the Brazilian Northeast. *Biodivers. Conserv.* 30, 819–845. doi: 10.1007/s10531-021-02119-5

Lessa, R., Batista, V. S., and Santana, F. M. (2016). Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrhynchus*) off Brazil. *Glob. Ecol. Conserv.* 7, 70–81. doi: 10.1016/j.gecco.2016.04.003

Liaw, A., and Wiener, M. (2002). Classification and Regression by randomForest. *R News* 2, 18–22.

Link, J., Segal, B., and Casarini, L. M. (2019). Abandoned, lost or otherwise discarded fishing gear in Brazil: A review. *Perspect. Ecol. Conserv.* 17, 1–8. doi: 10.1016/j.pecon.2018.12.003

Liu, P., Meng, P., Liu, L., Wang, J., and Leu, M. (2012). Impacts of human activities on coral reef ecosystems of southern Taiwan: A long-term study. *Mar. Pollut. Bull.* 64, 1129–1135. doi: 10.1016/j.marpolbul.2012.03.031

Magris, R. A., Costa, M. D. P., Ferreira, C. E. L., Vilar, C. C., Joel, J. J., Margareth, C. C., et al. (2021). A blueprint for securing Brazil's marine biodiversity and supporting the achievement of global conservation goals. *Divers. Distrib.* 27, 198–215. doi: 10.1111/ddi.13183

Marcovaldi, M., and Chaloupka, M. (2007). Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endanger. Species Res.* 3, 133–143. doi: 10.3354/esr003133

Marcovaldi, M. A., and Marcovaldi, G. G. (1999). Marine turtles of Brazil The history and structure of Projeto TAMAR—IBAMA. *Biol. Conserv.* 91, 35–41. doi: 10.1016/s0006-3207(99)00043-9

Marcovaldi, M. A., Sales, G., Thome, J. C. A., DiasdaSilva, A. C. C., Gallo, B. M. G., Lima, E. H. S. M., et al. (2006). Sea Turtles and Fishery Interactions in Brazil: Identifying and Mitigating Potential Conflicts. *Mar. Turt. Newsl.* 112, 4–8.

Marshall, N., Barnes, M. L., Birtles, A., Brown, K., Cinner, J., Curnock, M., et al. (2018). Measuring what matters in the Great Barrier Reef. *Front. Ecol. Environ.* 16:271–277. doi: 10.1002/fee.1808

Mies, M., Francini-Filho, R. B., Zilberberg, C., Garrido, A. G., Longo, G. O., Laurentino, E., et al. (2020). South atlantic coral reefs are major global warming refugia and less susceptible to bleaching. *Front. Mar. Sci.* 7:1–13. doi: 10.3389/fmars.2020.00514

Miranda, R. J., Cruz, I. C. S., and Barros, F. (2016). Effects of the alien coral *Tubastraea tagusensis* on native coral assemblages in a southwestern Atlantic coral reef. *Mar. Biol.* 163, 1–12. doi: 10.1007/s00227-016-2819-9

Morais, R. A., Ferreira, C. E. L., and Floeter, S. R. (2017). Spatial patterns of fish standing biomass across Brazilian reefs. *J. Fish Biol.* 91, 1642–1667. doi: 10.1111/jfb.13482

Moura, R. L. (2000). Brazilian reefs as priority areas for biodiversity conservation in the Atlantic Ocean. 9th Int. *Coral Reef. Symp.* 2, 917–920.

Muldrow, M., Parsons, E. C. M., and Jonas, R. (2020). Shifting baseline syndrome among coral reef scientists. *Humanit. Soc. Sci. Commun.* 7, 1–8. doi: 10.1057/s41599-020-0526-0

Myers, G. (2003). Discourse studies of scientific popularization: Questioning the boundaries. *Discour. Stud.* 5, 265–279. doi: 10.1177/1461445603005002006

Neto, A. Q., Lohmann, G., Scott, N., Dimmock, K., Queiroz, A., Lohmann, G., et al. (2017). Rethinking competitiveness: important attributes for a successful scuba diving destination. *Tour. Recreat. Res.* 42, 356–366. doi: 10.1080/02508281.2017.1308086

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). *vegan: Community Ecology Package*. Available online at: https://cran.r-project.org/package=vegan (accessed November 28, 2020).

Outeiro, L., Rodrigues, J. G., Damásio, L. M. A., and Lopes, P. F. M. (2019). Is it just about the money? A spatial-economic approach to assess ecosystem service tradeoffs in a marine protected area in Brazil. *Ecosyst. Serv.* 38:100959. doi: 10.1016/j.ecoser.2019.100959

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. Vienna: R Core Team.

Reis, E. G., and D'Incao, F. (2000). The present status of artisanal fisheries of extreme southern Brazil: An effort towards community-based management. *Ocean Coast. Manag.* 43, 585–595. doi: 10.1016/S0964-5691(00)00048-X

Riul, P., Targino, C. H., Júnior, L. A. C., Creed, J. C., Horta, P. A., and Costa, G. C. (2013). Invasive potential of the coral *Tubastraea coccinea* in the southwest Atlantic. *Mar. Ecol. Prog. Ser.* 480, 73–81. doi: 10.3354/meps10200

Roos, N., Taylor, B., Carvalho, A., and Longo, G. (2020). Demography of the largest and most endangered Brazilian parrotfish, *Scarus trispinosus*, reveals overfishing. *Endanger. Species Res.* 41, 319–327. doi: 10.3354/esr01024

Silva, F. C., Da Ferreira Júnior, A. L., Artoni, R. F., and Bessa, E. (2020). Impact of feeding fish as a tourist attraction on a coral reef invertivorous fish's diet and growth. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 30, 2327–2335. doi: 10.1002/aqc.3398

Slowikowski, K. (2019). *ggrepel: Automatically Position Non-overlapping Text Labels With "ggplot2." R Packag. Version 0.8.1*. Available online at: https://cran.r-project.org/package=ggrepel (accessed April 13, 2021).

Spence, A., Poortinga, W., Butler, C., and Pidgeon, N. F. (2011). Perceptions of climate change and willingness to save energy related to flood experience. *Nat. Clim. Chang.* 1, 46–49. doi: 10.1038/nclimate1059

Suárez de Vivero, J. L., Rodríguez Mateos, J. C., and Florido del Corral, D. (2008). The paradox of public participation in fisheries governance. The rising number of actors and the devolution process. *Mar. Policy* 32, 319–325. doi: 10.1016/j.marpol.2007.06.005

Teixeira, C. D., Chiroque-Solano, P. M., Ribeiro, F. V., Carlos-Júnior, L. A., Neves, L. M., Salomon, P. S., et al. (2021). Decadal (2006-2018) dynamics of Southwestern Atlantic's largest turbid zone reefs. *PLoS One* 16:247111. doi: 10.1371/journal.pone.0247111

Tuya, F., Haroun, R. J., Boyra, A., and Sanchez-Jerez, P. (2005). Sea urchin *Diadema antillarum*: Different functions in the structure and dynamics of reefs on both sides of the Atlantic. *Mar. Ecol. Prog. Ser.* 302, 307–310. doi: 10.3354/meps302307

Uyarra, M. C., Watkinson, A. R., and Côté, I. M. (2009). Managing dive tourism for the sustainable use of coral reefs: Validating diver perceptions of attractive site features. *Environ. Manage.* 43, 1–16. doi: 10.1007/s00267-008-9198-z

Vaclavikova, M., Vaclavik, T., and Kostkan, V. (2011). Otters vs. fishermen: Stakeholders' perceptions of otter predation and damage compensation in the Czech Republic. *J. Nat. Conserv.* 19, 95–102. doi: 10.1016/j.jnc.2010.07.001

Vieira, E. A., Souza, L. R., and Longo, G. O. (2020). Diving into science and conservation: recreational divers can monitor reef assemblages. *Perspect. Ecol. Conserv.* 18, 51–59. doi: 10.1016/j.pecon.2019.12.001

Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer.

Yandle, T. (2003). The challenge of building successful stakeholder organizations: New Zealand's experience in developing a fisheries co-management regime. *Mar. Policy* 27, 179–192. doi: 10.1016/S0308-597X(02)00071-4

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Farmers' Perceptions of the Effects of Extreme Environmental Changes on Their Health: A Study in the Semiarid Region of Northeastern Brazil

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People living in areas vulnerable to diseases caused by extreme climate change events, such as semiarid regions, tend to recognize them quickly and, consequently, develop strategies to cope with their effects. Our study investigated the perception of diseases by farmers living in the semiarid region of Northeastern Brazil and the adaptive strategies locally developed and used. To this end, the effect of the incidence and severity of locally perceived diseases on the frequency of adaptive responses adopted by the farmers was tested. The research was conducted in rural communities in the Pernambuco State, Northeastern Region of Brazil. Semi-structured interviews with 143 farmers were conducted to collect information about major drought and rainfall events, the perceived diseases related to these events, and the adaptive strategies developed to mitigate them. The incidence and severity of diseases perceived by farmers were calculated using the Participatory Risk Mapping method and the frequency of adaptive strategies. Our findings demonstrated that few climate change-related diseases were frequently mentioned by farmers, indicating low incidence rates. Among them, direct transmission diseases were the most frequently mentioned. Adaptive strategies to deal with the mentioned diseases related to prophylactic behavior were less mentioned, except if already utilized. Our model demonstrated that incidence was the only explanatory variable with a significant impact on the adaptive strategies used to deal with the effects of these risks on health. Our findings suggest that the estimated incidence of diseases should be considered in the development of predictive climate change models for government policy measures for the public health security of populations in areas of greater socio-environmental vulnerability.

Keywords: climate change, semi-arid, smallholder—farming sector, disease perception, adaptive strategies

INTRODUCTION

There is extensive evidence that the global climate is changing rapidly. A recent survey by the World Meteorological Organization (WMO, 2020) demonstrated that 2015 to 2019 were the five warmest years on record compared to any other equivalent period in history. Such changes drive the incidence of heatwaves, floods, and storms and affect the dynamics of air, water, and food supply, which are key drivers of human health (WHO, 2009).

Human health problems caused by extreme climate change events (e.g., prolonged droughts and rainfall) are diverse, ranging from heatwave related diseases and mortalities to infections transmitted by different vectors, causing respiratory problems and mental illness (McMichael et al., 2006; Younger et al., 2008; McMichael, 2013). According to data from the World Health Organization (WHO), an increase of up to 250,000 deaths is expected between 2030 and 2050 due to climate change impacts on human health (Watts et al., 2015). Climate change impacts pose significant global threats to human health, and the projections are staggering (e.g., McMichael et al., 2006; Costello et al., 2009; Hayes et al., 2018; Watts et al., 2018; Austin et al., 2020).

Diseases arising from climate change risks are diverse and transmitted directly and indirectly (Smith et al., 2014; Watts et al., 2018). Direct transmission occurs primarily with changes in the frequency of non-seasonal weather conditions, such as droughts and intense, prolonged rainfall. Indirect transmission occurs through natural systems, such as disease vectors and infections transmitted through water and air pollution, or by human systems, such as occupational factors, malnutrition, and mental stress (Smith et al., 2014). Some authors also prefer to categorize the impacts of climate change on human health into primary, secondary, and tertiary risks (Butler and Harley, 2010; McMichael, 2013). The primary, secondary, and tertiary risks correspond to direct transmission; indirect transmission mediated by biophysical and ecological processes and systems (such as variation in water flow) and by vectors of infectious diseases; and indirect transmission that arises, for example, as consequences of tensions and conflicts arising from factors related to climate change, such as migration and shortage of basic resources (these risks include mental health problems; McMichael, 2013) respectively. This study uses both classification criteria, considering secondary and tertiary risks as subcategories of indirect risks.

The health of vulnerable human populations tends to be more impacted by extreme climate change events, largely due to reduced access to health services and the barriers in seeking these services (Handley et al., 2014; Hayes et al., 2018). This includes rural populations living in semiarid regions, which, in addition to low rainfall totals and annual and inter-annual irregularities in rainfall patterns, have poor infrastructure for coping with the adversities of climate change (Banerjee, 2014; Dhanya and Ramachandran, 2016). In the semiarid region of Northeastern Brazil, for example, the dependence on forest resources and the low income of rural populations have already been documented, factors that make rural populations more vulnerable to climate change (de Albuquerque et al., 2012; dos Santos et al., 2013; Silva et al., 2017; Gonçalves et al., 2021).

Vulnerability, according to the Intergovernmental Panel on Climate Change (IPCC), corresponds to the predisposition of a given population and/or locality to be impacted by changes in climate and occurs as a function of three main factors: sensitivity, adaptive capacity, and exposure (IPCC, 2007). Sensitivity corresponds to the way a system can be affected (negatively or not); adaptive capacity corresponds to the ability to cope (minimizing or avoiding) with damage; and exposure corresponds to the presence of people, systems, and their relationships, which can be potentially impacted by the effects of climate change (IPCC, 2007). Thus, it is acknowledged that semiarid regions are more vulnerable because local human populations depend more on the natural resources provided locally for their subsistence and because they are more sensitive and exposed to the adverse effects of climate change. Based on this premise, these populations tend to recognize incident diseases associated with climate change more quickly (McMichael et al., 2006; Lafferty, 2009; Bhatta et al., 2020). Thus, in addition to the search for understanding how climate change interferes with people's way of life, it is essential to evaluate the perception of human populations in this context because people tend to develop knowledge and practices related to health to prevent the spread of diseases, modifying local medical systems (Ferreira et al., 2015). Therefore, local medical systems may offer clues about recent changes in disease incidences on a time scale (Estomba et al., 2006; Ferreira et al., 2015; Santoro et al., 2015; Santoro and Albuquerque, 2020).

Considering diseases as risks to human health, which can be caused or enhanced by extreme climate events, this study defines risks as potentially unfavorable or harmful circumstances arising from the effects generated by environmental changes in people's daily lives (Smith et al., 2000). According to the United Nations Office for Disaster Risk Reduction (UNDRR), risk can also correspond to the probability of the occurrence of an adverse effect arising from an environmental phenomenon (UNDRR, 2009). Thus, the risk perception can be used to anticipate change and enable the development of adaptive strategies to deal with potential negative effects. These adaptive strategies can be characterized as reactions or adjustments to situations perceived as risky at the collective or individual level (Smith et al., 2000; Smit and Wandel, 2006; Boillat and Berkes, 2013; Oliveira et al., 2017). This study considered both long-term (prophylactic) and short-term (therapeutic/treatment) adaptive strategies.

In relation to risk perceptions arising from climate change, whether on a local or regional scale, there is evidence that disease incidence may be related to the adoption of adaptive mitigation strategies (e.g., Lafferty, 2009; Oloukoi et al., 2014; de Perez et al., 2015; Bhatta et al., 2020). Although the severity assigned to diseases has received little attention in the literature, it is believed that adaptive strategies may be adopted based on the classification of diseases according to their severity, as has been recorded in studies on environmental risk perception (e.g., Smith et al., 2000; Quinn et al., 2003; Baird et al., 2009). Identifying popular strategies to adjust to climate change and avoid health risks is a gap to be filled in scientific knowledge, potentially contributing to collective public health management.

Thus, understanding how residents of semiarid regions—areas having a high probability of extreme climate change events and their direct implications, such as water scarcity (Martins et al., 2015)—perceive health risks and manage them amidst increasingly accelerated climate change is essential for the development and implementation of more effective adaptive responses (Austin et al., 2020). Thus, our study aimed to investigate the perception of farmers living in the northeastern

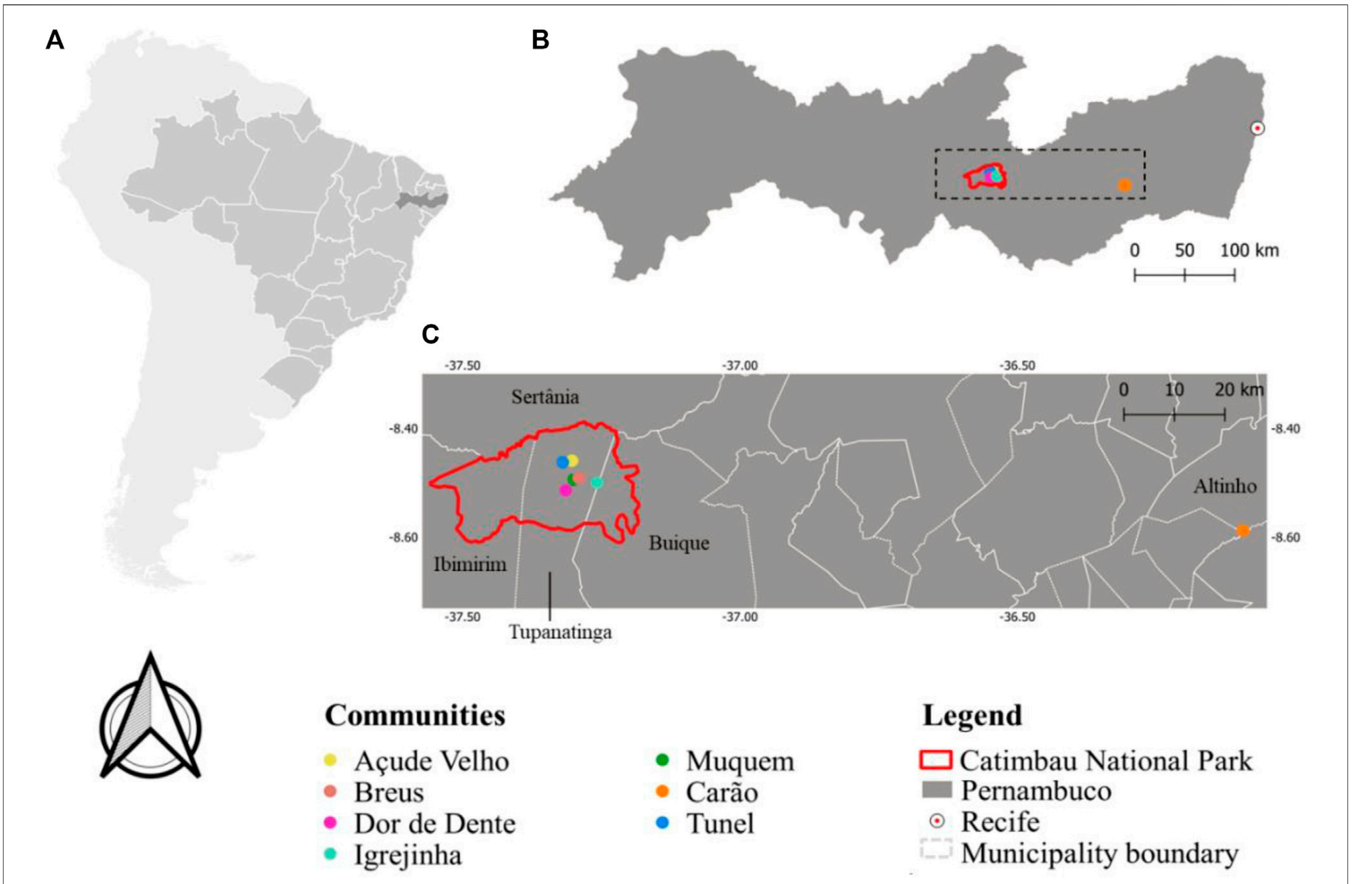

FIGURE 1 | Map of the Catimbau National Park location, highlighting the rural communities of the research (Açude Velho, Breus, Dor de Dente, Igrejinha, Muquem, and Tunel) and Carão, Altinho Municipality (Pernambuco State, semiarid region of Northeastern Brazil). All elements highlighted on the map (study area locations) have been revised and are correctly flagged in the legend.

semiarid region about local diseases, highlighting the adaptive strategies developed locally and used to mitigate health problems. For this, we tested the hypothesis that the incidence and severity of diseases related to climate change drive the adopted adaptive responses. It is expected that there is a higher frequency of adaptive strategies developed for more incidents and more severe diseases.

MATERIALS AND METHODS

Study Area

The study was conducted in two semiarid areas in the Pernambuco State, Northeastern Brazil (**Figure 1**). The first select area was the Catimbau National Park (Catimbau NAPAR), a Conservation Unit that covers 62,294.14 hectares, located between the "agreste" and "sertão" of the Pernambuco State in the domain of three municipalities in the São Francisco River Basin: Buíque, Tupanatinga, and Ibimirim (ICMBio, 2002) (**Figure 2**). In the Catimbau NAPAR, six rural communities were selected: Muquem (8.49414° S; 37.2999° W), Breus (8.49076° S; 37.29059° W), Açude Velho (8.4592° S; 37.30289° W), Tunel (8.46208° S; 37.31967° W), Dor de Dente (8.51355° S; 37.31413° W) and Igrejinha (8.49966° S; 37.25743° W). The total number of local adult residents in each of these communities, according to data obtained through the Family Health Program (FHP) of the Buíque Municipality, were: Muquem (n = 38), Breus (n = 32), Açude Velho (n = 17), Tunel (n = 6), Dor de Dente (n = 13), and Igrejinha (n = 112), totaling 218 people.

The second selected area was the Carão (08° 35′13.5″ S and 36° 05′ 34.6″ W), a rural community located in the Altinho Municipality, Pernambuco State, in the center of the "agreste," 168 km from the state capital. According to information obtained through the Carão health center, the local population currently consists of 140 people (27 were under 18 years old) in 55 family units (households; **Figure 3**).

The semiarid tropical climate (BSh), according to the Köppen-Geiger Scale, typical of the semiarid region of Northeastern Brazil (Alvares et al., 2013), is predominant in both the Catimbau NAPAR (ME, 2015) and Carão (Cruz et al., 2014). In the Catimbau NAPAR, the mean annual temperature is 23°C, with great interannual irregularity in rainfall, varying from 650 to 1,100 mm annually (ME, 2015). All rural communities selected

FIGURE 2 | Landscape of Igrejinha, rural community located in the Catimbau National Park (Pernambuco State, semiarid region of Northeastern Brazil). Photo: Henrique F. Magalhães.

FIGURE 3 | Landscape of the Carão rural community, located in the Altinho Municipality (Pernambuco State, semiarid region of Northeastern Brazil). Photo: Regina C. S. Oliveira.

for the study in the Catimbau NAPAR are located in the driest strip of the park (PELD Catimbau, 2016). The annual temperature in Carão is around 25°C, with an average rainfall of around 622 mm between March and July (BDE, 2017).

Droughts are recurrent climatic events in Northeastern Brazil and are generally associated with the El Niño phenomenon, which results in lower rainfall than the historical average in this semiarid region, which is about 800 mm per year (Magalhães, 2016; Marengo et al., 2018). Additionally, the precipitation is concentrated in a few months and evapotranspiration levels exceed 2,000 mm per year. As the semiarid region is a climatic Frontier area, any decrease in relation to the average may have a large impact (Magalhães, 2016). Based on historical records, as illustrated in **Table 1**, in the

TABLE 1 | History of drought periods in the Northeastern Region of Brazil.

16th century	17th century	18th century	19th century	20th century	21st century
1,583	1,603	1707	1804	1900	2001–2002
1,587	1,608	1710–1711	1808–1809	1902–1903	2005–2007
-	1,614	1721–1727	1810	1907	2010
-	1,624	1730	1814	1915	2012–2018
-	1,645	1736–1737	1816–1817	1919	-
-	1,652	1744–1747	1824–1825	1932–1933	-
-	1,692	1751	1827–1829	1936	-
-	-	1754	1830–1833	1941–1944	-
-	-	1760	1844–1845	1951–1953	-
-	-	1766	1870	1958	-
-	-	1771–1772	1877–1879	1966	-
-	-	1777–1778	1888–1889	1970	-
-	-	1783–1784	1891	1976	-
-	-	1791–1793	1897–1899	1979–1981	-
-	-	-	-	1982–1983	-
-	-	-	-	1986–1987	-
-	-	-	-	1990–1993	-
-	-	-	-	1997–1998	-

Source: *Marengo et al. (2020).*

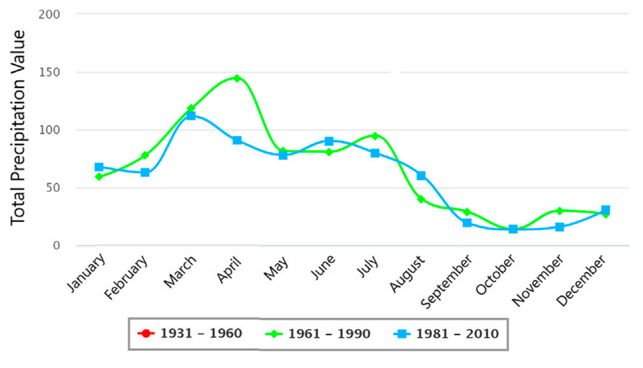

FIGURE 4 | Comparative graph of historical variations in accumulated precipitation (mm) in the Pernambuco State in three annual intervals of 30 years. Source: Adapted from INMET (2021).

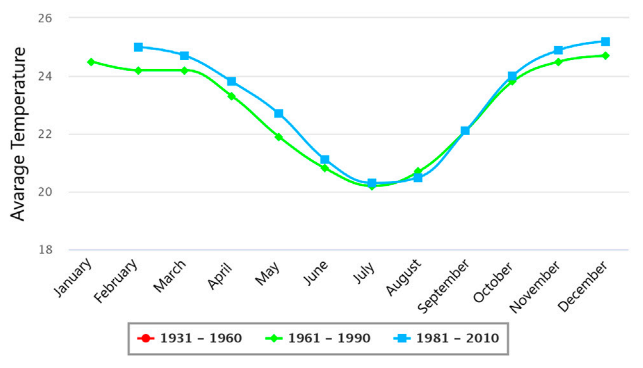

FIGURE 5 | Comparative graph of historical variations in average temperature (°C) in the Pernambuco State in three annual intervals of 30 years. Source: Adapted from INMET (2021).

last 50 years, there were at least nine periods of prolonged drought in the semiarid region of the Brazilian Northeast, which brought intensive losses to both the ecosystem and people's livelihoods: 1979–1983, 1986–1987, 1992–1993, 1997–1999, 2002–2003, 2005, 2007–2008, 2010, and 2012–2017 (Marengo et al., 2017; Lima and Magalhães, 2018; Marengo et al., 2018; Cunha et al., 2019). Since 2010, the region has experienced the longest and most severe drought periods in its history, especially since 2015, due to the El Niño phenomenon (Marengo et al., 2018). According to data from the Instituto Nacional de Meteorologia (INMET, 2021), the Pernambuco State had lower precipitation and higher temperature averages in some months of an otherwise average year (**Figures 4**, **5**).

In the Catimbau NAPAR and Carão, this research was carried out with small farmers whose main source of local income is derived from subsistence agriculture and livestock, with emphasis on the planting of corn and beans and the operation of small goat, cattle, pig, and poultry farms. However, both areas have suffered agricultural losses and water resource shortages, characterizing them as risk areas for extreme drought events (Martins et al., 2015; Marengo et al., 2018), which may imply the proliferation of diseases related to extreme events of climate change (WHO, 2009). In the Catimbau NAPAR, this situation is aggravated by socio-environmental conflicts that have distinguished the area since it was founded (in 2002), involving the park management body—the Chico Mendes Institute for Biodiversity Conservation (ICMBio) —and residents, who had never been compensated since the park's foundation and continue to live within the area, which is not legally permitted, according to the National System of Conservation Units (Brasil, 2000). Such a scenario made it very difficult for us to access some people living in the region because our presence was interpreted as an intervention by the environmental agency responsible for the park's administration. To alleviate this situation, we adopted a cautious approach to residents, based on informal conversations and by explaining our project. For this reason,

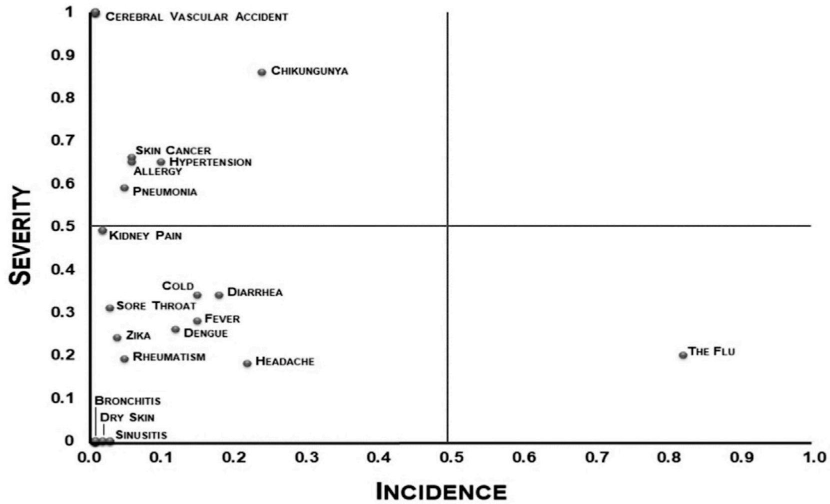

FIGURE 6 | Map of disease incidence and severity perceived by farmers in the Catimbau NAPAR.

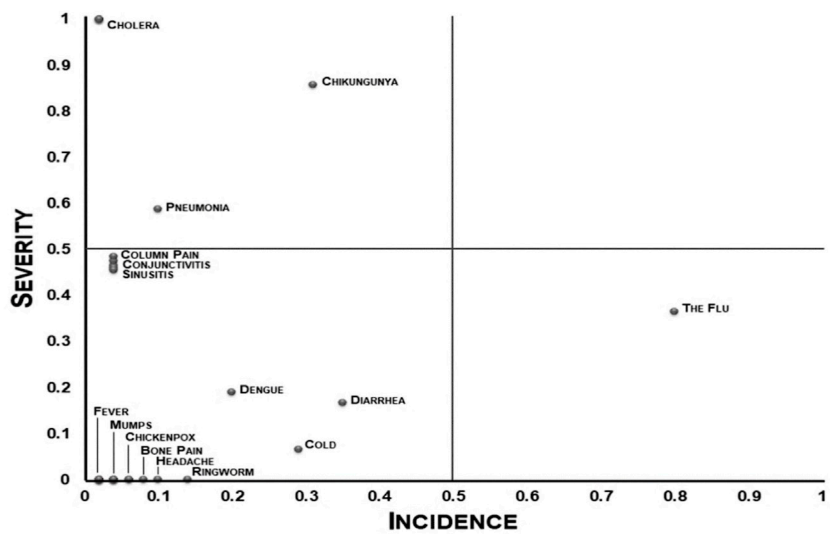

FIGURE 7 | Map of disease incidence and severity perceived by farmers in Carão.

we also started our data collection in Carão, as we wanted to obtain a larger sample and, for the reasons mentioned above, Catimbau NAPAR was no longer a viable alternative. We chose Carão because our team has been conducting research in the region for 13 years and, therefore, has extensive knowledge about the site and a good relationship with residents.

Legal Procedures and Informant Selection

To meet the legal aspects of research involving humans, this study was submitted and approved by the Research Ethics Committee of the University of Pernambuco, according to the Certificate of Submission for Ethics Appreciation (CSEA) number 89890617.1.0000.5207. All residents who agreed to participate in the research were asked to sign a free and informed consent form, as governed by the current legislation of the National Health Council (Resolution No. 466/2012).

The initial contact with both rural communities was made through a previous survey on the number of households in each of the seven communities in the study (in the case of Carão, this step was not necessary due to long-term studies conducted by our team in the region for at least 10 years). Data regarding the number of people living in each rural community were obtained through the Family Health Program (FHP) of Catimbau Village, Buíque Municipality (PE), and the health center of Carão, Altinho Municipality (PE). Adults and older people (above 18 years old) living in rural communities were chosen.

Data Collection and Processing

Data collection for the study occurred between July 2018 and September 2019. Of the 358 residents in the two study areas (218 in the Catimbau NAPAR and 140 in Carão, as mentioned above), it is important to note that some of these residents are above 60 years old and have health problems. Additionally, some residents were not available at the time of the survey and refused to participate in the research (especially in the Catimbau NAPAR, a scenario of numerous socio-environmental conflicts, as previously mentioned). Thus, our sample was ultimately composed of 143 people who agreed to participate in the study, comprising 94 people living in the Catimbau NAPAR in the six selected rural communities: Muquem (n = 30), Breus (n = 20), Açude Velho (n = 9), Tunel (n = 6), Dor de Dente (n = 4), and Igrejinha (n = 25); and 49 people living in Carão.

Before our fieldwork, the study's aims and methods were explained to informants to clarify doubts. After this step, people would be free to voluntarily accept (or refuse) to participate in the research. We also conducted a pilot study to ensure that the interviewers understood the questions.

The selection of the sample of the population that accepted to participate in the research was made from a census (Espinosa et al., 2014), as well as the collection of socioeconomic data from the selected informants (see **Supplementary Table S1**). Thus, residents who had relevant information for our study were interviewed, including people who lived in the same household. The information collected was carefully evaluated by removing inconsistencies or biases that compromised the validity of the information. Based on our observations and information from the scientific literature, people from the same family or who live in the same household do not necessarily have the same experiences or develop the same adaptive climate change strategies. This depends on other correlated factors, such as agriculture and risk experience (e.g., Weber, 2010; Bryan et al., 2013; Rodriguez et al., 2017).

To analyze perceptions on climate change-related diseases, semi-structured interviews were conducted with the participants due to the flexibility of the previously elaborated questions (Albuquerque et al., 2014; Magalhães et al., 2019). The field interviews were organized in two stages, which are described below. In the first stage, each participant was identified and asked about the years in which major extreme weather events (non-seasonal) occurred, such as droughts and rainfall. Without this design, the participants could have cited diseases related to environmental change in general and not those specifically related to climate change. Extreme droughts were the most characteristic climate change events faced in semiarid regions, with the period between 2012 and 2015 being pointed out as the most critical in the last 50 years (Martins et al., 2015). By comparing historical data on drought events in Northeastern Brazil (**Table 1**), the historical data cited by our informants were validated because they corresponded with the scientific data (such as the year 1993 and the period 2012–2014, the most mentioned by farmers in both study areas). Thereafter, using the free list technique (da Silva et al., 2014), the participants were asked to name or list diseases perceived as a result of the extreme drought and rainfall events in the region. We emphasize here that because the focus of the proposal of our experimental design was diseases "perceived by people" and not "scientifically designated" diseases, we do not use previously cataloged information regarding the incident diseases in the regions.

In the second stage, based on the list of mentioned diseases, each participant was asked to classify and organize them according to their severity i.e., the degree of impact on their lives (Smith et al., 2000). The severity of the diseases was represented by numbers following a decreasing ordinal classification (for example, number 1 represented the disease considered the most severe; number 2, the disease considered the second most severe; and so on). Additionally, based on each disease mentioned, the participants were asked about adaptive strategies used (if any) to mitigate them. In this study, the adaptive strategies, to paraphrase Smit and Wandel (2006), were considered responses developed by the participants to mitigate the potentially harmful effects arising from the diseases they perceived.

Although age was one of the main differences between our two areas of study, as Carão has a higher proportion of older people (80.7%), we chose not to categorize the sample sizes according to the age for each place of study due to the diverse evidence from scientific literature demonstrating that age is not a good predictor of the number of extreme weather events or perceived risks related to these weather phenomena. In this sense, a person's experience in agriculture explains much more than age (Slegers, 2008; Gbetibouo, 2009; Fosu-Mensah et al., 2012). For example, a 60-year-old person may have lived for 40 years outside the community and participated in activities unrelated to agriculture; and a 35-year-old person could have worked in agriculture for 30 years. In this case, the younger person has more experience in agriculture than the older person and, therefore, would tend to perceive a greater number of extreme weather events and risks related to these phenomena. We believe that studies that consider categorizing sampling units according to the length of experience in agriculture (which was not our study proposal), can provide interesting insights.

Data Analysis

The incidence index (Ii) and the severity index (Sj) attributed to each perceived illness were initially calculated to test our hypothesis using the method suggested by Baird et al. (2009), adapted from Smith et al. (2000) (see **Supplementary Table S2**), and the objective was to understand and describe the local risk perception (in this case, diseases and risks to human health). Originally, this method—Participatory Risk Mapping (PRM)—was developed to access and quantitatively evaluate perceived environmental risks (see Smith et al., 2000; Baird et al., 2009). Compared to other methods used for this same purpose, the PRM stands out for being an extremely accurate and easily applicable method, which enables the researcher to assess the potential that a particular risk has of affecting people's lives (da Silva et al., 2014;

Magalhães et al., 2019). To the best of our knowledge, this is the first time the PRM has been applied to the perception of specific risks to human health (diseases).

The incidence index (Ii) corresponds to the ratio between the number of people who mentioned a certain disease (nr) and the total number of people in the sample (nj), represented by the equation:

$$Ii = \frac{nr}{nj}$$

The values assumed by Ii can vary between 0 and 1, which corresponds to the lowest and 1 corresponds to the highest incidence respectively.

Following the method proposed by Baird et al. (2009), the disease severity indexes (Sj) were calculated in two steps. Initially, the individual value of the risk severity index (Rij) was obtained by the equation:

$$Rij = 1 - rij - \frac{1}{ni}$$

where ni represents the total number of risks mentioned by each informant (i), and rij represents the classification of each risk individually. Next, all the results found for Rij were summed and divided by the number of times the risk was mentioned as the most severe (Nj). Next, the severity index (Sj) was obtained, with values ranging between 0 (risks that are not considered severe) and 1 (risks considered extremely severe), using the following equation:

$$Sj = \sum_{i-1} Nj = 1 - \frac{Rij}{Nj}$$

Some of the obtained Ij and Sj results were represented using risk maps, graphical representations that allow the analysis of the space and distribution of incidence and severity of the mentioned diseases. As observed in the risk maps (**Figures 6**, **7**), the upper part of the graph illustrates the first quadrant (where it is possible to observe the diseases classified as low incidence and very severe) and the second quadrant (where the diseases locally considered as high incidence and very severe appear); and the lower part displays the third quadrant (where the diseases perceived as low incidence with low severity are illustrated) and the fourth quadrant (where flu, a disease classified as not very severe, although with high local incidence is illustrated). Here, influenza is highlighted because it was the only disease mentioned in the fourth quadrant whose incidence was high. For this purpose, the PRM proposed by Baird et al. (2009) is the most recommended because the type of severity index (Sj) classification used facilitates both the elaboration and interpretation of risk maps (Baird et al., 2009) due to the similarity of the type of values presented by the incidence indices (Ii) and severity (Sj). For that reason, we opted for this model.

To calculate the incidence of adaptive strategies used to mitigate the diseases perceived by farmers, a similar logic to that used to calculate the incidence of risk (Ij), mentioned earlier, was adopted. The difference was to divide the number of adaptive strategies mentioned for each disease by the participants' total number of adaptive strategies (see **Supplementary Table S2**). The indexes obtained in relation to the incidence of adaptive strategies (whose values could also vary from 0 to 1) were used in our analysis as dependent variables. The values of Ij and Sj were used as independent variables.

Subsequently, the data regarding perceived diseases were categorized (into direct and indirect diseases), and the mentioned adaptive strategies were classified (into therapeutic and prophylactic behavioral strategies) by the resident farmers of the Catimbau NAPAR (see **Tables 1**, **3**) and Carão (see **Tables 2**, **4**) regions to facilitate the explanation and discussion of our results. Finally, our hypothesis was tested for both areas using generalized linear models (GLM) with Gaussian distribution, in which the data were processed by calculating the logarithm (base 10) of n + 1 value to reduce the possible effects of large variation amplitudes. The statistical test was performed using the software R, version 3.6.3 (R Development Core Team 2019).

RESULTS

Perceived Diseases Related to Climate Change and Adopted Adaptive Strategies

A total of 42 diseases related to drought and prolonged rainfall events were mentioned by farmers living in the Catimbau NAPAR. The farmers in Carão mentioned 31 diseases related to extreme climate change events. These diseases were listed in two categories based on their sources of transmission: direct (or primary) and indirect (subcategorized into secondary and tertiary), when transmission occurs through climatic phenomena, such as rain and heatwaves, and mediation of natural processes or systems (such as contaminated water or vectors) or human systems (fatigue caused by the need to walk long distances in the intense heat to work) respectively.

In both Catimbau NAPAR and Carão, most of the diseases mentioned were from direct transmission (n = 34, 26), followed by secondary indirect transmission (n = 6,4) and tertiary indirect transmission (n = 2, 1). Influenza stands out in the first category as the most frequently mentioned disease among residents of the rural communities of the Catimbau NAPAR (NC (number of citations) = 77) and Carão (NC = 39). The most mentioned diseases in the second category in both areas were chikungunya (NC = 23,15) and dengue (NC = 11, 10) (**Table 3**).

It is evident that all diseases perceived by farmers living in the two study areas are considered to have a low local incidence (except for influenza, whose incidence is very high, although with low severity; **Figures 6**, **7**). Among these, diseases of low severity, such as dengue and cold predominated. Diseases perceived as having high severity were also mentioned, such as pneumonia and chikungunya, a disease of indirect transmission perceived as more severe.

Adaptive strategies were listed in two categories referring to the behavior adopted for developing the strategy: therapeutic behavior, subcategorized according to the origin of the behavior; and prophylactic behavior (**Tables 4**, **5**). In the Catimbau

TABLE 2 | Climate change-related diseases perceived by small-scale farmers living in the Catimbau NAPAR, Pernambuco State, Northeastern Brazil.

Category	Subcategory	Disease (n = 42)	Citations (NC)
Direct (Primary) (n = 34)	-	Flu	77
		Headache	21
		Diarrhea	17
		Fever	14
		Cold	14
		Hypertension	9
		Allergy	6
		Skin cancer	6
		Pneumonia	5
		Rheumatism	5
		Asthma	3
		Sore throat	3
		Sinusitis	3
		Leg pain	2
		Kidney pain	2
		Breathlessness	2
		Infarction	2
		Dry skin	2
		Cerebral Vascular Accident	1
		Bronchitis	1
		Chickenpox	1
		Dehydration	1
		Earache	1
		Back pain	1
		Body pain	1
		Eye pain	1
		Bone pain	1
		Rheumatic Fever	1
		Skin wounds	1
		Prostate inflammation	1
		Stuffy nose	1
		Rhinitis	1
		Measles	1
		Cough	1
Indirect	Secondary (n = 6)	Chikungunya	23
		Dengue	11
		Zika	4
		Diabetes	1
		Intestinal infection	1
		Urinary Infection	1
	Tertiary (n = 2)	Fatigue	3
		Insomnia	1

NAPAR, 19 adaptive strategies were mentioned, including therapeutic (n = 10) and prophylactic behavior strategies (n = 9). In Carão, 14 adaptive strategies were mentioned by local farmers, including therapeutic (n = 8) and prophylactic behavioral strategies (n = 6).

Among the therapeutic strategies, the subcategory that obtained the highest number of mentions, both in the Catimbau NAPAR (n = 4) and Carão (n = 3), is related to the use of pharmaceutical drugs: NC = 112 in the Catimbau NAPAR used for the treatment of 30 locally perceived diseases; and NC = 80 in Carão, used for the treatment of 21 locally perceived diseases. Among the adaptive therapeutic strategies related to the local medical system, the number of citations referring to treatment with local herbal medicines is noteworthy: NC = 89, 63 in the Catimbau NAPAR and Carão, used for the treatment of 19 and 17 locally perceived diseases respectively. It is also worth noting that adaptive strategies were also cited related to individual care, such as resting (NC = 5, two in the Catimbau NAPAR, and Carão); and taboo/beliefs in Carão such as using "magic" medicine (NC = 2).

Among the adaptive strategies of prophylactic behavior (n = 9 in the Catimbau NAPAR and n = 6 in Carão), the most frequently mentioned was hydration (NC = 4 in the Catimbau NAPAR and NC = 9 in Carão). This category demonstrates the significance of strategies related to escape/evasion behaviors to avoid sources or vectors that transmit diseases.

Relationship Between the Incidence and Severity of Perceived Illnesses and the Frequency of Used Adaptive Strategies

The incidence and severity attributed to perceived diseases related to climate change explained the frequency of adaptive strategies used among farmers in both the Catimbau NAPAR ($z = 5.221$; $p =$

TABLE 3 | Climate change-related diseases perceived by smallholder farmers living in Carão, Pernambuco State, Northeastern Brazil.

Category	Subcategory	Disease (n = 31)	Citations (NC)
Direct (Primary) (n = 26)	-	Flu	39
		Diarrhea	17
		Cold	14
		Mycosis	7
		Headache	5
		Pneumonia	5
		Bone pain	4
		Chickenpox	3
		Virus Diseases	3
		Mumps	2
		Conjunctivitis	2
		Dehydration	2
		Back pain	2
		Breathlessness	2
		Rhinitis	2
		Measles	2
		Sinusitis	2
		Cough	2
		Asthma	1
		Chafing	1
		Bronchitis	1
		Migraine	1
		Leg pain	1
		Kidney pain	1
		Stomachache	1
		Fever	1
Indirect	Secondary (n = 4)	Chikungunya	15
		Dengue	10
		Worms	2
		Cholera	1
	Tertiary (n = 1)	Anxiety	1

6.22e - 06) and Carão (z = 5.617; p = 5.15e—06; **Tables 6**, **7**). Among the independent variables tested in our models, the incidence of perceived diseases had great predictive power in both the Catimbau NAPAR (z = 5.151; p = 7.77e - 06) and Carão (z = 5.288; p = 1.26e - 05). Severity did not demonstrate predictive power in the models, suggesting that severity may not influence people's perception of diseases related to extreme rainfall and drought events that affect them the most, rather than potentiating them, as expected.

DISCUSSION

The results obtained demonstrate that diseases with the highest incidents tend to be prioritized in relation to the adoption of adaptive strategies to deal with their effects, both in the Catimbau NAPAR and Carão. This information is extremely relevant for understanding the importance of local therapeutic and prophylactic behaviors. Few diseases were mentioned very often by farmers, and most diseases had a low incidence. A possible explanation is that the diseases experienced by the population and the resources used for their treatment vary within time scales, which points to the existence of dynamic medical systems that can influence the perception of local populations (Santoro and Albuquerque, 2020). A diachronic study (with data collected over an 8-year time interval) also conducted in Carão, Santoro and Albuquerque (2020) observed that although incidence has a positive effect on the number of adaptive strategies, both allopathic and traditional medicines, it does not explain the variation in knowledge associated with these treatments, nor their efficacy. Thus, we believe that diachronic variations should not be disregarded in the analysis of disease perception or the related factors because disease incidence can drive the evolution of medical systems at different time scales (Santoro and Albuquerque, 2020).

Another possible explanation is that the diseases identified in this study with low incidence (almost all of them) may correspond to diseases perceived as common locally. People's perception of these diseases is a complex phenomenon related to cognitive factors, such as judgment of environmental events and their local consequences on their way of life (Nyantakyi-Frimpong and Bezner-Kerr, 2015). Although common illnesses are considered to have less severity, data from the United Nations Children's Emergency Fund (UNICEF) and the World Health Organization (WHO) demonstrate that common conditions, such as diarrhea, are among the leading contributors to child mortality worldwide (WHO and UNICEF, 2004; Young et al., 2012). Therefore, this category of perceived diseases should not be neglected in the development of prophylactic and emergency adaptive measures by civil society or public authorities.

TABLE 4 | Adaptive strategies used to mitigate diseases perceived by farmers living in the Catimbau NAPAR, Pernambuco State, Northeastern Brazil.

Category	Subcategory	Adaptive strategy (n = 19)	Citations (NC)	Mitigated diseases (NC)
Therapeutic behavior (n = 10)	Western medicine	Treat with pharmaceutical drugs	112	30
		Seek medical assistance	18	7
		Get an injection	2	2
		Get the vaccination	3	3
	Local medical system	Treat with local herbal medicines	89	19
		Treating with home remedies	27	12
	Individual care	Rest	5	5
		Wash with water	1	1
		Dieting	1	1
	Welfarism	Dependence on external assistance	1	1
Prophylactic behavior (n = 9)	-	Hydrate	4	4
		Avoid standing water	4	3
		Avoid exposure to heat	2	2
		Avoid exposure to cold	2	2
		Avoid indigestible foods	2	1
		Avoid contact with vectors	1	1
		Avoid stress	1	1
		Avoid exposure to dust	1	1
		Measure pressure regularly	1	1

TABLE 5 | Adaptive strategies used to mitigate diseases perceived by farmers living in Carão, Pernambuco State, Northeastern Brazil.

Category	Subcategory	Adaptive strategy (n = 14)	Citations (NC)	Mitigated diseases (NC)
Therapeutic behavior (n = 8)	Western medicine	Treat with pharmaceutical drugs	80	21
		Seek medical assistance	10	6
		Get injection	4	4
	Local medical system	Treat with local herbal medicines	63	17
		Treating with home remedies	24	8
	Individual care	Rest	2	1
		Wash with water	1	1
	Taboo/belief	Appealing to "magic medicine"	2	2
Prophylactic behavior (n = 6)	-	Hydrate	9	8
		Avoid eating iced food	5	4
		Avoid accumulation of water (e.g., in vases or flowerbeds)	1	1
		Avoid exposure to heat	1	1
		Avoid drinking cold water	2	1
		Eating well	1	1

TABLE 6 | Generalized Linear Model used to test the effect of incidence and severity of diseases perceived by farmers in the Catimbau NAPAR on the frequency of used adaptive strategies. The *p*-values for the significant predictors are highlighted in bold. Significance code *p*-value: *** [0, 0.001]; ** (0.001, 0.01]; * (0.01, 0.05]; (0.05, 0.1]; (0.1, 1].

Sources of variation	Estimate	Error	Value of z	Value of p	AIC
Intercept	0.07676	0.01470	5.221	**6.22e-06 *** **	−103.79
Perceived disease incidence	0.39922	0.07751	5.151	**7.77e-06 *** **	-
Perceived severity of illness	0.04169	0.02639	1.579	0.122	-

In this study, although disease incidence and severity explained the frequency of adaptive strategies used to cope with their effects, the evidence also demonstrated that the predictive power of incidence is greater. This indicates that severity may not exert any influence on people's perception of the diseases that affect them the most in their social-ecological systems, instead of potentiating it, as expected. One possible explanation may be related to the vulnerability of the socio-ecological systems: recent and regular experiences of prolonged drought in the regions (Martins et al., 2015) and their harmful consequences on agroecosystems and farmers. Among these implications, the scarcity of water is highlighted, with

TABLE 7 | Generalized Linear Model used to test the effect of disease incidence and severity perceived by Carão farmers on the frequency of used adaptive strategies. The *p*-values for significant predictors are highlighted in bold. Significance code *p*-value: *** [0, 0.001]; ** (0.001, 0.01]; * (0.01, 0.05]; (0.05, 0.1]; (0.1, 1].

Sources of variation	Estimate	Error	Value of z	Value of p	AIC
Intercept	0.13081	0.02329	5.617	**5.15e-06 *** **	–54.959
Perceived disease incidence	0.56423	0.10670	5.288	**1.26e-05 *** **	-
Perceived severity of illness	–0.03816	0.04603	–0.829	0.414	-

implications for people's health; poor infrastructure, which does not meet local needs (the poor condition of local roads, for example); remoteness from the nearest urban centers; and the low purchasing power of farmers. Given this completely unfavorable scenario, it was observed that, as the farmers attested, they find themselves unmotivated or unable to seek adaptive strategies and treatments to deal with diseases perceived as more severe.

Observations about the lack of significance of severity in relation to people's perception of diseases arising from climate change in the Catimbau NAPAR and Carão demonstrate that local conceptions of severity may be related to people's previous experiences with certain diseases. This possible explanation finds support in evidence from the scientific literature (Miceli et al., 2008; Sachs et al., 2017; Scheideler et al., 2017; de Silva et al., 2019). For example, Sachs et al. (2017) demonstrated that diabetic patients' concerns about adverse health events that they consider severe are systematically related to their past personal experiences with the diseases. da Silva et al. (2019) observed that university students from Northeastern Brazil tend to store adaptive information regarding diseases considered common and have low severity, which might be related to their experience with the diseases in question. Haque et al. (2012) found that farmers in Bangladesh perceive of greater concern diseases whose incidence is correlated with local extreme climate change events that they have had past personal experiences, such as drought and floods. This correlates with our field observations. Thus, this study supports the authors' argument that these risks related to people's past experiences should receive greater attention when designing and implementing adaptive coping strategies (Haque et al., 2012).

Finally, it was observed that farmers use more adaptive prophylactic behavior strategies. This might be because they are well supported by health information and services, either through a non-governmental organization (in the case of the Catimbau NAPAR communities) or a community health post (in the case of Carão). Research has highlighted that the adoption of personal prophylactic measures is influenced by factors such as knowledge, experience with the disease, and beliefs about health (Weinstein, 1993; Beaujean et al., 2013). Kisomi et al. (2016) found that the low index and inefficiency of prophylactic practices adopted among Malaysian farm workers regarding tick bites, which are transmitters of diseases in humans and animals, are related to low levels of knowledge and health beliefs, although they have extensive experience with the disease. Jin et al. (2020) highlighted the role of emotional factors, negatively correlated with risk communication, in the adoption of prophylactic behaviors related to the COVID-19 contagion. In this case, people's experience with the disease and the amount of information about the risk of contamination is low because it is an emerging disease. Our study concluded that adequate prophylactic planning should be based on an open, honest, and updated flow of information, which can positively direct the adoption of adaptive measures, both prophylactic and therapeutic.

CONCLUSION

Our findings can provide useful information regarding the proposal and development of projects aimed at controlling and mitigating the diseases that most affect local populations in a scenario of increasingly extreme climate change in terms of speed and intensity. Hence, the growing importance of the dialogue between local ecological knowledge and scientific knowledge. The absence of this information can hinder understanding how people behave in these risk contexts and, consequently, the proposition of government policy measures favorable to social development in affected regions.

Our results suggest that some people's understanding of incidence and severity may differ from the scientific community's consensus. In this sense, it is advisable to conduct studies at local and global levels to identify the criteria people residing in different sociocultural contexts use to understand the concepts of incidence and severity. We also believe that diachronic studies that consider the influence of disease perception on the number of adaptive measures to treat them and the variation of knowledge associated with these treatments and their efficacy can help unravel the different factors that direct the evolution of medical systems. This can help fill gaps in the health literature.

Methodologically, our research introduced the PRM as a new approach for specific studies on the perception of human health risks. However, although it is a method that has a simple application and great practicality allowing researchers to analyze and evaluate results easily, these results may offer a limited and biased scope if not applied optimally or not considering an ideal scenario. In this sense, some considerations must be acknowledged. Although the low population density of the investigated communities, in addition to the low heterogeneity and the context of socio-environmental conflict evidenced in some communities of the Catimbau NAPAR, did not invalidate our results and conclusions, they may have limited its scope. Thus, further studies are recommended to compare more heterogeneous scenarios with more robust population densities. If the studies occur in conflict areas, we suggest that this factor must be considered in the experimental design of the research (which was not the case in our study).

Finally, it is recommended that this study is replicated, considering all the previously mentioned considerations, in different scenarios of prolonged climate change events (with high rainfall variation, for example) and, consequently, new diseases. Although our study focused only on diseases "perceived by people" and not "scientifically designated" diseases, we believe that further studies that compare these two types of information can provide broader insights. These additional studies may provide a more accurate understanding of the effect of the perception of diseases (especially those with the highest incidents) on the development of adaptive measures adopted to deal with their adverse effects and evaluate which strategies are more efficient. This information is essential for the proposition, elaboration, and application of predictive models based on people's experiences in socio-environmental vulnerable contexts enhanced by extreme environmental changes and more efficient and favorable governmental policy measures for social development in affected regions.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

This study was submitted and approved by the Research Ethics Committee of the University of Pernambuco, according to the Certificate of Submission for Ethics Appreciation (CSEA) number 89890617.1.0000.5207, in order to meet the legal aspects of research involving human beings. All residents who agreed to participate in the research were asked to sign a free and informed consent form, as governed by the current legislation of the National Health Council (Resolution No. 466/2012). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

HM, IF, EdL, and UA designed and conceived the experimental design of the study. HM collected the data, performed the analyses, and wrote the initial manuscript. All authors contributed significantly to improving the manuscript and gave their final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2021.735595/full#supplementary-material

REFERENCES

Albuquerque, U. P., Ramos, M. A., de Lucena, R. F. P., and Alencar, N. L. (2014). "Methods and Techniques Used to Collect Ethnobiological Data," in *Methods and Techniques in Ethnobiology and Ethnoecology*. Editors U. P. Albuquerque, L. V. F. Cruz da Cunha, R. F. P. Lucena, and R. R. N. Alves (New York: Springer Protocols Handbooks), 15–37. doi:10.1007/978-1-4614-8636-7_2

Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes Gonçalves, J. L., and Sparovek, G. (2013). Köppen's Climate Classification Map for Brazil. *Metz* 22, 711–728. doi:10.1127/0941-2948/2013/0507

Austin, E. K., Rich, J. L., Kiem, A. S., Handley, T., Perkins, D., and Kelly, B. J. (2020). Concerns about Climate Change Among Rural Residents in Australia. *J. Rural Stud.* 75, 98–109. doi:10.1016/j.jrurstud.2020.01.010

Baird, T. D., Leslie, P. W., and McCabe, J. T. (2009). The Effect of Wildlife Conservation on Local Perceptions of Risk and Behavioral Response. *Hum. Ecol.* 37, 463–474. doi:10.1007/s10745-009-9264-z

Banerjee, R. R. (2014). Farmers' Perception of Climate Change, Impact and Adaptation Strategies: a Case Study of Four Villages in the Semi-arid Regions of India. *Nat. Hazards* 75, 2829–2845. doi:10.1007/s11069-014-1466-z

BDE (2017). Perfil Municipal. Altinho. Base de Dados Do Estado, Governo Do Estado de Pernambuco. Available at: http://www.bde.pe.gov.br/estruturacaogeral/PerfilMunicipios.aspx (Accessed November 9, 2020).

Beaujean, D. J. M. A., Bults, M., Van Steenbergen, J. E., and Voeten, H. A. C. M. (2013). Study on Public Perceptions and Protective Behaviors Regarding Lyme Disease Among the General Public in the Netherlands: Implications for Prevention Programs. *BMC Public Health* 13, 225. doi:10.1186/1471-2458-13-225

Bhatta, L. D., Udas, E., Khan, B., Ajmal, A., Amir, R., and Ranabhat, S. (2019). Local Knowledge Based Perceptions on Climate Change and its Impacts in the Rakaposhi valley of Gilgit-Baltistan, Pakistan. *Ijccsm* 12, 222–237. doi:10.1108/IJCCSM-05-2019-0024

Boillat, S., and Berkes, F. (2013). Perception and Interpretation of Climate Change Among Quechua Farmers of Bolivia: Indigenous Knowledge as a Resource for Adaptive Capacity. *E and S* 18, 21. doi:10.5751/ES-05894-180421

Brasil (2000). *Lei n. 9.985, de 18 de julho de 2000. Regulamenta o art. 225, § 1o, incisos I, II, III e VII da Constituição Federal, institui o Sistema Nacional de Unidades de Conservação da Natureza e dá outras providências*. Brasília: Presidência da República, Casa Civil, Subchefia para Assuntos Jurídicos.

Bryan, E., Ringler, C., Okoba, B., Roncoli, C., Silvestri, S., and Herrero, M. (2013). Adapting Agriculture to Climate Change in Kenya: Household Strategies and Determinants. *J. Environ. Manage.* 114, 26–35. doi:10.1016/j.jenvman.2012.10.036

Butler, C. D., and Harley, D. (2010). Primary, Secondary and Tertiary Effects of Eco-Climatic Change: The Medical Response. *Postgrad. Med. J.* 86, 230–234. doi:10.1136/pgmj.2009.082727

Costello, A., Abbas, M., Allen, A., Ball, S., Bell, S., Bellamy, R., et al. (2009). Managing the Health Effects of Climate Change. *The Lancet* 373, 1693–1733. doi:10.1016/s0140-6736(09)60935-1

Cruz, M. P., Medeiros, P. M., Sarmiento-Combariza, I., Peroni, N., and Albuquerque, U. P. (2014). "I Eat the Manofê So it Is Not Forgotten": Local Perceptions and Consumption of Native Wild Edible Plants from Seasonal Dry Forests in Brazil. *J. Ethnobiol. Ethnomedicine* 10, 45. doi:10.1186/1746-4269-10-45

Cunha, A. P. M. A., Zeri, M., Deusdará Leal, K., Costa, L., Cuartas, L. A., Marengo, J. A., et al. (2019). Extreme Drought Events over Brazil from 2011 to 2019. *Atmosphere* 10, 642. doi:10.3390/atmos10110642

da Silva, R. H., da Ferreira, W. S., Jr, Ferreira Júnior, W. S., Muniz de Medeiros, P., and Albuquerque, U. P. (2019). Adaptive Memory and Evolution of the Human Naturalistic Mind: Insights from the Use of Medicinal Plants. *PLoS ONE* 14, e0214300. doi:10.1371/journal.pone.0214300

da Silva, T. C., Cruz, M. P., de Sousa Araújo, T. A., Schwarz, M. L., and Albuquerque, U. P. (2014). "Methods in Research of Environmental Perception," in *Methods and Techniques in Ethnobiology and Ethnoecology*. Editors U. P. Albuquerque, L. V. F. Cruz da Cunha, R. F. P. Lucena, and R. R. N. Alves (New York: Springer Protocols Handbooks), 99–109. doi:10.1007/978-1-4614-8636-7_7

de Albuquerque, U. P., de Lima Araújo, E., El-Deir, A. C. A., de Lima, A. L. A., Souto, A., Bezerra, B. M., et al. (2012). Caatinga Revisited: Ecology and Conservation of an Important Seasonal Dry Forest. *Scientific World J.* 2012, 1–18. doi:10.1100/2012/205182

de Perez, E, C., Nerlander, L., Monasso, F., van Aalst, M., Mantilla, G., Muli, E., et al. (2015). Managing Health Risks in a Changing Climate: Red Cross Operations in East Africa and Southeast Asia. *Clim. Dev.* 7, 197–207. doi:10.1080/17565529.2014.951012

Dhanya, P., and Ramachandran, A. (2016). Farmers' Perceptions of Climate Change and the Proposed Agriculture Adaptation Strategies in a Semi Arid Region of South India. *J. Integr. Environ. Sci.* 13, 1–18. doi:10.1080/1943815X.2015.1062031

dos Santos, D. M., da Silva, K. A., de Albuquerque, U. P., dos Santos, J. M. F. F., Lopes, C. G. R., and Araújo, E. d. L. (2013). Can Spatial Variation and Inter-annual Variation in Precipitation Explain the Seed Density and Species Richness of the Germinable Soil Seed Bank in a Tropical Dry forest in north-eastern Brazil? *Flora - Morphol. Distribution, Funct. Ecol. Plants* 208, 445–452. doi:10.1016/j.flora.2013.07.006

Espinosa, M. M., Bieski, I. G. C., and Martins, D. T. O. (2014). "Sampling in Ethnobotanical Studies of Medicinal Plants," in *Methods and Techniques in Ethnobiology and Ethnoecology*. Editors U. P. Albuquerque, L. V. F. Cruz da Cunha, R. F. P. Lucena, and R. N. Alves (New York: Springer Protocols Handbooks), 197–212. doi:10.1007/978-1-4614-8636-7_13

Estomba, D., Ladio, A., and Lozada, M. (2006). Medicinal Wild Plant Knowledge and Gathering Patterns in a Mapuche Community from North-western Patagonia. *J. Ethnopharmacology* 103, 109–119. doi:10.1016/j.jep.2005.07.015

Ferreira, W. S., Jr., Nascimento, A. L. B., Ramos, M. A., Medeiros, P. M., Soldati, G. T., Santoro, F. R., et al. (2015). "Resilience and Adaptation in Social-Ecological Systems," in *Evolutionary Ethnobiology*. Editors U. P. Albuquerque, P. M. Medeiros, and A. Casas (New York: Springer), 105–119. doi:10.1007/978-3-319-19917-7

Fosu-Mensah, B. Y., Vlek, P. L. G., and MacCarthy, D. S. (2012). Farmers' Perception and Adaptation to Climate Change: a Case Study of Sekyedumase District in Ghana. *Environ. Dev. Sustain.* 14, 495–505. doi:10.1007/s10668-012-9339-7

Gbetibouo, G. A. (2009). *Understanding Farmers' Perceptions and Adaptations to Climate Change and Variability: The Case of the Limpopo Basin, South Africa*. Washington, D.C.: International Food Policy Research Institute Discussion.

Gonçalves, P. H. S., da Cunha Melo, C. V. S., de Assis Andrade, C., de Oliveira, D. V. B., de Moura Brito Junior, V., Jr, Rito, K. F., et al. (2021). Livelihood Strategies and Use of forest Resources in a Protected Area in the Brazilian Semiarid. *Environ. Dev. Sustain.* 24, 1–21. doi:10.1007/s10668-021-01529-3

Handley, T. E., Kay-Lambkin, F. J., Inder, K. J., Lewin, T. J., Attia, J. R., Fuller, J., et al. (2014). Self-reported Contacts for Mental Health Problems by Rural Residents: Predicted Service Needs, Facilitators and Barriers. *BMC Psychiatry* 14, 1–12. doi:10.1186/s12888-014-0249-0

Haque, M. A., Yamamoto, S. S., Malik, A. A., and Sauerborn, R. (2012). Households' Perception of Climate Change and Human Health Risks: A Community Perspective. *Environ. Health* 11, 1. doi:10.1186/1476-069X-11-1

Hayes, K., Blashki, G., Wiseman, J., Burke, S., and Reifels, L. (2018). Climate Change and Mental Health: Risks, Impacts and Priority Actions. *Int. J. Ment. Health Syst.* 12, 1–12. doi:10.1186/s13033-018-0210-6

ICMBio (2002). *Decreto s/no de 13 de dezembro de 2002. Cria o Parque Nacional do Catimbau, nos Municípios de Ibirimirim, Tupanatinga e Buíque, no Estado de Pernambuco, e dá outras providências*. Brasília: Instituto Chico Mendes de Conservção da Biodiversidade, Ministério do Meio Ambiente.

INMET (2021). Gráficos climatológicos: Pernambuco. Instituto Nacional de Meteorologia. Available at: https://clima.inmet.gov.br/GraficosClimatologicos/PE/82890 (Accessed August 28, 2021).

IPCC (2007). "Climate Change 2007: Synthesis Report," in *Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Editors C. W. Team, R. K. Pachauri, and A. Reisinger (Geneva: IPCC), 104. doi:10.1038/446727a

Jin, Z., Zhao, K.-b., Xia, Y.-y., Chen, R.-j., Yu, H., Tamunang Tamutana, T., et al. (2020). Relationship between Psychological Responses and the Appraisal of Risk Communication during the Early Phase of the COVID-19 Pandemic: a Two-Wave Study of Community Residents in China. *Front. Public Health* 8, 550220. doi:10.3389/fpubh.2020.550220

Kisomi, M. G., Wong, L. P., Tay, S. T., Bulgiba, A., Zandi, K., Kho, K. L., et al. (2016). Factors Associated with Tick Bite Preventive Practices Among Farmworkers in Malaysia. *PLoS ONE* 11, e0157987. doi:10.1371/journal.pone.0157987

Lafferty, K. D. (2009). The Ecology of Climate Change and Infectious Diseases. *Ecology* 90, 888–900. doi:10.1890/08-0079.1

Lima, J. R. d., and Magalhães, A. R. (2018). "Secas no Nordeste: registros históricos das catástrofes econômicas e humanas Do século 16 ao século 21," in *Parcerias Estratégicas*. Editor CGEE (Brasília: Centro de Gestão e Estudos Estratégicos), 191–212.

Magalhães, A. R. (2016). "Vida e seca no Brasil," in *Secas no Brasil: política e gestão proativas*. Editors E. De Nys, N. L. Engle, and A. R. Magalhães (Brasília: Centro de Gestão e Estudos Estratégicos; Banco Mundial), 19–35.

Magalhães, H. F., Oliveira, R. C. S., Feitosa, I. S., and Albuquerque, U. P. (2019). "Collection and Analysis of Environmental Risk Perception Data," in *Methods and Techniques in Ethnobiology and Ethnoecology*. Editors U. P. Albuquerque, R. F. P. Lucena, L. V. F. Cruz da Cunha, and R. R. N. Alves (New York, NY: Springer Protocols Handbooks), 149–159. doi:10.1007/978-1-4614-8636-7

Marengo, J. A., Alves, L. M., Alvala, R. C. S., Cunha, A. P., Brito, S., and Moraes, O. L. L. (2018). Climatic Characteristics of the 2010-2016 Drought in the Semiarid Northeast Brazil Region. *Acad. Bras. Ciênc.* 90, 1973–1985. doi:10.1590/0001-3765201720170206

Marengo, J. A., Cunha, A. P. M. A., Nobre, C. A., Ribeiro Neto, G. G., Magalhaes, A. R., Torres, R. R., et al. (2020). Assessing Drought in the Drylands of Northeast Brazil under Regional Warming Exceeding 4 °C. *Nat. Hazards* 103, 2589–2611. doi:10.1007/s11069-020-04097-3

Marengo, J. A., Torres, R. R., and Alves, L. M. (2017). Drought in Northeast Brazil-past, Present, and Future. *Theor. Appl. Climatol* 129, 1189–1200. doi:10.1007/s00704-016-1840-8

Martins, E. S. P. R., De Nys, E., Molejón, C., Biazeto, B., Silva, R. F. V., and Engle, N. (2015). *Monitor de Secas do Nordeste, em busca de um novo paradigma para a gestão de secas*. 1st ed. Brasília: Banco Mundial. doi:10.13140/RG.2.1.4238.8886

McMichael, A. J. (2013). Globalization, Climate Change, and Human Health. *N. Engl. J. Med.* 368, 1335–1343. doi:10.1056/NEJMra1109341

McMichael, A. J., Woodruff, R. E., and Hales, S. (2006). Climate Change and Human Health: Present and Future Risks. *The Lancet* 367, 859–869. doi:10.1016/S0140-6736(06)68079-3

Miceli, R., Sotgiu, I., and Settanni, M. (2008). Disaster Preparedness and Perception of Flood Risk: a Study in an alpine valley in Italy. *J. Environ. Psychol.* 28, 164–173. doi:10.1016/j.jenvp.2007.10.006

ME (2015). *Mapeamento e análise espectro-temporal das Unidades de Conservação de Proteção Integral da Administração Federal no Bioma Caatinga. Parque Nacional do Catimbau*. Editor N. C. F. Freire Recife: Ministério da Educação, Fundação Joaquim Nabuco, Universidade Federal de Campina Grande).

Nyantakyi-Frimpong, H., and Bezner-Kerr, R. (2015). The Relative Importance of Climate Change in the Context of Multiple Stressors in Semi-arid Ghana. *Glob. Environ. Change* 32, 40–56. doi:10.1016/j.gloenvcha.2015.03.003

Oliveira, R. C. d. S., Albuquerque, U. P., da Silva, T. L. L., Ferreira Júnior, W. S., Chaves, L. d. S., and Araújo, E. d. L. (2017). Religiousness/spirituality Do Not Necessarily Matter: Effect on Risk Perception and Adaptive Strategies in the Semi-arid Region of NE Brazil. *Glob. Ecol. Conservation* 11, 125–133. doi:10.1016/j.gecco.2017.05.004

Oloukoi, G., Bob, U., and Jaggernath, J. (2014). Perception and Trends of Associated Health Risks with Seasonal Climate Variation in Oke-Ogun Region, Nigeria. *Health & Place* 25, 47–55. doi:10.1016/j.healthplace.2013.09.009

PELD Catimbau (2016). Projeto Ecológico de Longa Duração Sítio Parque Nacional Do Catimbau. Mapas temáticos. PELD-PRONEX Catimbau. Available at: https://www.peldcatimbau.org/mapas-tematicos (Accessed November 4, 2020).

Quinn, C. H., Huby, M., Kiwasila, H., and Lovett, J. C. (2003). Local Perceptions of Risk to Livelihood in Semi-arid Tanzania. *J. Environ. Manage.* 68, 111–119. doi:10.1016/S0301-4797(03)00013-6

R Development Core Team (2019). *The R Project for Statistical Computing News via Twitter*. Vienna: R Development Core Team.

Rodriguez, N., Eakin, H., and De Freitas Dewes, C. (2017). Perceptions of Climate Trends Among Mexican maize Farmers. *Clim. Res.* 72, 183–195. doi:10.3354/cr01466

Sachs, M. L., Sporrong, S. K., Colding-Jørgensen, M., Frokjaer, S., Helboe, P., Jelic, K., et al. (2017). Risk Perceptions in Diabetic Patients Who Have Experienced Adverse Events: Implications for Patient Involvement in Regulatory Decisions. *Pharm. Med.* 31, 245–255. doi:10.1007/s40290-017-0200-z

Santoro, F. R., and Albuquerque, U. P. (2020). What Factors Guide Healthcare Strategies over Time? A Diachronic Study Focused on the Role of Biomedicine and the Perception of Diseases in the Dynamics of a Local Medical System. *Acta Bot. Bras.* 34, 720–729. doi:10.1590/0102-33062020abb0002

Santoro, F. R., Ferreira Júnior, W. S., Jr, Araújo, T. A. d. S., Ladio, A. H., and Albuquerque, U. P. (2015). Does Plant Species Richness Guarantee the Resilience of Local Medical Systems? A Perspective from Utilitarian Redundancy. *PLoS ONE* 10, e0119826–18. doi:10.1371/journal.pone.0119826

Scheideler, J. K., Taber, J. M., Ferrer, R. A., Grenen, E. G., and Klein, W. M. P. (2017). Heart Disease versus Cancer: Understanding Perceptions of Population Prevalence and Personal Risk. *J. Behav. Med.* 40, 839–845. doi:10.1007/s10865-017-9860-0

Silva, J. M. C. d., Barbosa, L. C. F., Leal, I. R., and Tabarelli, M. (2017). "The Caatinga: Understanding the Challenges," in *Caatinga: The Largest Tropical Dry Forest Region in South America*. Editors J. M. C. Silva, I. R. Leal, and M. Tabarelli (Berlin: Springer International Publishing), 3–19. doi:10.1007/978-3-319-68339-3_1

Slegers, M. F. W. (2008). "If Only it Would Rain": Farmers' Perceptions of Rainfall and Drought in Semi-arid central Tanzania. *J. Arid Environments* 72, 2106–2123. doi:10.1016/j.jaridenv.2008.06.011

Smit, B., and Wandel, J. (2006). Adaptation, Adaptive Capacity and Vulnerability. *Glob. Environ. Change* 16, 282–292. doi:10.1016/j.gloenvcha.2006.03.008

Smith, K., Barrett, C. B., and Box, P. W. (2000). Participatory Risk Mapping for Targeting Research and Assistance: With an Example from East African Pastoralists. *World Dev.* 28, 1945–1959. doi:10.1016/S0305-750X(00)00053-X

Smith, W. J., Jr., Liu, Z., Safi, A. S., and Chief, K. (2014). Climate Change Perception, Observation and Policy Support in Rural Nevada: A Comparative Analysis of Native Americans, Non-native Ranchers and Farmers and Mainstream America. *Environ. Sci. Pol.* 42, 101–122. doi:10.1016/j.envsci.2014.03.007

UNDRR (2009). "Summary and Recommendations: 2009 Global Assessment Report on Disaster Risk Reduction," in *Risk and Poverty in a Changing Climate: Invest Today for a Safer Tomorrow* (Geneva, Switzerland: United Nations Office for Disaster Risk Reduction, International Strategy for Disaster Reduction), 24. doi:10.1037/e522342010-005

Watts, N., Adger, W. N., Agnolucci, P., Blackstock, J., Byass, P., Cai, W., et al. (2015). Health and Climate Change: Policy Responses to Protect Public Health. *Lancet* 386, 1861–1914. doi:10.1016/S0140-6736(15)60854-6

Watts, N., Amann, M., Ayeb-Karlsson, S., Belesova, K., Bouley, T., Boykoff, M., et al. (2018). The Lancet Countdown on Health and Climate Change: from 25 Years of Inaction to a Global Transformation for Public Health. *The Lancet* 391, 581–630. doi:10.1016/S0140-6736(17)32464-9

Weber, E. U. (2010). What Shapes Perceptions of Climate Change? *Wires Clim. Change* 1, 332–342. doi:10.1002/wcc.41

Weinstein, N. D. (1993). Testing Four Competing Theories of Health-Protective Behavior. *Health Psychol.* 12, 324–333. doi:10.1037/0278-6133.12.4.324

WHO (2009). *Protecting Health from Climate Change: Global Research Priorities*. Editor WHO (Geneva, Switzerland: World Health Organization, WHO Library Cataloguing-in-Publication Data).

WHO; UNICEF (2004). *Joint Statement: Clinical Management of Acute Diarrhoea (WHO/FCH/CAH/04.07)*. Geneva, Switzerland: World Health Organization, Department of Child and Adolescent Health and Development, and United Nations Children's Fund, Programme Division.

WMO (2020). *The Global Climate in 2015-2019. WMO Statements on Climate, 1249*. Geneva, Switzerland: World Meteorological Organization.

Young, M., Wolfheim, C., Marsh, D. R., and Hammamy, D. (2012). World Health Organization/United Nations Children's Fund Joint Statement on Integrated Community Case Management: An Equity-Focused Strategy to Improve Access to Essential Treatment Services for Children. *Am. J. Trop. Med. Hyg.* 87, 6–10. doi:10.4269/ajtmh.2012.12-0221

Younger, M., Morrow-Almeida, H. R., Vindigni, S. M., and Dannenberg, A. L. (2008). The Built Environment, Climate Change, and Health. Opportunities for Co-benefits. *Am. J. Prev. Med.* 35, 517–526. doi:10.1016/j.amepre.2008.08.017

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Indigenous and Traditional Management Creates and Maintains the Diversity of Ecosystems of South American Tropical Savannas

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The tropical South American savannas have been occupied and manipulated by humans since the late Pleistocene. Ecologists consider that soils, hydrology, and seasonal precipitation influence the structure and composition of plants and the fire-proneness of savannas. However, the human influence on these dynamics remains uncertain. This is because little is known about human activities and what influence they have on the diversity of ecosystems. Considering this, our study sought to synthesize the management practices used by small-scale societies of the South American savannas, compile the species that are the focus of direct management, and demonstrate the role of this management in maintaining the diverse ecosystems that make up the savannas. We also set out to test the hypotheses that forms of management differ depending on the ecosystem and cultural matrices. To do so, we conducted a systematic review, in which we collected 51 articles with information about the management carried out by small-scale societies. From this, we categorized 10 management practices directed to ecosystems: protection of the ecosystem, enrichment of species, topographic changes, increased soil fertility, cleaning, prevention of fire, resource promotion, driving of game, swidden-fallow, and maintenance of ecosystem structure. We identified 19 native plant species whose populations are managed *in-situ*. These management practices have proven capable of keeping savanna and grassland ecosystems open and increasing the occurrence of forest ecosystems in the mosaic, as well as favoring plants of human interest in general. We note that there is a relationship between management practices with ecosystems and cultures, which suggests that both factors influence the management of landscapes. We conclude that management practices of small-scale societies are responsible for domesticating South American tropical savannas and that these savannas are composed of a mosaic of culturally constructed niches. The small-scale societies that inhabit these environments have important traditional ecological knowledge and strategies that enable the use, conservation, and restoration of savannas, extremely threatened by agribusiness today.

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INTRODUCTION

Humans across the planet evolved in different ecosystems and their activities influenced these habitats, as well as the evolution of populations in numerous taxonomic groups (Cooke, 1998; Boivin et al., 2016; Roberts, 2019). Within the diversity of environments in the Neotropical region, savannas were a key part of early occupations (Lombardo et al., 2020), either because of their diversity of ecosystems and resources, or because of the evolutionary preferences inherited from Pleistocene hominids (Ellenberg and Mueller-Dombois, 1967; Eiten, 1972; Orians, 1980; Harris and Hillman, 2014; Roberts, 2019). The prevailing ecological thinking considers that the ecosystems that make up tropical savannas are mainly influenced by soils, hydrology, and seasonal precipitation, as these factors determine the structure and composition of plants and their propensity to fire (Staver et al., 2011; Hoffmann et al., 2012; Silva et al., 2013). Some authors draw attention to the fact that humans can influence these dynamics, as they can modify floristic composition and edaphic conditions (Hirota et al., 2011; Pinho et al., 2011; Lombardo et al., 2020) and they are mostly responsible for the appearance of fire (Ramos-Neto and Pivello, 2000). However, the extent of human influence on savannas remains unclear, as it is not known which practices are used, in what combinations, how they influence different ecosystems, and which plant species are most affected in this process.

Human influences on environments occur from the moment humans settle in new territories (Lombardo et al., 2020), and tropical South American savannas have a diverse occupation history (Denevan, 1966; Morey, 1976; Bueno and Isnardis, 2018). Early records are sparse, but make clear that the savannas were inhabited in the late Pleistocene and that, in this period, human activities were characterized by a dynamic of high mobility and initial recognition of environments (Bocanegra and Mora, 2012; Bueno and Dias, 2015; Vialou et al., 2017). In the Holocene, there is a greater number of archaeological records, which suggests sedentarization associated with population growth and diversification of strategies to adapt to the temperature oscillations and rainfall variations common in the period (Erickson, 1995; Gassón, 2002; Mayle et al., 2004; Rostain, 2008; Bueno and Dias, 2015; Bueno and Isnardis, 2018; Lombardo et al., 2020; Stier et al., 2020).

At present, the tropical savannas of South America are the focus of urban expansion and intensive agriculture and ranching; these activities take advantage of open ecosystems and eliminate native vegetation, endangering biodiversity in general (Klink and Machado, 2005; Hernández-Hernández et al., 2011; Eufemia et al., 2019). On the other hand, parts of these regions continue to be occupied by small-scale societies, who base their lifestyles on an intimate relationship with nature (Ploeg, 2009). Smith (2012) points out that these people, in the past or the present, share the following behavioral patterns: have well-defined territories; maintain and update knowledge about local ecosystems, passing it on to future generations; create strategies to control wild resources; have the inherent capacity to modify ecosystems; and, through these modifications, increase the abundance and accessibility of resources of interest.

These modifications made by small-scale societies generally do not result in a decrease in plant diversity (Balée, 2006). However, these modifications reduce the impact of existing natural selection pressures, making it easier for humans to adapt (Albuquerque et al., 2015). These modifications also influence other species that interact with resources of human interest, directly or indirectly (Laland et al., 2016; Albuquerque et al., 2019). This process is the basis of Niche Construction Theory (NCT), which affirms that living beings can change environmental conditions at different scales, consequently becoming more adapted to the transformed environment (Laland and O'Brien, 2010; Odling-Smee et al., 2013; Albuquerque et al., 2019). When humans are the agents of landscape transformation, it is necessary to recognize that cultural aspects also influence their activities (Albuquerque et al., 2015; Coca et al., 2021). NCT helps explain and substantiate the process of plant domestication (Smith, 2012), which consists of humans selecting and managing phenotypes in wild populations, resulting in genetic, morphological, and demographic changes in the resulting populations (Clement, 1999).

This relationship between humans and plants is mutualistic and occurs through selection combined with management; it can occur in different locations and not only in food production systems, such as cultivated areas (Clement et al., 2021). By domesticating plant populations in their natural environments, even if at incipient levels, humans also domesticate landscapes (Casas et al., 1997; Clement, 1999; Allaby et al., 2021; Clement et al., 2021). Domesticated landscapes are created by the conscious and unconscious processes of manipulating ecosystems and the plants that compose them, resulting in more productive environments suitable for humans (Terrell et al., 2003; Casas et al., 2017; Hecht, 2017; Clement et al., 2021). This feedback between practice and result is one of the differentials of NCT (Matthews et al., 2014; Huebert and Allen, 2020; Davis and Douglass, 2021).

According to recent research, domesticated landscapes are formed and maintained as a result of a set of management practices that alter vegetation structure, floristic composition, and ecological processes (Smith, 2011; Levis et al., 2018). For tropical humid forests, theoretical models explain the mechanisms of management of species of human interest by indigenous and traditional communities that result in richer and more diverse forests (Clement, 1999; Levis et al., 2018). Similarly, Smith (2011), who focused his investigation on the rich diversity of environments in North America, presented another conceptual model on the set of strategies focused on making environments richer in food. In the case of savannas, there are reports of small-scale societies in northern Australia that have a set of organized and directed burning practices, aimed at maintaining grasslands and savannas (Russell-Smith et al., 1997; Yibarbuk et al., 2001; Fletcher et al., 2020). In the savannas of northern Tanzania, there are reports of non-fire management practices, where the Chagga constantly manage their forest yards employing practices such as the toleration of species of interest and the removal of species of no use to humans (Fernandes et al., 1985). In general, these management practices are responsible for lasting legacies in ecosystems (Arroyo-Kalin, 2016), another feature of niche construction (Albuquerque et al., 2015).

In these varied theoretical perspectives, the process of constructing niches and domesticating landscapes is the result of valuing and promoting species and environments (Smith, 2012; Harris and Hillman, 2014; Allaby et al., 2021). Once occupied by humans, ecosystems become dependent on complex interactions with human societies, which can be described by interactive matrices of species and management strategies over time (Terrell et al., 2003; Crumley, 2007; Albuquerque et al., 2019). Valuation procedures, also called management practices, are learned collectively and created through an intimate relationship with the landscape, common in small-scale societies (Abraão et al., 2010; Smith, 2011; Silva et al., 2016; Balée, 2018; Levis et al., 2018). For a long time, it has been debated which factors guide these practices; some authors argue that practices are developed in the social environment and consequently are influenced by different cultures (Smith, 2012; Albuquerque et al., 2015); others adopted deterministic thinking where the environment would be the main factor related to this set of practices and strategies (Meggers, 2001). Today, historical ecology proposes a middle ground by assuming that environments and cultures evolved together and that landscapes are the result of this relationship, and therefore it is impossible to separate their effects (Arroyo-Kalin, 2016; Balée, 2018).

Considering this context, our study uses a systematic review to: 1) synthesize the management practices carried out by small-scale societies in South American savannas; 2) highlight the role of this management in maintaining the diversity of ecosystems that make up the savannas; and 3) compile the focus species for human management. We also propose to test the hypotheses that management strategies vary with the type of vegetation formation (H1) and the cultural matrices that use them (H2). From this effort, we hope to contribute to the understanding of how humans domesticate landscapes and plants, with reference to savannas, which are characterized by specific ecological processes, limiting environmental factors and their own taxonomic composition.

MATERIALS AND METHODS

Definition of Terms

Savannah formations expanded globally in the late Miocene, about eight million years ago, due to the decrease in atmospheric CO_2 and the arid climate at the time, factors that favored the occurrence of fires and, consequently, savannas (Keeley and Rundel, 2005; Beerling and Osborne, 2006). Today, tropical savannas cover one-eighth of the earth's terrestrial surface, with representation in the Americas, Africa, and Australia (Scholes and Archer, 1997). The present study is focused on South American tropical savannas, which include the following areas (**Figure 1**): 1) the Cerrado, the largest savanna in Brazilian territory 2) the Orinoco Llanos, with parts in the territories of Colombia and Venezuela; 3) the Magdalena Valley in Colombia; 4) the savannas of the Guianas, located in the Guiana shield; 5) the Beni Savanna, located in Bolivia, also known as Llanos de Mojos. Besides these larger areas, there are small fragments of savanna within the boundaries of Amazonia, called 6) Amazonian Savannas (Huber, 1987; Olson et al., 2001; Adeney et al., 2016; ONF, 2017).

Broadly, savannas can be defined as terrestrial domains or ecosystems whose herbaceous stratum is ecologically predominant and continuous, and woody individuals may or may not be present (Huber, 1987; FAO, 2000). The climate of these regions is classified as tropical savanna, Aw or As in the Köppen system, determined by having a well-marked dry season, in winter or summer (Kottek et al., 2006). The length of the dry season is one of the most important factors in the occurrence and current distribution of savannas (Walter et al., 2008). Soils are generally classified as dystrophic to acidic because they have base saturation of less than 50%, low to medium fertility, and high aluminum contents (Cole, 1986; Reatto et al., 2008). Other determinants of savanna distribution are fire and herbivory; both play strong roles in continental-scale tree cover (Staver et al., 2011).

More detailed definitions exist which propose that savannas are made up of forest, savanna and grassland ecosystems distributed as a mosaic across the landscape (Ellenberg and Mueller-Dombois, 1967; Eiten, 1972; Ribeiro and Walter, 2008). In these different ecosystems there are environmental variations in the general characteristics described above.

Forest ecosystems have a predominant arboreal stratum and a continuous canopy, with heights varying between 3 and 30 m (Oliveira-Filho, 2009). Included in this category are moist tropical forest enclaves that occur within the domain of savannas and forested savannas; both types do not have a dense and continuous herbaceous layer and have a sub-canopy layer that covers a large part of the terrain (FAO, 2000; IBGE, 2012). This type of ecosystem commonly occurs in mesotrophic soils, with moderate nutrient contents, and in places where water is available year-round; these forests are species-rich compared to other savanna ecosystems (Oliveira-Filho and Ratter, 2002). These characteristics mean that these forests do not burn easily and consequently their species are not adapted to fire, being considered fire-sensitive ecosystems (Pivello et al., 2021).

Savanna ecosystems, the predominant formation from which the domain's name originates, occur in interfluves with well-drained and low-fertility soils (Oliveira-Filho and Ratter, 2002). These environments have two representative strata, herbaceous and arboreal-bushy, the latter reaching heights of up to 8 m (Kauffman et al., 1994). The flora of the savannas presents adaptations to fire and drought, such as the presence of underground organs for water storage, protection of the buds below ground or by a dense arrangement of the leaves, thickening

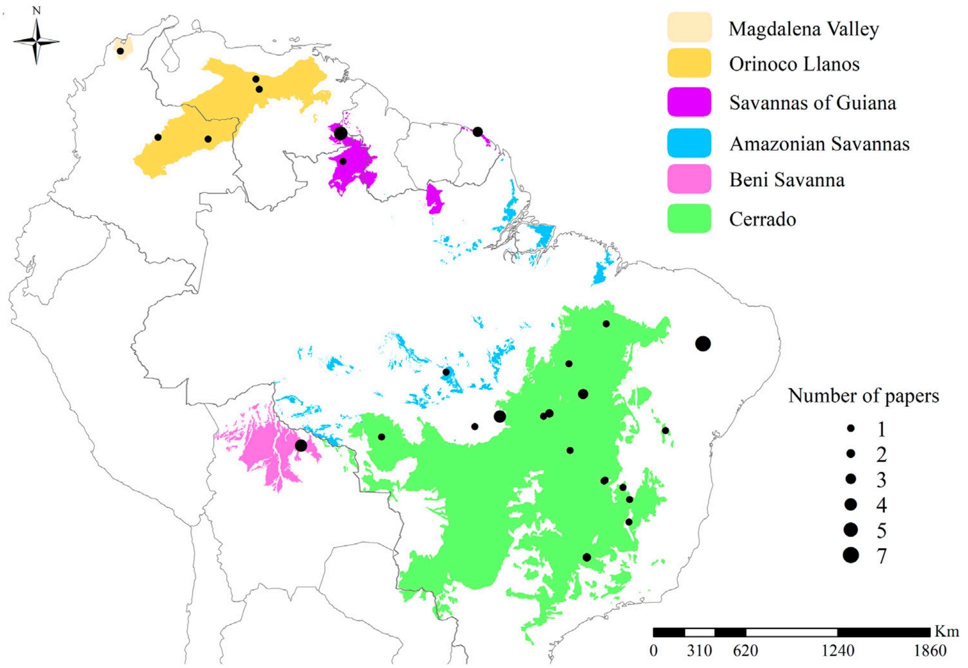

FIGURE 1 | Map showing the location of tropical savannas in South America. To compose this map, we combined the following classifications: from Adeney et al. (2016) for Amazonian savannas; from Huber (1987) for the Magdalena valley; from ONF (2017) for the coastal savannas of the Guianas; and from Olson et al. (2001) for the remaining areas. The black dots represent the sampling sites, the size of the dots corresponds to the number of papers included in this review at each site. The point located in northeastern Brazil corresponds to seven studies carried out in a patch of savannah detached from the main Cerrado area; the point overlaps the patch and cannot be seen on the map, differing from the others.

of the bark and sclerophilia, resulting in a set of evergreen or semideciduous species (Oliveira-Filho and Ratter, 2002). These adaptations to fire demonstrate that the flora of these environments co-evolved with this disturbance and benefited from it, being considered fire-dependent (Pivello et al., 2021). There is, however, a subclass in savanna ecosystems considered to be fire-sensitive (Flores et al., 2021; Pivello et al., 2021), the swamp savannas also called *veredas*, a pioneer formation without canopy where the arboreal palm *Mauritia flexuosa* L. f. is dominant to the shrub-herbaceous stratum; these occur on hydromorphic and floodable soils (Ribeiro and Walter, 1998).

Grassland ecosystems are dominated by the herbaceous and subshrub strata, being poor in woody vegetation that reaches a maximum of 5 m in height. (Kauffman et al., 1994; Filgueiras, 2002). These ecosystems can occur on very well-drained, dystrophic sites or in areas that experience seasonal flooding (Oliveira-Filho and Ratter, 2002). Grasslands tend to have a high diversity of herbaceous species, and it is rare to find monodominant grasslands (Filgueiras, 2002). Like savannas, grasslands are adapted to and dependent on fire, and benefit from its action (Pivello et al., 2021).

Data Collection

We conducted a systematic literature review, using the practices recommended by PRISMA-EcoEvo (O'Dea et al., 2021) and Collaboration for Environmental Evidence (CEE, 2018). For this we used the online search engines Web of Science, Scielo and Scopus. The survey was conducted in June 2021, using the following search key in the fields 1) title, 2) abstract and 3) keywords: (traditional OR local OR indigen*) NEAR/4 (management OR manejo OR practi* OR pratic* OR colet* OR harvest* OR cosecha) (OR domestic*) AND (savanna OR savana OR sabana OR llanos OR cerrado), which returned 1,555 documents. We initially refined the results so that only papers about South America were displayed, leaving 597 articles. We excluded duplicate articles and were left with 393 unique articles (for details see **Figure 1**; **Supplementary Material**).

We first evaluated these documents by reading their titles and abstracts, selecting 1) peer-reviewed articles, 2) written in English, Portuguese or Spanish, 3) that addressed the management carried out by small-scale societies. We excluded from our review all documents developed 1) outside the scope of the study, and 2) outside our spatial frame. We selected 147 documents, which were read in their entirety and excluded those that: 1) did not detail how the management is done; 2) did not mention ways of managing ecosystems or native plants; 3) did not make explicit the ecosystem in which management occurred; 4) did not mention management with species *in situ;* and 5) did not make clear which human group performed a particular form of management (for list of documents evaluated and specific exclusion criteria see **Supplementary Table S1**). As a result of this process, 37 articles were included in our review.

To increase coverage, we included in our sample 14 articles previously known to contain relevant information on savanna management, but which did not appear in the search strategy described above. We evaluated these articles individually to understand why they did not appear in our systematic search and observed that five of them presented our key search terms but were published in non-indexed journals, and nine did not present our key search terms in the title, abstract, or keywords, but contained them in the body of the text (**Supplementary Table S1**). Thus, our final sample size was 51 articles.

The objectives of the papers were not always to investigate the management of ecosystems or plant populations, but all those included in our sample included this information to support or complete the main objective; thus, there were differences in the detailing of the information. Such differences may also be related to the different methodologies used by the researchers.

Data Extraction and Categorization of Information

We extracted from the selected articles: 1) the types of ecosystems managed; 2) the human groups investigated; 3) all forms of management cited; and 4) the species targeted for individual or population management. These data were categorized according to the following criteria:

Ecosystems*:* We categorized the ecosystems where the work was carried out into: 1) Forests: papers whose authors cited the terms gallery forests, riparian forests, forest islands and patches, secondary forests, inundated forests, cerradão or just forests; 2) Savannas: papers in which the authors used the terms savannas, cerrado-like vegetation, and swamp savannas (*veredas*); and 3) Grasslands: articles whose authors referred to grasslands, open savanna, treeless open savannas, seasonally flooded savannas or wet grasslands, and natural pastures. For the main structural and ecological differences between these ecosystems see *Definition of Terms*.

Cultural Matrices: Human communities were assigned to the following groups: *1*) Indigenous peoples: human groups that self-identify as indigenous and that inhabited the country or a geographical region belonging to the country at the time of European colonization or the establishment of current state borders. Included in this group are pre-Columbian peoples and their descendants who, regardless of their legal status, retain their own social, economic, cultural, and political institutions, or parts of them (ILO, 1989; ISA, 2005; Brondízio et al., 2021). 2) Local communities: human groups acting collectively in a way that defines a territory and culture over time (Brondízio et al., 2021). In this group were included family farmers and local communities that do not necessarily agree on one concept of political self-determination. 3) Traditional communities: groups that maintain knowledge, identities, and territorialities linked to a historical, collective, and communal territory (Brasil, 1988; Colombia, 1997; Brandão, 2012; Eidt and Udry, 2019; Brondízio et al., 2021). In this group were included "geraizeiros," "apanhadores de sempre-vivas," groups formed from the historical mixture between indigenous, black and European people, and "quilombolas" groups that originated from enslaved black people who resisted slavery (Monteiro, 2011; Dayrell, 2012; CPI-SP, 2021). It is important to emphasize that all groups share the behavioral patterns of small-scale societies, such as direct dependence on biological resources from a rural territory (Ploeg, 2009; Smith, 2012), and yet they have unique traditions passed down through generations (Almeida, 2004).

Management citations: Based on the information from the selected articles, we grouped the various citations of ways to manage ecosystems into categories, called management practices. Citations were considered: observations of management practices made by the researcher responsible for the article, and practices reported by small-scale societies to the researchers. Our grouping was based on the following criteria: 1) similarity among the citations, 2) result of the management practice, and 3) use or not of fire as a tool (**Supplementary Table S2**).

Target species: We list the target species for some types of management in the different ecosystems of the savannas. In this list we include information about the species, such as popular names, scientific name, life form and uses; and on indicators of patterns and processes of plant domestication, based on categories that already exist in the literature (Casas et al., 1997, 2017; Clement, 1999; Levis et al., 2018; Clement et al., 2021). We follow this categorization: 1) Patterns: genetic or phenotypic differences, occurrence of intraspecific diversity or evidence of pre-Columbian use; and 2) Processes: evidence of protection or tolerance, techniques to reduce competition, evidence of propagule dispersal, selection, cultivation, soil preparation, evidence of fire management.

Quantitative Analyses

To test whether the different ecosystems and cultural matrices are associated with management practices we used a chi-square test of independence. For this, we used the number of records in each category organized in a contingency table. The correlation between the predictor variables was also evaluated using the chi-square test for independence. All analyses were performed in the R (R Team Core, 2021) and p values ≤ 0.05 were considered significant.

RESULTS

Management Practices

We registered 147 citations of management practices distributed in the 10 categories summarized in **Supplementary Table S2** and presented in detail below:

Protection of the ecosystem—This involves avoiding actions that damage systems that are more sensitive to fire, especially dry season fires (Mistry et al., 2005; Welch, 2015; Figueira et al., 2016; Eloy et al., 2018a). This protection is done essentially without fire, by establishing firebreaks (Bilbao et al., 2010; Falleiro, 2011; Batista et al., 2018), and in some cases secured by collective agreements (Sletto and Rodriguez, 2013). The fires near these protected sites are closely monitored; if the flames approach they are put out with natural smothering devices, such as branches of native trees (Posey, 1985). Fire-protected sites are also considered areas rich in resources, such as fruits and animals, with high potential for gathering and hunting (Mistry et al., 2005). The practice of protecting the system as a whole can also be designed to protect some species and resources, such as water (Eloy et al., 2018a). In addition to protecting the resources present, certain sites are also protected from burning because they are considered sacred (Sletto and Rodriguez, 2013).

Enrichment of species—This consists of planting seeds and transplanting seedlings of species of human interest. It can extend to the creation of home gardens and forest islands, in which arboreal individuals are intentionally planted to enrich the vegetation of an area (Rostain, 2010; Pinho et al., 2011; Dayrell, 2012; Iriarte et al., 2012; Lombardo et al., 2020). This practice can also be characterized by the accidental dumping of food waste, such as seeds and fruits, by humans or non-humans (Lúcio et al., 2014). This practice does not use fire and creates resource-rich supporting points for living, hiking, and camping (Posey, 1985). These places are used by humans and species with some utility are protected and tolerated, making the area even more favorable (Posey, 1985).

Topographic changes—This consists in the movement of earth with the intention of creating elevated environments that do not suffer from the action of floods or sunken areas to store water. In this practice earth mounds are raised, often following structural and geometric patterns (Erickson, 2000). Fire is not used (Iriarte et al., 2012). Mounds often occur beside ditches and have complementary purposes, for example growing food on the mound and raising fish in the ditch (Posey, 1985; Iriarte et al., 2010; Rostain, 2010; Carson et al., 2014; Leal et al., 2019). Large mounds may have human settlements and even forest islands (Lombardo et al., 2013, Lombardo et al., 2020). After these changes in topography are established, other practices can be carried out in the same locations, such as system protection and/or species enrichment. These patterns are common among the peoples who inhabited South America before the arrival of Europeans and were discovered mainly through archaeological research.

Increased soil fertility—This consists in improving the nutritional characteristics of the soil of a certain place in the ecosystem, thus favoring plant species of human interest (Pinho et al., 2011). It often occurs through the creation of piles of organic matter, prepared from sticks, branches, and leaves, remains of termite mounds, and anthills (Posey, 1985; Rostain, 2010; Lombardo et al., 2020). This practice also involves the conservation of fertility in cultivated areas by covering the soil to avoid its exposure (Hernández-Hernández et al., 2011). In this practice, fire is not used.

Cleaning—This practice uses fire in a controlled manner with the intention of making the place safe and comfortable. It consists of removing part of the herbaceous layer, especially removing excess dry materials, as these make walking and hunting difficult (Bilbao et al., 2010; Sletto and Rodriguez, 2013; Carson et al., 2014). Not cleaning the place makes it dangerous, because it increases the chance of finding venomous animals, such as snakes and scorpions (Posey, 1985; Mistry et al., 2005). Thus, it is common to maintain clean sites near habitations There are no reports on when this practice is carried out.

Prevention—This strategy literally fights fire with fire. It is carried out in fire-dependent ecosystems adjacent to fire-sensitive ones; for this reason, it is directly linked to the practice of protection of the ecosystem (Bilbao et al., 2010; Sletto and Rodriguez, 2013; Eloy et al., 2018a, Eloy et al., 2018b). It is intended to reduce combustible material loads, which are responsible for large, out-of-control fires that commonly occur in the dry season (Mistry et al., 2005; Rodríguez, 2007; Falleiro, 2011; Melo and Saito, 2011; Welch et al., 2013; Lúcio et al., 2014; Batista et al., 2018). Prevention is done through controlled burning in the transition from the rainy to the dry season when the savannas and grasslands still have ideal amounts of moisture (Rodríguez, 2007; Melo and Saito, 2011; Batista et al., 2018). The records of this practice make it clear that it is necessary to understand the climatic conditions, such as the seasonality of rainfall and wind direction, so that the fires do not get out of control and turn into megafires.

Resource promotion—This practice has the purpose of maintaining the herbaceous vegetation with new leaves, promoting and accelerating regrowth. This renewal is mainly aimed at stimulating animal feed for wild and domestic species, because new leaves are more palatable (Rodríguez, 2007; Falleiro, 2011; Hernández-Hernández et al., 2011; Sampaio et al., 2012; Sletto and Rodriguez, 2013; Welch et al., 2013; Eloy et al., 2018a; Batista et al., 2018). It is done using controlled burning and, like the previous practice, is carried out in the transition from the rainy to the dry season. This practice goes beyond promoting the regrowth of important herbaceous species for livestock; it also stimulates flowering and fruiting in the following year of species of economic importance that are adapted to fire (Posey, 1985; Mistry et al., 2005; Falleiro, 2011; Schmidt et al., 2011; Monteiro et al., 2012; Schmidt and Ticktin, 2012; Figueira et al., 2016; Assunção et al., 2017; Eloy et al., 2018b).

Game driving—This practice uses controlled fire in order to drive hunted animals in a specific direction, thus facilitating slaughter in a desired location (Mistry et al., 2005; Bilbao et al., 2010; Melo and Saito, 2011; Welch et al., 2013; Figueira et al., 2016; Leal et al., 2019). This type of hunting is done collectively and is associated with indigenous ceremonies at the beginning of the dry season (Welch, 2015; Welch and Coimbra Jr, 2019).

Swidden-fallow—This practice involves the felling of vegetation and subsequent burning of the area (Rosa et al., 2018). The intention is to open areas for horticulture, known as slash-and-burn cultivation (Bilbao et al., 2010; Iriarte et al., 2012; Miller, 2016). It is part of a rotational system of shifting cultivation, in which prescribed burning occurs in small cleared areas, followed by a period of cultivation and harvest (Mistry et al., 2005; Rodríguez, 2007; Schmidt et al., 2011, 2018; Sampaio et al., 2012; Leal et al., 2019). After harvest, the fields go through a regeneration period (fallow) to recover soil nutrients and the pre-existing ecosystem (Kingsbury, 2003; Dayrell, 2012).

Maintenance of ecosystem structure—This consists of setting fire to fire-dependent ecosystems at the beginning of the dry season or the beginning of the rainy season in order to keep them open (Falleiro, 2011), preventing the proliferation of tree species (Rodríguez, 2007).

Ecosystem Use and Management

The management practices presented above are related to the types of ecosystems in which they are carried out ($x^2 = 71.5$; $p < 0.001$) (**Figure 2**). We observed 32 citations of management of forest ecosystems; there were no reports of prevention with fire, nor of fire for maintenance of ecosystem structure. Savanna ecosystems had 44 management citations, with no reports of increased soil fertility. The grassland ecosystems, on the other hand, had 71 management citations, with the only practice not reported being swidden-fallow.

The two most cited management practices for forests are complementary, since the first one prioritizes their protection to conserve resources (32.2%) and the second consists in using fire to open areas for swidden-fallow cultivation (32.2%). In addition to these practices, forests undergo management that favors characteristics considered important to humans, such as increasing the abundance of managed species (9.4%) and increasing soil fertility and changing topography (6.3% each). The other practices with fire were rarely mentioned in this type of ecosystem.

Forests had 25 cited uses, with transformation into food cultivation areas (56%) being the most significant. These are also used for gathering (28%) and non-fire hunting (12%). This type of ecosystem is used as a resting or security point, serving as a shelter in times of conflict, or even as a barrier to protect housing areas that are in more open formations (4%).

The savannah ecosystems had management citations focused mainly on management with fire to promote resources of both human and animal interest (25%), and with prescribed fire for wildfire prevention (20.5%). Fire in savannas is also used for hunting (9%) and to keep the physiognomies open (11.4%). The practices of swidden-fallow (15.9%) and protection against fire (11.4%) were cited mainly in one sub-class of savanna ecosystems, the swampy areas (*veredas*). The other management practices in the savannas were not mentioned or were rare.

The savannas had 56 reports of use. These areas are mainly used for gathering and hunting (32.1 and 23.2%, respectively). Savannah ecosystems are also used for cattle raising (16.1%), due to their abundant herbaceous stratum, and sporadically for housing construction (3.6%). The swamps are much sought after for cultivating food (16.1%) and provide drinking water for humans and domestic and wild animals, which makes it common to use them as water reservoirs (8.9%).

The most cited practice for managing grassland areas is promoting resources with fire (32.4%), followed by wildfire prevention (18.3%). Besides these, the other practices with fire were also expressive, cleaning (4.2%), game driving (7%) and maintaining the ecosystem (5.6%). The grasslands are also managed without burning, through species enrichment, topographic changes (11.3% each) and changes in soil fertility (8.5%). Other forms of management are rare or absent.

We recorded 73 citations of uses for the grasslands. These are mainly used for gathering and cattle raising (24.7% each). As open areas, they are used for hunting (16.4%) and are preferred sites for establishing camps and dwellings (11%). In addition to these uses, grasslands, especially humid ones, were used by pre-Columbian indigenous peoples for cultivation on raised fields without the use of fire (11%). Grasslands with rocky outcrops, a subclass of the category, are considered by some peoples as ritualistic sites (5.5%).

We recorded in our survey that these ecosystem management practices are carried out by 26 human groups, including 16 indigenous peoples, six local communities and four traditional communities (see **Supplementary Table S2**). We observed no correlation between the ecosystems and the cultural matrices recorded ($p = 0.24$), that is, all cultures manage forests, savannas and grasslands in some way.

These practices are also related to the cultural matrices that practice them ($x^2 = 36.2$; $p = 0.007$) (**Figure 3**). Five practices were recorded in all recorded human groups: protection of the ecosystem, enrichment of species, prevention, resource promotion, and swidden-fallow. The practices of topographic changes, increased soil fertility, and game driving with fire were cited only by indigenous peoples and local communities. In addition, two practices were recorded exclusively among indigenous peoples, using fire for cleaning and for maintaining open ecosystems.

Use, Management and Domestication of Plant Species

In addition to the ecosystem management practices, 81 citations were registered for management practices directed to 19 species of human interest. Eight species occur only in forest ecosystems and five in savannas; two occur in both environments. In grasslands only four species are the focus of some type of management, two of them are herbs from the most representative stratum of this ecosystem. Most of them are food resources (12), of which four were registered only for food and eight have complementary uses, three are used exclusively for folk medicine, three are used only for making handicrafts for self-consumption and for sale, and 1 is exploited as fuel and for ritualistic purposes (**Table 1**).

We observed that the different management practices that demonstrate the process of domestication of plant populations of human interest were cited in different proportions. The practice of protection by keeping individuals of different ages represented 24.7% of the citations and was reported for 9 species. Cultivation, which consists of planting seeds and seedlings, represented 19.8% of the reports and is carried out with 12 species, two of which reported the additional practice of improving soil structure and fertility. The tolerance strategy, which occurs when a species is not removed from the environment, accounted for 13.6% and is directed at 10 species. Transplanting seedlings or intentional seedling exchange accounted for 8.6% and targeted six species. This process can also occur unintentionally (8.6%) and occurs with seven species. Management using fire to encourage a certain resource, such as fruits or flowers, represented 8.6% of the citations and is aimed at five species. The practice of avoiding competition, which consists of removing useless plants to benefit species of human interest, represented 4.9% of the citations and is aimed at only three species. Selection of specific phenotypes of plants of interest by promoting morphological and/or genetic divergence from wild populations represented 3.7% of the citations and was reported

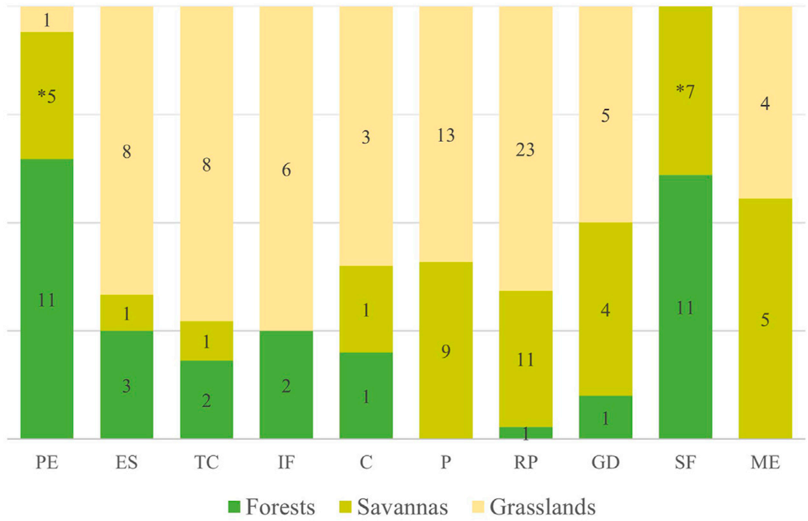

FIGURE 2 | Proportions and variation of management categories according to the ecosystem in which it occurs. The acronyms represent the different categories: protection of the ecosystem (PE), enrichment of species (ES), topographic changes (TC), increased soil fertility (IF), cleaning (C), prevention (P), resource promotion (RP), game driving (GD), swidden-fallow (SF), maintenance of ecosystem structure (ME). The values within the bars represent the number of citations in each ecosystem; and the asterisk represents that the practice is carried out in a subclass of savannas, swampy areas (veredas), with only one citation for typical savannas.

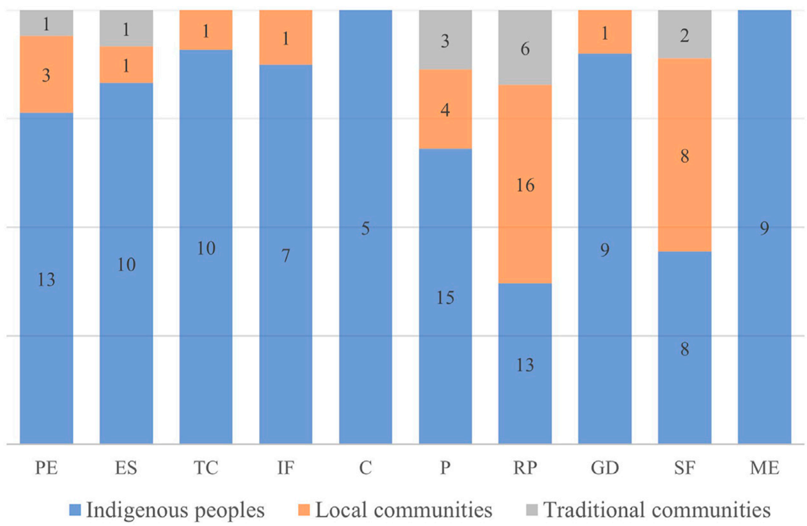

FIGURE 3 | Proportions and variation of management categories according to the culture that practices it. The acronyms represent the different categories: protection of the ecosystem (PE), enrichment of species (ES), topographic changes (TC), increased soil fertility (IF), cleaning (C), prevention (P), resource promotion (RP), game driving (GD), swidden-fallow (SF), maintenance of ecosystem structure (ME). The values within the bars represent the number of citations in each cultural matrix.

for three species. The strategy of attracting dispersers of plants of human interest was also recorded (3.7%) for three species. The practice of breaking seed dormancy to accelerate the germination process represented 1.2% of the citations and was recorded for only one specie.

Our review found, through nine citations, that only four species showed the expected patterns in plant populations with some degree of domestication: *Mauritia flexuosa*, *Caryocar brasiliense*, *Caryocar coriaceum* and *Dimorphandra gardneriana*. For the first three species, evidence of pre-Columbian use was recorded, and phenotypic differences only for the latter three.

DISCUSSION

Our review identified a diverse set of management practices carried out by small-scale societies that are co-responsible for

TABLE 1 | List of target species for management in South American savannas, including: scientific name and botanical family, accepted by Plants of the World Online; popular names; uses, the codes represent categories (F, food; AG, attracts game animals; AF, animal food; MN, manufacturing, tool making; CO, construction; ME, medicinal; RI, ritualistic; FU, fuel; HD, handicraft; RT, Roofing thatch); habit; ecosystem of occurrence; domestication patterns; management that indicates the domestication process; and references. Indicators of domestication follow the categories proposed by Casas et al. (1997, 2017), Clement (1999), and Levis et al. (2018).

Species	Family	Popular name	Uses	Habit	Ecosystem	Indicators of domestication		References
						Patterns	Processes	
Acrocomia aculeata (Jacq.) Lodd. ex R.Keith	Arecaceae	macaúba; mucajá	F	Palm	Forest	—	Unintended transplant; Tolerance	Pinho et al. (2011)
Alibertia edulis (Rich.) A.Rich.	Rubiaceae	marmelada-lisa	F; AG	Tree	Forest	—	Attraction of dispersers; Intentional transplant; Fire management; Cultivation	Posey, (1985)
Astrocaryum tucuma Mart.	Arecaceae	tucum	F	Palm	Forest	—	Unintended transplant; Fire management; Tolerance	Posey, (1985); Pinho et al. (2011)
Attalea butyracea (Mutis ex L.f.) Wess.Boer	Arecaceae	wine-palm	F; AF; MN; CO; ME; RI	Palm	Grassland	—	Protection; Cultivation	Bernal et al. (2010)
Byrsonima crassifolia (L.) Kunth	Malpighiaceae	murici	F	Tree	Forest	—	Attraction of dispersers; Intentional transplant; Unintended transplant; Fire management; Cultivation; Tolerance	Posey, (1985); Pinho et al. (2011)
Caryocar brasiliense A.St.-Hil.	Caryocaraceae	pequi	F; RI	Tree	Savanna	Phenotypic differences; Evidence of pre-Columbian use	Protection; Cultivation; Selection	Lopes et al. (2003); Azevedo et al. (2009); Smith and Fausto, (2016)
Caryocar coriaceum Wittm.	Caryocaraceae	pequi	F; ME; CO; FU; AF	Tree	Forest; Savanna	Phenotypic differences; Evidence of pre-Columbian use	Avoid competition; Protection; Dormancy break; Intentional transplant; Selection; Cultivation; Improving soil; Tolerance	Sousa Júnior et al. (2013), 2018; Silva et al. (2017)
Copernicia tectorum (Kunth) Mart.	Arecaceae	palma-sará	HD	Palm	Savanna	—	Avoid competition; Protection; Cultivation	Torres et al. (2016)
Dimorphandra gardneriana Tul.	Fabaceae	fava-d'anta; faveira	ME	Tree	Forest	Phenotypic differences	Avoid competition; Selection; Cultivation; Improving soil	Alcântara et al. (2020)
Genipa americana L.	Rubiaceae	genipapo	F; ME; RI	Tree	Forest	—	Unintended transplant; Tolerance	Pinho et al. (2011)
Guacamaya superba Maguire	Rapateaceae	flor-de-inírida	HD	Herb	Grassland	—	Protection	Fernández-Lucero et al. (2016)
Hancornia speciosa Gomes	Apocynaceae	mangaba	F; ME	Tree	Savanna	—	Intentional transplant; Cultivation; Tolerance	Pinho et al. (2011)
Himatanthus drasticus (Mart.) Plumel	Apocynaceae	janaguba	ME	Tree	Forest; Savanna	—	Protection; Intentional transplant; Cultivation	Baldauf and dos Santos, (2013), Baldauf and dos Santos, (2014); Baldauf et al. (2015)
Hymenaea courbaril L.	Fabaceae	jatobá	F; ME; CO	Tree	Forest	—	Unintended transplant; Tolerance	Silva et al. (2017)
Mauritia flexuosa L.f.	Arecaceae	buriti; moriche	F; AG; HD; RT; ME; MN	Palm	Savanna	Evidence of pre-Columbian use	Protection; Attraction of dispersers; Unintended transplant; Cultivation; Tolerance	Erickson, (2000); Sampaio et al. (2008); Sampaio et al. (2012); Pinho et al. (2011); Schmidt et al. (2011); Rull and Montoya, (2014)
Spondias mombin L.	Anacardiaceae	cajá; taperebá	F	Tree	Forest	—	Unintended transplant; Tolerance	Pinho et al. (2011)
Stryphnodendron rotundifolium Mart.	Fabaceae	barbatimão	ME	Tree	Savanna	—	Intentional transplant; Cultivation; Tolerance	Silva et al. (2017)
Syngonanthus nitens (Bong.) Ruhland	Eriocaulaceae	capim-dourado	HD	Herb	Grassland	—	Protection; Fire management; Cultivation	Schmidt et al. (2011); Schmidt and Ticktin, (2012); Eloy et al. (2018b)
Vellozia sincorana L.B.Sm. & Ayensu	Velloziaceae	candombá	FU; RI	Shrub	Grassland	—	Protection; Fire management	Souza et al. (2018)

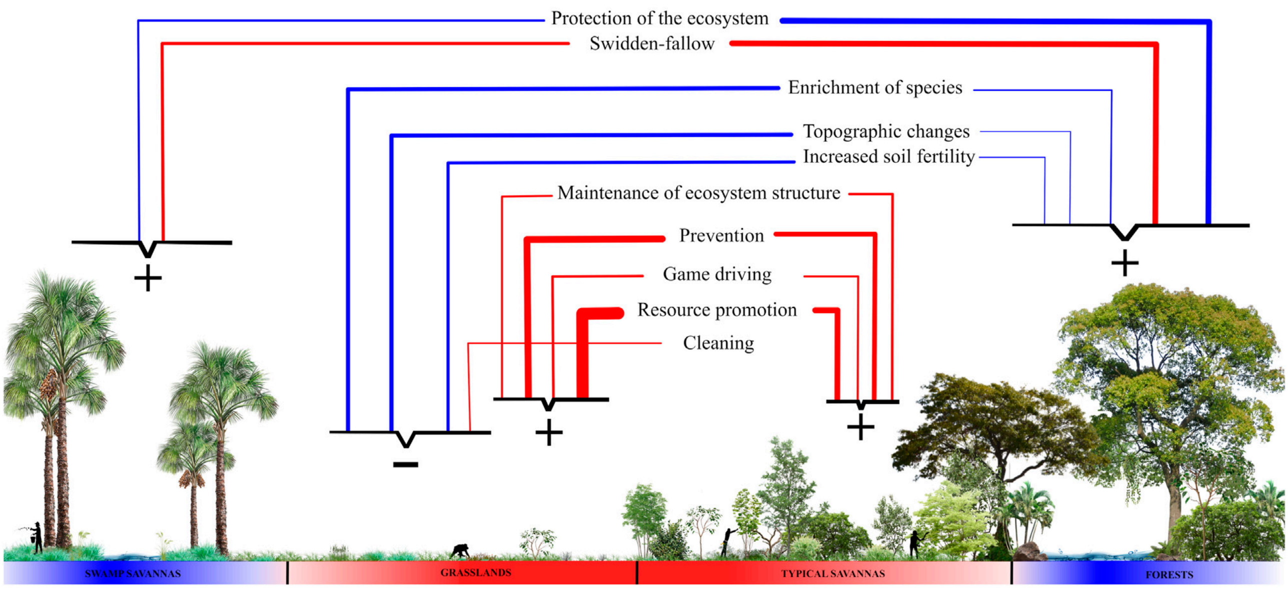

FIGURE 4 | Summary diagram of how the most expressive management practices are distributed and influence the following ecosystems: swamp savannas (veredas), grasslands, typical savannas, and forests. The direction of the lines indicates which ecosystem is the focus of each management practice, and the thickness of the lines the number of citations; those considered rare were excluded for having only one citation (see **Figure 2**). The colors of the lines indicate whether the practice uses fire (red) or not (blue). On the basis of the diagram, we categorize ecosystems according to the classification by Pivello et al. (2021), in blue the fire-sensitive and in red the fire-dependent. Each ecosystem is targeted by a subset of practices grouped by keys and the signs represent the influence that each subset exerts on the ecosystem: maintenance due to management (positive) or ecosystems altered by management (negative).

creating and maintaining the diversity of ecosystems of South American savannas; these practices vary with both environments and cultural matrices, corroborating our hypotheses. In addition, there is a set of native species that are being favored by human management. Thus, it is possible to affirm that these small-scale societies play a fundamental role not only in maintaining the savannas, but also in transforming them into more favorable environments for humans themselves.

Influence of Management on the Diversity of Ecosystems

Management practices were distributed heterogeneously, forming subsets by ecosystems, and these ecosystems tend to be influenced by these interventions in different ways (**Figure 4**). Protection of the ecosystem is a practice aimed at forest ecosystems and savanna swamps (*veredas*). This practice is also common among the Akan people of the Ghana savannas, where forests are protected because they are sacred and provide food, medicine, wood and other resources important for subsistence (Sarfo-Mensah and Oduro, 2007). Besides not allowing burning, another practice, the non-extraction of plants of human interest, is carried out to protect these ecosystems (Sarfo-Mensah and Oduro, 2007); in South American savannas this practice was also cited for six forest species, but we categorized it as protection and tolerance (**Table 1**). The protection of the ecosystem favors the structure and floristic composition, because fire significantly affects both in these environments (Pivello et al., 2021). Furthermore, when uncontrolled, fire in these ecosystems causes chemical and water stress in the soil, which drastically alters the amount of biomass, making these ecosystems more susceptible to megafires, which—when recurrent—convert forests into more open vegetation ecosystems (Dezzeo and Chacón, 2005). With this, we can affirm that the practice of protection maintains these fire-sensitive ecosystems, also known as "Fire refugia" (Meddens et al., 2018), and consequently conserves important ecological functions for the entire biome, because these sites help maintain trophic chains, act as a refuge for fauna, and function as a seed bank to repopulate burned areas (Meddens et al., 2018; Flores et al., 2021).

Complementary to protection, prevention is done in savanna and grassland ecosystems. It can reduce the accumulated fine fuel load, composed of leaves and thinner branches, alive or dead, of the herbaceous layer and from the lower part of the arboreal-shrub layer (Miranda, 2010). Fuel accumulation, together with extreme droughts and hot weather events, are responsible for the megafires (Fidelis et al., 2018), which are those with a large extension of burning, that are difficult to control, and that cause a negative impact on biodiversity (Fidelis et al., 2018). This practice has the consequence of maintaining structure and floristic composition because excluding fire permanently from the ecosystems dependent on it generates negative social and ecological consequences (Aslan et al., 2018; Pivello et al., 2021), which explains why protection management is rarely applied to them. Studies in Australian savannas show that this practice is common among small-scale tropical savanna societies and that, in addition to intentionally preventing large fires, it protects food resources of unburned ecosystems (Russell-Smith et al., 1997; Yibarbuk et al., 2001; Hill and Baird, 2003; Fletcher et al., 2020). The negative ecological consequences of fire exclusion are related to the breaking of the circular dynamics present in grasslands and savannas, which regulate the establishment of woody plants (Kauffman et al., 1994). This relationship occurs as follows: grassland ecosystems that contain fewer woody plants tend to have intense fires, which result in higher mortality of living tissue and consequently less chance for woody plants to establish themselves and remain structurally open; in savanna ecosystems that are woodier, fires tend to be mild, because they do not consume shrubs and trees completely, which consequently facilitates the persistence of these individuals, remaining structurally denser (Kauffman et al., 1994).

Fire-sensitive ecosystems are also sought after and preferred by savanna inhabitants for swidden-fallow; this practice was not reported in articles on grasslands and rarely in typical savannas. This can be explained by the fact that forests and swamp savannas (*veredas*) have wetter soils and higher levels of organic matter, important attributes for the soil's capacity to retain and exchange cations and keep the microbiota in balance, which consequently facilitates the establishment of plants of human interest (Reatto et al., 2008). Fire in these ecosystems is considered destructive (Pivello et al., 2021), but in this practice, it is used in a controlled manner on a small scale to remove the original vegetation before planting and to further improve soil characteristics through the ash that provides an initial nutritional increase of K and Ca (Kauffman et al., 1994). Another important point is that this practice involves the rotation of areas and long fallow periods, which makes it less aggressive to the soil, since it leads to the eventual reestablishment of the vegetation, creating a mosaic of heterogeneous areas in different regenerative stages, increasing diversity as a whole (Kingsbury, 2003; Adamou et al., 2007). This food production system is common throughout the Neotropics and in tropical savannas, and allows the soil to regain its fertility and native species to re-establish themselves (Sarfo-Mensah and Oduro, 2007; Clement et al., 2021); From then on, these recovering forests are protected again. We can affirm that this practice is favorable for the ecosystems in which it is carried out because even if it partially alters ecosystems in the short term, in the long term it allows for their recovery and favors species of human interest.

Species enrichment is mainly done in grasslands, occasionally mentioned in forests, and rarely in savannas. This practice was considered to alter the structure and floristic composition of the grasslands, because the establishment of woody species in these ecosystems can alter nutrient cycling, soil structure, biomass levels, and organic matter concentration, resulting in changes to the entire local microclimate (Scholes and Archer, 1997; Ayalew and Mulualem, 2018). Giles et al. (2021) evaluated the process of invasion of woody plants into grassland ecosystems used for grazing and proposed that a management approach to remove woody species would be ideal to conserve the characteristics of these ecosystems. We observe that the practice of enrichment with woody species is done in or near inhabited grasslands, that is, the intention here is not to maintain the grassland structure but to bring the environment closer to the forest structure rich in human interest resources and to create a milder microclimate around the dwellings. Similarly, there are records in the savannas of West Africa of non-forested areas being enriched with tree species to become forest patches because this type of ecosystem is considered the most important to the people who inhabit the region (Sarfo-Mensah and Oduro, 2007).

Two other practices done near dwellings are cleaning and increasing soil fertility, also recorded for the grassland ecosystems, the preferred areas to establish human habitation. Both change the structure of the grasslands, as the cleaning reduces competition between trees and herbs, favoring the trees, as it allows them to have more access to nutrients and water, and their roots reach deeper into the soil. (Scholes and Archer, 1997). The increase in fertility also favors the establishment of trees, because it reduces nutritional stress and allows their growth by providing greater nutritional support (Scholes and Archer, 1997). In the savannas of Western Sudan, small-scale farmers have developed similar practices aimed at increasing soil fertility, such as creating mounds of organic matter and fertilizing with home-grown organic residues, which allow for the support of arboreal individuals (Adamou et al., 2007).

The wet grasslands close to human dwellings also had more citations of alteration of topography, mainly by indigenous peoples before European colonization. These people significantly changed the shape and ecology of these grasslands, which made human population growth possible throughout the Holocene (Erickson, 2000; Rostain, 2010), but did not change their structure to the point of becoming forest or savanna ecosystems. Paleoenvironmental research has shown that the Holocene climate favored the expansion of forests, but human care meant that the grassland structure was maintained (Carson et al., 2014). Hence this practice was considered to maintain the structure of the grasslands. In addition, it was common in tropical savannas, as it occurred locally in the humid grasslands of the Amazonian savannas, the Beni Savannah, the Guianas savannas (Erickson, 2000; Iriarte et al., 2010, 2012; Rostain, 2010; Pinho et al., 2011; Carson et al., 2014; Leal et al., 2019; Rodrigues et al., 2020).

In our review, we observed that the most cited activities for grassland and savannah ecosystems are cattle raising and gathering, and the peoples of the South American savannas have developed management practices that differ from those proposed by Giles et al. (2021). Four practices are geared towards these ecosystems and make use of prescribed fire: prevention, resource promotion, game drives, and ecosystem maintenance. Fire, the central element of these practices, consumes the fine, flammable tissues of the grasses quickly enough to not kill them and the heat remains at the surface, which allows seeds and perennial parts to survive (Pivello et al., 2021). The mature shrub layer present in savannas is also able to recover because the accumulation of bark prevents the trunks from dying (Hoffmann et al., 2012). After the fire event, the herbaceous stratum, the focus of human interest in this case, quickly regrows and recovers its flammability, becoming susceptible to another fire event (Miranda, 2010). These practices with fire are commonly used recurrently (Schmidt et al., 2011; Schmidt et al., 2018; Monteiro et al., 2012; Sletto and Rodriguez, 2013), which ends up favoring that the dominance of the herbaceous layer over the arboreal, as the fire-sensitive woody trees, which could change the structure of these ecosystems, have no chance of establishing themselves, as they cannot thicken their bark before the next fire (Hoffmann et al., 2012).

Moreover, these fire practices are done in the transitions between the rainy and dry seasons. The time when a fire event occurs influences its intensity and is directly linked to the chances of it getting out of human control and reaching fire-sensitive ecosystems (Schmidt and Eloy, 2020). Fire at the end of the dry season, a period of low humidity, tends to be more aggressive and cause mortality of woody individuals more than fires at the beginning of the dry season, when management is done, because at this time the environments still contain moisture and occasional rainfall occurs, which makes the fire milder (Miranda, 2010). According to Ramos-Neto and Pivello (2000), fires in the rainy season are mainly caused by lightning and not by human action; this causes only small areas to be burned, as the rain that proceeds or follows the lightning does not allow the fire to spread over large areas. Furthermore, it is known that management practices that use fire in an organized and controlled manner are essential for open formations to continue to occur in tropical savannas (Russell-Smith et al., 1997; Hill and Baird, 2003; Roberts et al., 2021). Considering these factors, we can say that in general these four practices, prevention, resource promotion, game driving, and ecosystem maintenance, tend to maintain the grassland and savanna ecosystems used for cattle grazing and gathering.

The influence of the practices presented above allowed us to observe feedbacks between practice and result, an important dynamic for confirming the niche construction process (Baedke et al., 2021). In simplified form, we can affirm that fire-dependent ecosystems are managed mainly with fire and fire-sensitive ones are managed without it. Over time, this influenced the evolution of the ecosystems and consequently the evolution of the practices used by the small-scale societies of the South American savannas, making explicit the evolutionary feedback present in this process (Spengler, 2021).

Cultural Influence: Construction of Niches

In addition to management practices varying between ecosystems, our results also showed that the different cultural matrices of South America share only a few ways of managing these ecosystems (**Figure 3**). Two of these widely used practices are aimed at increasing the abundance of edible species: species enrichment and swidden-fallow. This can be explained by the fact that, in general, humans tend to optimize environments by increasing food resources, transforming them into domesticated landscapes (Clement, 1999; Hill and Baird, 2003; Terrell et al., 2003; Clement et al., 2021). Furthermore, of the 19 species managed *in-situ*, 12 are used for food; of these, 12 are cultivated or transplanted intentionally or not, and two are protected in their original ecosystems (**Table 1**). All these forms of management aimed at food acquisition corroborate the analysis of Smith (2011), who says that niche constructing humans create strategies to increase the abundance of food resources. While in the tropical savannas of South America we have found that enriching areas with plants of interest is common, this is not the case in the savannas of Nigeria where rural communities claim that the food trees of the forests are only planted by God, but should always be preserved (Olorunfemi et al., 2016). Swidden-fallow in turn is a system widely used for food production by small-scale societies in the Neotropics, but it is not the only one (Terrell et al., 2003; Clement et al., 2021). For example, in the Bolivian savannas, food production was done by indigenous people on raised fields without the use of fire (Iriarte et al., 2012). This system of topographic changes for cultivation without fire has also been recorded today in the savannas of Congo (Rodrigues et al., 2020).

Two other practices performed by all cultural matrices are resource promotion and prevention. Our review found no records of savanna or grassland patches created by humans, however, the practice of burning open environments is described by Laland and O'Brien (2010) as one of the most efficient ways of constructing niches by humans. Clark (1980) reported that in the early Holocene African savannas and grasslands were burned regularly and seasonally by hunters and gatherers, a practice that encouraged the growth of herbaceous plants and consequently maintained the structure of these ecosystem types. We, therefore, defend that these environments in South America occur naturally due to environmental factors and are perpetuated by anthropic action.

Complementarily, the practice of protecting forest ecosystems is also common to all the cultures sampled in our study, because these environments are rich in important resources for human survival. In parallel, we have observed that some forest patches in our survey were constructed by indigenous people through a combination of the following practices: increased soil fertility, topographic changes, followed by species enrichment. Research suggests that the extent of savannas is not entirely the result of human action, but the location and extent of ecotones, forests and grasslands, may have been determined by human actions in the past (Hammond, 1980). In the same sense, Casas et al. (1997) observed that forms of management aimed at wild plants *in situ* influence regeneration processes and may be responsible for the creation of anthropogenic forests. As observed by these authors, our review showed that ten species are managed in different ways in South American savanna forests (**Table 1**), which suggests that—even if they were not intentionally constructe—forests can be considered legacies of human management (Arroyo-Kalin, 2016), and are therefore protected due to their importance.

These common practices are widely spread across the continent and this can be explained by the fact that Neotropical savannas were connected in the past (Silva and Bates, 2002) and people were able to exchange information. The distribution of these practices among different human cultures is maintained today, and this may be related to the fact that humans, when successful niche constructors, inherit from their ancestors information about how to manage these environments, thus favoring more than one generation (Smith, 2011; Albuquerque et al., 2015; Coca et al., 2021). This makes explicit one of the principles of NCT, relocation, which affirms that practices can migrate with constructing organisms and be adopted by other populations when they meet in time and space (Davis and Douglass, 2021). Moreover, these common practices refute one of the current criticisms of NCT, because they are not merely singular human behaviors but behaviors that are regularly repeated at the population level (Spengler, 2021).

Together with these management practices aimed at ecosystems, we recorded the occurrence of practices aimed at 19 species important for humans (**Table 1**). Management practices aimed at plant populations may be responsible for altering landscapes as a whole, transforming them into domesticated landscapes (Casas et al., 1997; Clement, 1999; Terrell et al., 2003; Levis et al., 2018). This is because management practices favor these species in the environment, which can make them more abundant, and consequently the environments more favorable to humans (Smith, 2012). In conjunction with changes in the environment, population management can generate phenotypic and genetic changes, indicating the occurrence of a domestication process (Casas et al., 1997; Clement, 1999; Allaby et al., 2021; Clement et al., 2021). We observed that only four species present some component of the domestication syndrome (Meyer et al., 2012), but the other 16 managed species may be under-going domestication, even if in early stages (Terrell et al., 2003; Clement et al., 2021). All these plant populations are domesticated as components of the landscape and not separately (i.e., not necessarily in cultivation), because the domestication process is the result of interactions between cultural matrices and selection over time; this results in increased gene flow even with incipient changes in phenotypic traits (Rindos, 2013; Allaby et al., 2021). Clement et al. (2021) showed that 2,384 plant species are used in the Brazilian Cerrado and other Neotropical savannas and some may be undergoing domestication, but our review found a much smaller number. This may be related to our search methodology, as we included in our review only articles that detailed the forms of management and not those that only cited plants used by small-scale societies; we also did not search for information in databases like the cited authors. However, this restricted number indicates which species are in fact managed in the natural ecosystems of the South American savannas and which may be at different stages of the domestication process, thus being able to guide further studies on this theme.

Traditional Ecological Knowledge: a Tool for Conservation and Restoration

The extent and durability of human manipulations, and the diversity and specificity of management practices demonstrate extensive traditional knowledge about the ecological processes of the South American savannas. Small-scale societies have this knowledge due to the intimate relationship they have with their respective territories, a relationship marked by long periods of observation and use (Abraão et al., 2010; Smith, 2011; Silva et al., 2016).

The practice of fire management to keep these ecosystems open demonstrates traditional knowledge about the ecological processes of savanna succession. These peoples have a clear understanding that savanna and grassland areas left without human manipulation for even a short period can change due to the establishment of arboreal individuals, becoming denser (Pinheiro and Durigan, 2009; Santos et al., 2017). Another factor that seems well understood by small-scale societies is tree-herb interaction in the savannas, very relevant knowledge for restoration of degraded environments. According to Hoffmann et al. (2012), for forest seedlings to establish naturally in savanna ecosystems, long periods without fire are required and for saplings typical of savannas to establish themselves in forest ecosystems, prolonged droughts and intense fires are required. However, these authors point out that humans can induce changes in this process. Our survey confirmed this argument, as it showed that humans are actively transplanting species of interest between environments and subsequently caring for them to reach adulthood. Furthermore, we observed that there is protection of already established trees in both environments (**Table 1**), which proves that humans do indeed know how to influence the distribution dynamics of woody individuals.

Of the 10 management practices aimed at ecosystems, six of them have fire as a central element. Traditional knowledge of fire is extremely complex and involves a detailed understanding of several elements: seasons, effect of fire on fauna, rainfall seasonality, current legislation, moisture of combustible material, fire intensity, heat production, necessary intervals between fires, consequences of not burning, how to control fires, and plant phenology of each ecosystem (Huffman, 2013). This set of details makes it possible to say that fire management is reliable, but it is also dependent on extensive knowledge acquired over many generations.

Drastic changes in the planet's climate are a real problem to be mitigated (IPCC, 2021) and several studies have shown that high temperatures, extreme droughts and accumulation of combustible material are the main causes of the megafires that have been occurring more frequently in tropical savannas and that prescribed burning may be a feasible solution for this problem (Eloy et al., 2018a; Fidelis et al., 2018; Mistry et al., 2018; Schmidt et al., 2018; Moura et al., 2019; Schmidt and Eloy, 2020; Pivello et al., 2021; Roberts et al., 2021). Flores et al. (2021) stated that integrated management plans require strategies that consider forests as a vulnerable element of the system. The practices proposed by scientists are part of the strategies carried out by small-scale societies throughout the history of occupation of the South American savannas, but our results show that prevention and ecosystem protection do not maintain ecosystems on their own (**Figure 4**). This suggests to us that other practices need to be further analyzed and possibly included in these conservation and restoration strategies. When incorporating these niche-construction practices into conservation and restoration plans, it is important to keep in mind that they go beyond the momentary and have long-term ecological consequences, including evolutionary consequences (Albuquerque et al., 2019).

Concluding Remarks

Our review demonstrated that small-scale societies of South American savannas have a diverse set of management practices that contribute, along with environmental factors, to keeping savanna and grassland ecosystems open and to increase the occurrence of forest ecosystems in the mosaic of ecosystems, favoring human sustenance. These practices vary with the ecosystems in which they are used and with the different cultures that use them. They have also proven to be a very useful sources of information for restoration, conservation, and integrated management programs for these endangered ecosystems.

We found that the small-scale societies of the South American savannas are remarkable niche constructors, changing the selective pressures of the ecosystems and leaving important legacies for following generations. These ranged from very expressive and persistent constructions, such as anthropogenic forests or raised fields, to less visible footprints, such as 19 native species being domesticated *in situ* by diverse cultures, consequently making the landscapes more favorable for humans. We conclude, therefore, that South American savannas are domesticated landscapes because they are composed of a mosaic not only of natural ecosystems, but also of culturally constructed niches.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MF, GS, CC, and CL designed the study; MF and LC designed and executed the methodological part; MF collected and synthesized the data; MF and LC analyzed the data; MF wrote the manuscript and designed the graphics; CC, GS, and CL supervised the study; and all authors contributed to previous versions and approved the final one.

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SUPPLEMENTARY MATERIAL

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Abraão, M. B., Shepard, G. H., Nelson, B. W., Baniwa, J. C., Andrello, G., and Yu, D. W. (2010). "Baniwa Vegetation Classification in the white-sand Campinarana Habitat of the Northwest Amazon, Brazil," in *Landscape Ethnoecology: Concepts Of Biotic And Physical Space*. Editors L. M. Johnson and E. S. Hunn (New York, NY: Berghahn Books), 83–115.

Adamou, I., Pierre, N. J., Pogenet, P., Tchimbi, B., and Gonlaina, G. (2007). Soil Degradation in the Sudano-guinea Savannas of Mbe, Cameroon: Farmers' Perception, Indicators and Soil Fertility Management Strategies. *Res. J. Agric. Biol. Sci.* 3, 907–916.

Adeney, J. M., Christensen, N. L., Vicentini, A., and Cohn-Haft, M. (2016). White-sand Ecosystems in Amazonia. *Biotropica* 48, 7–23. doi:10.1111/btp.12293

Albuquerque, U. P., do Nascimento, A. L. B., da Silva Chaves, L., Feitosa, I. S., de Moura, J. M. B., Gonçalves, P. H. S., et al. (2019). A Brief Introduction to Niche Construction Theory for Ecologists and Conservationists. *Biol. Conservation* 237, 50–56. doi:10.1016/j.biocon.2019.06.018

Albuquerque, U. P., Júnior, W. S. F., Santoro, F. R., Torres-Avilez, W. M., and Júnior, J. R. S. (2015). "Niche Construction Theory and Ethnobiology," in *Evolutionary Ethnobiology*. Editors U. P. Albuquerque, P. M. De Medeiros, and A. Casas (Cham: Springer International Publishing), 73–87. doi:10.1007/978-3-319-19917-7_6

Allaby, R. G., Stevens, C. J., Kistler, L., and Fuller, D. Q. (2021). "Genetic Revelations of a New Paradigm of Plant Domestication as a Landscape Level Process," in *Plant Breeding Reviews*. Editor I. Goldman (Oxford, UK: John Wiley & Sons), 321–343. doi:10.1002/9781119828235.ch8

Almeida, A. W. B. d. (2004). Terras tradicionalmente ocupadas: processos de territorialização e movimentos sociais. *Rbeur* 6, 9–32. doi:10.22296/2317-1529.2004v6n1p9

Arroyo-Kalin, M. (2016). "Landscaping, Landscape Legacies, and Landesque Capital in Pre-columbian Amazonia," in *The Oxford Handbook of Historical Ecology and Applied Archaeology*. Editors C. Isendahl and D. Stump (Oxford University Press), 90–109. doi:10.1093/oxfordhb/9780199672691.013.16

Aslan, C. E., Samberg, L., Dickson, B. G., and Gray, M. E. (2018). Management Thresholds Stemming from Altered Fire Dynamics in Present-Day Arid and Semi-arid Environments. *J. Environ. Manage.* 227, 87–94. doi:10.1016/j.jenvman.2018.08.079

Assunção, R. de., Tetto, A. F., and Batista, A. C. (2017). O Uso Tradicional Do Fogo No Assentamento Vale Verde, Em Gurupi/TO. *Espacios* 38, 19–32.

Ayalew, S., and Mulualem, G. (2018). A Review on Bush Encroachment Effect on Cattle Rearing in Rangelands. *J. Rangel. Sci.* 8, 403–415.

Azevedo, A. I. d., Martins, H. T., and Drummond, J. A. L. (2009). A dinâmica institucional de uso comunitário dos produtos nativos Do cerrado no município de japonvar (Minas Gerais). *Soc. Estado.* 24, 193–228. doi:10.1590/s0102-69922009000100009

Baedke, J., Fábregas-Tejeda, A., and Prieto, G. I. (2021). Unknotting Reciprocal Causation Between Organism and Environment. *Biol. Philos.* 36, 1–29. doi:10.1007/s10539-021-09815-0

Baldauf, C., Corrêa, C. E., Ferreira, R. C., and dos Santos, F. A. M. (2015). Assessing the Effects of Natural and Anthropogenic Drivers on the Demography of

Himatanthus Drasticus (Apocynaceae): Implications for Sustainable Management. *For. Ecol. Manag.* 354, 177–184. doi:10.1016/j.foreco.2015.06.022
Baldauf, C., and Dos Santos, F. A. M. (2014). The Effect of Management Systems and Ecosystem Types on Bark Regeneration in Himatanthus Drasticus (Apocynaceae): Recommendations for Sustainable Harvesting. *Environ. Monit. Assess.* 186, 349–359. doi:10.1007/s10661-013-3378-x
Baldauf, C., and Maës dos Santos, F. A. (2013). Ethnobotany, Traditional Knowledge, and Diachronic Changes in Non-timber Forest Products Management: A Case Study of Himatanthus Drasticus (Apocynaceae) in the Brazilian Savanna1. *Econ. Bot.* 67, 110–120. doi:10.1007/s12231-013-9228-5
Balée, W. (2018). Brief Review of Historical Ecology. *Les Nouv. L'archéologie* 152, 1–11. doi:10.4000/nda.4150
Balée, W. (2006). The Research Program of Historical Ecology. *Annu. Rev. Anthropol.* 35, 75–98. doi:10.1146/annurev.anthro.35.081705.123231
Batista, E. K. L., Russell-Smith, J., França, H., and Figueira, J. E. C. (2018). An Evaluation of Contemporary savanna Fire Regimes in the Canastra National Park, Brazil: Outcomes of Fire Suppression Policies. *J. Environ. Manage.* 205, 40–49. doi:10.1016/j.jenvman.2017.09.053
Beerling, D. J., and Osborne, C. P. (2006). The Origin of the Savanna Biome. *Glob. Chang. Biol.* 12, 2023–2031. doi:10.1111/j.1365-2486.2006.01239.x
Bernal, R., Galeano, G., García, N., Olivares, I. L., and Cocomá, C. (2010). Uses and Commercial Prospects for the Wine Palm, Attalea Butyracea, in Colombia. *Ethnobot. Res. App.* 8, 255–268. doi:10.17348/era.8.0.255-268
Bilbao, B. A., Leal, A. V., and Méndez, C. L. (2010). Indigenous Use of Fire and Forest Loss in Canaima National Park, Venezuela. Assessment of and Tools for Alternative Strategies of Fire Management in Pemón Indigenous Lands. *Hum. Ecol.* 38, 663–673. doi:10.1007/s10745-010-9344-0
Bocanegra, F. J. A., and Mora, S. R. (2012). Del paleoindio al formativo: 10.000 años para la historia de la tecnología lítica en Colombia. *Boletín Antropol* 26, 124–156.
Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., et al. (2016). Ecological Consequences of Human Niche Construction: Examining Long-Term Anthropogenic Shaping of Global Species Distributions. *Proc. Natl. Acad. Sci. USA* 113, 6388–6396. doi:10.1073/pnas.1525200113
Brandão, C. R. (2012). "A Comunidade Tradicional," in *Cerrado, Gerais, Sertão: Comunidades Tradicionais Nos Sertões Roseanos*. Editors J. B. de. A. Costa and C. L. de Oliveira (São Paulo: Editora Intermeios), 367–380.
Brasil (1988). *Constituição da República Federativa do Brasil: texto constitucional promulgado em 5 de outubro de 1988, com as alterações determinadas pelas Emendas Constitucionais de Revisão nos 1 a 6/94, pelas Emendas Constitucionais nos 1/92 a 91/2016 e pelo Decreto*. Brasília, DF: Senado Federal: Centro Gráfico, 496.
Brondízio, E. S., Aumeeruddy-Thomas, Y., Bates, P., Carino, J., Fernández-Llamazares, Á., Ferrari, M. F., et al. (2021). Locally Based, Regionally Manifested, and Globally Relevant: Indigenous and Local Knowledge, Values, and Practices for Nature. *Annu. Rev. Environ. Resour.* 46, 481–509. doi:10.1146/annurev-environ-012220-012127
Bueno, L., and Dias, A. (2015). Povoamento inicial da América Do Sul: contribuições Do contexto brasileiro. *Estud. Av.* 29, 119–147. doi:10.1590/S0103-40142015000100007 10.1590/s0103-40142015000100009
Bueno, L., and Isnardis, A. (2018). Peopling central Brazilian Plateau at the Onset of the Holocene: Building Territorial Histories. *Quat. Int.* 473, 144–160. doi:10.1016/j.quaint.2018.01.006
Cardoso Da Silva, J. M., and Bates, J. M. (2002). Biogeographic Patterns and Conservation in the South American Cerrado: A Tropical Savanna Hotspot. *Bioscience* 52, 225–233. doi:10.1641/0006-3568(2002)052[0225:bpacit]2.0.co;2
Carson, J. F., Whitney, B. S., Mayle, F. E., Iriarte, J., Prumers, H., Soto, J. D., et al. (2014). Environmental Impact of Geometric Earthwork Construction in Pre-columbian Amazonia. *Proc. Natl. Acad. Sci.* 111, 10497–10502. doi:10.1073/pnas.1321770111
Casas, A., Caballero, J., Mapes, C., and Zárate, S. (1997). Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Bot. Sci.* 61, 31–47. doi:10.17129/botsci.1537
Casas, A., Torres-Guevara, J., and Parra-Rondinel-Rondinel, F. (2017). in *Domesticación en el continente americano*. Editors A. Casas, J. Torres-Guevara, and F. Parra-. Rondinel-Rondinel.
CEE (2018). Guidelines and Standards for Evidence Synthesis in Environmental Management. Version 5.0. AS Pullin GK Fram. B Livoreil G Petrokofsky. Available at: www.environmentalevidence.org/information-for-authors. Acessed in: 03/16/2021.
Clark, J. D. (1980). "Early Human Occupation of African savanna Enviroment," in *Human Ecology in savanna Enviroments*. Editor D. R. Harris (London: Academic Press), 41–71.
Clement, C. R. (1999). 1492 and the Loss of Amazonian Crop Genetic Resources. I. The Relation Between Domestication and Human Population Decline. *Econ. Bot.* 53, 188–202. doi:10.1007/BF02866498
Clement, C. R., Casas, A., Parra-Rondinel, F. A., Levis, C., Peroni, N., Hanazaki, N., et al. (2021). Disentangling Domestication from Food Production Systems in the Neotropics. *Quaternary* 4, 4–35. doi:10.3390/quat4010004
Coca, J. R., Soto, A., Mesquita, C., Lopes, R. P., and Cordero-Rivera, A. (2021). Biosociological Ethodiversity in the Social System. *BioSystems* 210, 104552. doi:10.1016/j.biosystems.2021.104552
Cole, M. M. (1986). in *The Savannas: Biogeography and Geobotany*. Editor M. M. Cole (London: Academic Press). Available at: https://www.jstor.org/stable/635398?origin=crossref.
Colombia (1997). *Constitución política Colombia 1991 (con reforma de 1997)*, 164.
Cooke, R. (1998). Human Settlement of Central America and Northernmost South America (14,000-8000Bp). *Quat. Int.* 49-50, 177–190. doi:10.1016/s1040-6182(97)00062-1
CPI-SP (2021). Direitos quilombolas. Comissào pr□-ךndio Sào Paulo. Available at: https://cpisp.org.br/direitosquilombolas/. Acessed: September 06, 2021.
Crumley, C. L. (2007). "Historical Ecology: Integrated Thinking at Multiple Temporal and Spatial Scales," in *The World System and the Earth System: Global Socioenvironmental Change and Sustainability since the Neolithic*. Editors A. Hornborg and C. L. Crumley (Abingdon: The Routledge), 1–13. doi:10.1017/CBO9781107415324.004
da Silva, T. C., Medeiros, M. F. T., Peroni, N., and Paulino Albuquerque, U. (2016). Folk Classification as Evidence of Transformed Landscapes and Adaptative Strategies: a Case Study in the Semiarid Region of Northeastern Brazil. *Landscape Res.* 42, 521–532. doi:10.1080/01426397.2016.1258047
Davis, D. S., and Douglass, K. (2021). Remote Sensing Reveals Lasting Legacies of Land-Use by Small-Scale Foraging Communities in the Southwestern Indian Ocean. *Front. Ecol. Evol.* 9, 689399. doi:10.3389/fevo.2021.689399
Dayrell, C. A. (2012). Agricultura geraizeira, identidade e educação. *Trab. Educ.* 21, 99–120.
de Alcântara, M. S., Duarte, A. E., Boligon, A. A., de Campos, M. M. A., de Lucena, R. F. P., Pinheiro, M. A., et al. (2020). Effects of Different Levels of Exploration on the Ecological Processes of Dimorphandra Gardneriana, a Tropical savanna Tree. *Environ. Monit. Assess.* 192, 1–15. doi:10.1007/s10661-020-08344-9
Denevan, W. M. (1966). *The Aboriginal Cultural Geography of the Llanos de Mojos of Bolivia*.
Dezzeo, N., and Chacón, N. (2005). Carbon and Nutrients Loos in Aboveground Biomass along a Fire Induced forest-savanna Gradient in the Gran Sabana, Southern Venezuela. *For. Ecol. Manag.* 209, 343–352. doi:10.1016/j.foreco.2005.02.008
Eidt, J. S., and Udry, C. (2019). *Sistemas Agrícolas Tradicionais No Brasil*. Editors J. S. Eidt and C. Udry Brasília. 1st ed. (Embrapa: DF).
Eiten, G. (1972). The Cerrado Vegetation of Brazil. *Bot. Rev.* 38, 201–341. doi:10.1007/bf02859158
Ellenberg, H., and Mueller-Dombois, D. (1967). Tentative Physiognomic-Ecological Classification of Plant Formations of the Earth. *Berichte Des Geobot. Institutes der Eidg. Techn.* 37, 21–55. doi:10.5169/seals-377650
Eloy, L., Bilbao, A. B., Schmidt, I. B., and Schmidt, I. B. (2018a). From Fire Suppression to Fire Management: Advances and Resistances to Changes in Fire Policy in the Savannas of Brazil and Venezuela. *Geogr. J.* 185, 10–22. doi:10.1111/geoj.12245
Eloy, L., Schmidt, I. B., Borges, S. L., Ferreira, M. C., and dos Santos, T. A. (2018b). Seasonal Fire Management by Traditional Cattle Ranchers Prevents the Spread of Wildfire in the Brazilian Cerrado. *Ambio* 48, 890–899. doi:10.1007/s13280-018-1118-8
Erickson, C. L. (2000). An Artificial Landscape-Scale Fishery in the Bolivian Amazon. *Nature* 408, 190–193. doi:10.1038/35041555

Erickson, C. L. (1995). "Archaeological Methods for the Study of Ancient Landscapes of the Llanos de Mojos in the Bolivian Amazon," in *Archaeology In the Lowland American Tropics: Current Analytical Methods And Applications*. Editor P. Stahl (Cambridge University Press), 66–95. doi:10.1017/cbo9780511521188.004

Eufemia, L., Morales, H., Bonatti, M., Graser, M., Lana, M., and Sieber, S. (2019). Collective Perception of Anthropic and Extractive Interventions in the Colombian Llanos. *Soc. Sci.* 8, 259–315. doi:10.3390/socsci8090259

Falleiro, R. D. M. (2011). Resgate Do manejo tradicional Do Cerrado com fogo para proteção das terras indígenas Do oeste Do Mato Grosso: um estudo de caso. *Biodiversidade Bras* 1, 86–96.

FAO (2000). *Recursos Florestais Mundiais: Termos e definições*, 21.

Fernandes, E. C. M., Oktingati, A., and Maghembe, J. (1984). The Chagga Homegardens: a Multistoried Agroforestry Cropping System on Mt. Kilimanjaro (Northern Tanzania). *Agroforest Syst.* 2, 73–86. doi:10.1007/BF00131267

Fernández-Lucero, M., Madriñán, S., and Campbell, L. M. (2016). Morphology and Anatomy ofGuacamaya superba(Rapateaceae) and Schoenocephalieae with Notes on the Natural History of theFlor de inírida. *Harv. Pap. Bot.* 21, 105–123. doi:10.3100/hpib.v21iss1.2016.n9

Fidelis, A., Alvarado, S., Barradas, A., and Pivello, V. (2018). The Year 2017: Megafires and Management in the Cerrado. *Fire* 1, 49–11. doi:10.3390/fire1030049

Figueira, J. E. C., Ribeiro, K. T., Ribeiro, M. C., Jacobi, C. M., França, H., de Oliveira Neves, A. C., et al. (2016). "Fire in Rupestrian Grasslands: Plant Response and Management," in *Ecology and Conservation of Mountaintop Grasslands in Brazil*. Editor G. W. Fernandes (Cham: Springer International Publishing), 415–448. doi:10.1007/978-3-319-29808-5_18

Filgueiras, T. S. (2002). "Herbaceous Plant Communities," in *The Cerrados of Brazil: Ecology and Natural History of a Neotropical savanna*. Editors P. S. Oliveira and R. J. Marquis (Columbia University Press), 121–139.

Fletcher, M.-S., Hall, T., and Alexandra, A. N. (2020). The Loss of an Indigenous Constructed Landscape Following British Invasion of Australia: An Insight into the Deep Human Imprint on the Australian Landscape. *Ambio* 50, 138–149. doi:10.1007/s13280-020-01339-3

Flores, B. M., Sá Dechoum, M., Schmidt, I. B., Hirota, M., Abrahão, A., Verona, L., et al. (2021). Tropical Riparian Forests in Danger from Large savanna Wildfires. *J. Appl. Ecol.* 58, 419–430. doi:10.1111/1365-2664.13794

Gassón, R. A. (2002). Orinoquia: The Archaeology of the Orinoco. *J. World Prehistory* 16, 237–311. doi:10.1023/a:1020978518142

Giles, A. L., Flores, B. M., Rezende, A. A., Weiser, V. d. L., and Cavassan, O. (2021). Thirty Years of clear-cutting Maintain Diversity and Functional Composition of Woody-Encroached Neotropical Savannas. *For. Ecol. Manag.* 494, 119356. doi:10.1016/j.foreco.2021.119356

Hammond, N. (1980). "Prehistoric Human Utilization of the savanna Enviroments of Middle and South America," in *Human Ecology in savanna Enviroments*. Editor D. R. Harris (London: Academic Press), 73–105.

Harris, D. R., and Hillman, G. C. (2014). *Foraging and Farming - the Evolution of Plant Exploitation*. Editors D. R. . Harris and G. C. Hillman (London: Routledge).

Hecht, S. B. (2017). "Domestication, Domesticated Landscapes, and Tropical Nature," in *The Routledge Companion to the Environmental Humanities*. Editors U. K. Heise, J. Christensen, and M. Niemann (Abingdon: The Routledge), 23–36.

Hernández-Hernández, R. M., Morros, M. E., Medina, C. A. B., Pérez, Z. L., Díaz, P. E. H., Hernández, A. O., et al. (2011). The Integration of Local and Scientific Knowledge in the Sustainable Management of Soils in savanna Agroecosystems. *Interciencia* 36, 104–112.

Hill, R., and Baird, A. (2003). Kuku-Yalanji Rainforest Aboriginal People and Carbohydrate Resource Management in the Wet Tropics of Queensland, Australia. *Hum. Ecol.* 31, 27–52. doi:10.1023/A:1022830123349

Hirota, M., Holmgren, M., Van Nes, E. H., and Scheffer, M. (2011). Global Resilience of Tropical forest and savanna to Critical Transitions. *Science* 334, 232–235. doi:10.1126/science.1210657

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O. L., et al. (2012). Ecological Thresholds at the savanna-forest Boundary: How Plant Traits, Resources and Fire Govern the Distribution of Tropical Biomes. *Ecol. Lett.* 15, 759–768. doi:10.1111/j.1461-0248.2012.01789.x

Huber, O. (1987). Neotropical Savannas: Their flora and Vegetation. *Trends Ecol. Evol.* 2, 67–71. doi:10.1016/0169-5347(87)90151-0

Huebert, J. M., and Allen, M. S. (2020). Anthropogenic Forests, Arboriculture, and Niche Construction in the Marquesas Islands (Polynesia). *J. Anthropological Archaeology* 57, 101122. doi:10.1016/j.jaa.2019.101122

Huffman, M. R. (2013). The many Elements of Traditional Fire Knowledge: Synthesis, Classification, and Aids to Cross-Cultural Problem Solving in Fire-dependent Systems Around the World. *E&S* 18, 3. doi:10.5751/ES-05843-180403

IBGE (2012). *Manual técnico da vegetação brasileira*. second. , ed. I. B. de G and e. E. IBGE Rio de Janeiro.

ILO (1989). Indigenous and Tribal Peoples Convention. *The Foundations Mod. Int. L. Indigenous Tribal Peoples* 1989 (No. 169), 12. doi:10.1163/9789004289062_010

Iriarte, J., Glaser, B., Watling, J., Wainwright, A., Birk, J. J., Renard, D., et al. (2010). Late Holocene Neotropical Agricultural Landscapes: Phytolith and Stable Carbon Isotope Analysis of Raised fields from French Guianan Coastal Savannahs. *J. Archaeological Sci.* 37, 2984–2994. doi:10.1016/j.jas.2010.06.016

Iriarte, J., Power, M. J., Rostain, S., Mayle, F. E., Jones, H., Watling, J., et al. (2012). Fire-free Land Use in Pre-1492 Amazonian Savannas. *Proc. Natl. Acad. Sci.* 109, 6473–6478. doi:10.1073/pnas.1201461109

ISA (2005). Povos Indigenas No Brasil: Quem São? Available at: https://pib.socioambiental.org/pt/Quem_são Acessed in: 06/09/2021.

Kauffman, J. B., Cummings, D. L., and Ward, D. E. (1994). Relationships of Fire, Biomass and Nutrient Dynamics along a Vegetation Gradient in the Brazilian Cerrado. *J. Ecol.* 82, 519–531. doi:10.2307/2261261

Keeley, J. E., and Rundel, P. W. (2005). Fire and the Miocene Expansion of C4 Grasslands. *Ecol. Lett.* 8, 683–690. doi:10.1111/j.1461-0248.2005.00767.x

Kingsbury, N. D. (2003). Same Forest, Different Countries. *J. Sust. For.* 17, 171–188. doi:10.1300/J091v17n01_10

Klink, C. a., and Machado, R. B. (2005). A Conservação Do Cerrado Brasileiro. *Megadiversidade* 1, 147–155. doi:10.1590/S0100-69912009000400001

Kottek, M., Grieser, J., Beck, C., Rudolf, B., and Rubel, F. (2006). World Map of the Köppen-Geiger Climate Classification Updated. *metz* 15, 259–263. doi:10.1127/0941-2948/2006/0130

Laland, K., Matthews, B., and Feldman, M. W. (2016). An Introduction to Niche Construction Theory. *Evol. Ecol.* 30, 191–202. doi:10.1007/s10682-016-9821-z

Laland, K. N., and O'Brien, M. J. (2010). Niche Construction Theory and Archaeology. *J. Archaeol. Method Theor.* 17, 303–322. doi:10.1007/s10816-010-9096-6

Leal, A., Gassón, R., Behling, H., and Sánchez, F. (2019). Human-made Fires and forest Clearance as Evidence for Late Holocene Landscape Domestication in the Orinoco Llanos (Venezuela). *Veget Hist. Archaeobot* 28, 545–557. doi:10.1007/s00334-019-00713-w

Levis, C., Flores, B. M., Moreira, P. A., Luize, B. G., Alves, R. P., Franco-Moraes, J., et al. (2018). How People Domesticated Amazonian Forests. *Front. Ecol. Evol.* 5, 1–21. doi:10.3389/fevo.2017.00171

Lombardo, U., Denier, S., May, J.-H., Rodrigues, L., and Veit, H. (2013). Human-environment Interactions in pre-Columbian Amazonia: The Case of the Llanos de Moxos, Bolivia. *Quat. Int.* 312, 109–119. doi:10.1016/j.quaint.2013.01.007

Lombardo, U., Iriarte, J., Hilbert, L., Ruiz-Pérez, J., Capriles, J. M., and Veit, H. (2020). Early Holocene Crop Cultivation and Landscape Modification in Amazonia. *Nature* 581, 190–193. doi:10.1038/s41586-020-2162-7

Lopes, P. S. N., Souza, J. C. d., de, Reis, P. R., Reis, J. M., and Rocha, I. D. F. (2003). Caracterização Do ataque da broca dos frutos Do pequizeiro. *Rev. Bras. Frutic.* 25, 540–543. doi:10.1590/s0100-29452003000300046

Lúcio, S. L. B., Pereira, L. E. C., and Ludewigs, T. (2014). O Gado que circulava : Desafios da gestão participativa e impactos da proibição Do uso Do fogo aos criadores de gado de solta da Reserva de Desenvolvimento Sustentável Veredas Do Acari. *Biodiversidade Bras* 4, 130–155.

Matthews, B., De Meester, L., Jones, C. G., Ibelings, B. W., Bouma, T. J., Nuutinen, V., et al. (2014). Under Niche Construction: An Operational Bridge between Ecology, Evolution, and Ecosystem Science. *Ecol. Monogr.* 84, 245–263. doi:10.1890/13-0953.1

Mayle, F. E., Beerling, D. J., Gosling, W. D., and Bush, M. B. (2004). Responses of Amazonian Ecosystems to Climatic and Atmospheric Carbon Dioxide Changes since the Last Glacial Maximum. *Phil. Trans. R. Soc. Lond. B* 359, 499–514. doi:10.1098/rstb.2003.1434

Meddens, A. J. H., Kolden, C. A., Lutz, J. A., Smith, A. M. S., Cansler, C. A., Abatzoglou, J. T., et al. (2018). Fire Refugia: What Are They, and Why Do They Matter for Global Change? *Bioscience* 68, 944–954. doi:10.1093/biosci/biy103

Meggers, B. J. (2001). The Continuing Quest for El Dorado: Round Two. *Latin Am. Antiq.* 12, 304–325. doi:10.2307/971635

Melo, M. M. De., and Saito, C. H. (2011). Regime de queima das caçadas com uso Do fogo realizadas pelos Xavante no Cerrado. *Biodiversidade Bras* 1, 97–109.

Meyer, R. S., Duval, A. E., and Jensen, H. R. (2012). Patterns and Processes in Crop Domestication: An Historical Review and Quantitative Analysis of 203 Global Food Crops. *New Phytol.* 196, 29–48. doi:10.1111/j.1469-8137.2012.04253.x

Miller, T. L. (2016). Living Lists: How the Indigenous Canela Come to Know Plants through Ethnobotanical Classification. *J. Ethnobiol.* 36, 105–124. doi:10.2993/0278-0771-36.1.105

Miranda, H. S. (2010). "Efeitos Do regime Do fogo sobre a estrutura de comunidades de cerrado: Resultados Do Projeto Fogo," in *DF: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis*. Editor H. S. Miranda Brasília.

Mistry, J., Berardi, A., Andrade, V., Krahô, T., Krahô, P., and Leonardos, O. (2005). Indigenous Fire Management in the Cerrado of Brazil: The Case of the Krahô of Tocantíns. *Hum. Ecol.* 33, 365–386. doi:10.1007/s10745-005-4143-8

Mistry, J., Schmidt, I. B., Eloy, L., and Bilbao, B. (2018). New Perspectives in Fire Management in South American Savannas: The Importance of Intercultural Governance. *Ambio* 48, 172–179. doi:10.1007/s13280-018-1054-7

Monteiro, F. T. (2011). *Os (as) apanhadores(as) de flores e o parque nacional das sempre-vivas (MG): Travessias e contradições ambientais*, 241.

Monteiro, F. T., Pereira, D. B., and Del Gaudio, R. S. (2012). Os(as) apanhadores(as) de flores e o Parque Nacional das Sempre-Vivas: entre ideologias e territorialidades. *Soc. Nat.* 24, 419–433. doi:10.1590/s1982-45132012000300004

Morey, N. C. (1976). Ethnohistorical Evidence for Cultural Complexity in the Western Llanos of Venezuela and the Eastern Llanos of Colombia. *Antropologica* 45, 41–69.

Moura, L. C., Scariot, A. O., Schmidt, I. B., Beatty, R., and Russell-Smith, J. (2019). The Legacy of Colonial Fire Management Policies on Traditional Livelihoods and Ecological Sustainability in Savannas: Impacts, Consequences, New Directions. *J. Environ. Manage.* 232, 600–606. doi:10.1016/j.jenvman.2018.11.057

O'Dea, R. E., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., et al. (2021). Preferred Reporting Items for Systematic Reviews and Meta-analyses in Ecology and Evolutionary Biology: a PRISMA Extension. *Biol. Rev.* 96, 1695–1722. doi:10.1111/brv.12721

Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W., and Laland, K. N. (2013). Niche Construction Theory: A Practical Guide for Ecologists. *Q. Rev. Biol.* 88, 3–28. doi:10.1086/669266

Oliveira-Filho, A. T. (2009). Classificação das fitofisionomias da América Do Sul cisandina tropical e subtropical: proposta de um novo sistema - prático e flexível - ou uma injeção a mais de caos? *Rodriguésia* 60, 237–258. doi:10.1590/2175-7860200960201

Oliveira-Filho, A. T., and Ratter, J. A. (2002). "Vegetation Physiognomies and Woody flora of the Cerrado Biome," in *The Cerrados of Brazil: Ecology and Natural History of a Neotropical savanna*. Editors P. S. Oliveira and R. J. Marquis (Columbia University Press New), 91–120.

Olorunfemi, F., Fasona, M., Oloukoi, G., Elias, P., and Adedayo, V. (2016). Traditional Knowledge in the Use and Management of forest Ecosystem for Livelihoods and Food Security in Nigerian Savanna. *J. Hum. Ecol.* 53, 167–175. doi:10.1080/09709274.2016.11906969

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience* 51, 933–938. doi:10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2

ONF (2017). *Occupation du sol en 2015 sur la bande littorale de la Guyane et son évolution entre 2005 et 2015, 92*. Paris: Ministère de L'agriculture et de l'alimentation.

Orians, G. H. (1980). "Habitat Selection: General Theory and Applications to Human Behavior," in *The Evolution of Human Social Behavior*. Editor J. S. Lockard (Elsevier/North Holland), 49–66.

Pinheiro, E. D. S., and Durigan, G. (2009). Dinâmica espaço-temporal (1962-2006) das fitofisionomias em unidade de conservação Do Cerrado no sudeste Do Brasil. *Rev. Bras. Bot.* 32, 441–454. doi:10.1590/s0100-84042009000300005

Pinho, R. C., Alfaia, S. S., Miller, R. P., Uguen, K., Magalhães, L. D., Ayres, M., et al. (2011). Islands of Fertility: Soil Improvement Under Indigenous Homegardens in the Savannas of Roraima, Brazil. *Agroforest Syst.* 81, 235–247. doi:10.1007/s10457-010-9336-5

Pivello, V. R., Vieira, I., Christianini, A. V., Ribeiro, D. B., da Silva Menezes, L., Berlinck, C. N., et al. (2021). Understanding Brazil's Catastrophic Fires: Causes, Consequences and Policy Needed to Prevent Future Tragedies. *Perspect. Ecol. Conservation* 19, 233–255. doi:10.1016/j.pecon.2021.06.005

Ploeg, J. (2009). "Sete teses sobre a agricultura camponesa," in *Agricultura Familiar Camponesa Na Construção Do Futuro*. Editor P. Petersen (Rio de Janeiro: AS-PTA), 17–32.

Posey, D. A. (1985). Indigenous Management of Tropical forest Ecosystems: the Case of the Kayapó Indians of the Brazilian Amazon. *Agroforest Syst.* 3, 139–158. doi:10.1007/BF00122640

R Team Core (2021). R: A Language and Environment for Statistical Computing. Available at: https://www.r-project.org/.

Ramos-Neto, M. B., and Pivello, V. R. (2000). Lightning Fires in a Brazilian savanna national park: Rethinking Management Strategies. *Environ. Manage.* 26, 675–684. doi:10.1007/s002670010124

Reatto, A., Correia, J. R., Spera, S. T., and Martins, É. de. S. (2008). "Solos Do Bioma Cerrado: Aspectos Pedólogicos," in *Cerrado: Ecologia e flora*. Editor S. M. Sano (Brasília, DF: Embrapa Informação Tecnológica), 107–150.

Ribeiro, J. F., and Walter, B. M. T. (2008). "As Principais Fitofisionomias Do Bioma Cerrado," in *" in* Cerrado: Ecologia e flora. Editors S. M. Sano, S. P. de Almeida, and J. F. Ribeiro, 152–212.

Ribeiro, J. F., and Walter, B. M. T. (1998). "Fitofisionomias Do Bioma Cerrado," in *Cerrado: Ambiente e flora*. Editors S. M. Sano and S. P. de Almeida (Brasília, DF: Embrapa CPAC), 89–166.

Rindos, D. (2013). *The Origins of Agriculture: An Evolutionary Perspective*. San Diego: Academic Press.

Roberts, P., Buhrich, A., Caetano-Andrade, V., Cosgrove, R., Fairbairn, A., Florin, S. A., et al. (2021). Reimagining the Relationship between Gondwanan Forests and Aboriginal Land Management in Australia's "Wet Tropics". *iScience* 24, 102190. doi:10.1016/j.isci.2021.102190

Roberts, P. (2019). *Tropical Forests in Prehistory, History, and Modernity*. Oxford, UK: Oxford University Press.

Rodrigues, L., Sprafke, T., Bokatola Moyikola, C., Barthès, B. G., Bertrand, I., Comptour, M., et al. (2020). A Congo Basin Ethnographic Analogue of Pre-columbian Amazonian Raised fields Shows the Ephemeral Legacy of Organic Matter Management. *Sci. Rep.* 10, 10851. doi:10.1038/s41598-020-67467-8

Rodríguez, I. (2007). Pemon Perspectives of Fire Management in Canaima National Park, Southeastern Venezuela. *Hum. Ecol.* 35, 331–343. doi:10.1007/s10745-006-9064-7

Rosa, R. dos. S., Almeida, S. A. de., Araujo, A. C. de., and Moura, A. A. (2018). A agricultura tradicional na comunidade Kalunga Vão de Almas: Um estudo de caso. *Facit Bus. Technol. J.* 5, 121–141.

Rostain, S. (2008). "Agricultural Earthworks on the French Guiana Coast," in *"Agricultural Earthworks on the French Guiana Coast," in* Handbook Of South American Archaeology. Editors H. Silverman and W. Isbell (New York, NY: Springer), 217–233. doi:10.1007/978-0-387-74907-5_13

Rostain, S. (2010). Pre-Columbian Earthworks in Coastal Amazonia. *Diversity* 2, 331–352. doi:10.3390/d2030331

Rull, V., and Montoya, E. (2014). Mauritia Flexuosa palm Swamp Communities: Natural or Human-Made? A Palynological Study of the Gran Sabana Region (Northern South America) within a Neotropical Context. *Quat. Sci. Rev.* 99, 17–33. doi:10.1016/j.quascirev.2014.06.007

Russell-Smith, J., Lucas, D., Gapindi, M., Gunbunuka, B., Kapirigi, N., Namingum, G., et al. (1997). Aboriginal Resource Utilization and Fire Management Practice in Western Arnhem Land, Monsoonal Northern Australia: Notes for Prehistory, Lessons for the Future. *Hum. Ecol.* 25, 159–195. doi:10.1023/A:1021970021670

IPCC (2021). in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Editors B. Z. Masson-Delmotte, C. Péan, S. Berger, P. Zhai,

A. Pirani, S. L. Connors, et al. (Cambridge University Press). In Press. doi:10.1080/03736245.2010.480842
Sampaio, M. B., Schmidt, I. B., and Figueiredo, I. B. (2008). Harvesting Effects and Population Ecology of the Buriti Palm (Mauritia Flexuosa L. f., Arecaceae) in the Jalapão Region, Central Brazil1. *Econ. Bot.* 62, 171–181. doi:10.1007/s12231-008-9017-8
Sampaio, M. B., Ticktin, T., Seixas, C. S., and dos Santos, F. A. M. (2012). Effects of Socioeconomic Conditions on Multiple Uses of Swamp Forests in central Brazil. *Hum. Ecol.* 40, 821–831. doi:10.1007/s10745-012-9519-y
Santos, G. L. d., Pereira, M. G., Delgado, R. C., and Torres, J. L. R. (2017). Natural Regeneration in Anthropogenic Environments Due to Agricultural Use in the Cerrado, Uberaba, MG, Brazil. *Biosci. J.* 33, 169–176. doi:10.14393/BJ-v33n1a2017-35036
Sarfo-Mensah, P., and Oduro, W. (20072007). Traditional Natural Resources Management Practices and Biodiversity Conservation in Ghana: A Review of Local Concepts and Issues on Change and Sustainability. *SSRN J.* 90, 1–19. doi:10.2139/ssrn.1017238
Schmidt, I. B., and Eloy, L. (2020). Fire Regime in the Brazilian Savanna: Recent Changes, Policy and Management. *Flora* 268, 151613. doi:10.1016/j.flora.2020.151613
Schmidt, I. B., Moura, L. C., Ferreira, M. C., Eloy, L., Sampaio, A. B., Dias, P. A., et al. (2018). Fire Management in the Brazilian Savanna: First Steps and the Way Forward. *J. Appl. Ecol.* 55, 2094–2101. doi:10.1111/1365-2664.13118
Schmidt, I. B., Sampaio, M. B., Figueiredo, I. B., and Ticktin, T. (2011). Fogo e artesanato de Capim-dourado no Jalapão – Usos tradicionais e consequências ecológicas. *Biodiversidade Bras* 1, 67–85.
Schmidt, I. B., and Ticktin, T. (2012). When Lessons from Population Models and Local Ecological Knowledge Coincide - Effects of Flower Stalk Harvesting in the Brazilian savanna. *Biol. Conservation* 152, 187–195. doi:10.1016/j.biocon.2012.03.018
Scholes, R. J., and Archer, S. R. (1997). Tree-grass Interactions in Savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544. doi:10.1146/annurev.ecolsys.28.1.517
Silva, L. C. R., Hoffmann, W. A., Rossatto, D. R., Haridasan, M., Franco, A. C., and Horwath, W. R. (2013). Can Savannas Become Forests? A Coupled Analysis of Nutrient Stocks and Fire Thresholds in central Brazil. *Plant Soil* 373, 829–842. doi:10.1007/s11104-013-1822-x
Silva, T. C. d., Campos, L. Z. d. O., Balée, W., Medeiros, M. F. T., Peroni, N., and Albuquerque, U. P. (2017). Human Impact on the Abundance of Useful Species in a Protected Area of the Brazilian Cerrado by People Perception and Biological Data. *Landscape Res.* 44, 75–87. doi:10.1080/01426397.2017.1396304
Sletto, B., and Rodriguez, I. (2013). Burning, Fire Prevention and Landscape Productions Among the Pemon, Gran Sabana, Venezuela: Toward an Intercultural Approach to Wildland Fire Management in Neotropical Savannas. *J. Environ. Manage.* 115, 155–166. doi:10.1016/j.jenvman.2012.10.041
Smith, B. D. (2012). A Cultural Niche Construction Theory of Initial Domestication. *Biol. Theor.* 6, 260–271. doi:10.1007/s13752-012-0028-4
Smith, B. D. (2011). General Patterns of Niche Construction and the Management of 'wild' Plant and Animal Resources by Small-Scale Pre-industrial Societies. *Phil. Trans. R. Soc. B* 366, 836–848. doi:10.1098/rstb.2010.0253
Smith, M., and Fausto, C. (2016). Socialidade e diversidade de pequis (Caryocar brasiliense, Caryocaraceae) entre os Kuikuro Do alto rio Xingu (Brasil). *Bol. Mus. Para. Emílio Goeldi. Ciênc. Hum.* 11, 87–113. doi:10.1590/1981.81222016000100006
Sousa Júnior, J. R., Albuquerque, U. P., and Peroni, N. (2013). Traditional Knowledge and Management of Caryocar Coriaceum Wittm. (Pequi) in the Brazilian Savanna, Northeastern Brazil1. *Econ. Bot.* 67, 225–233. doi:10.1007/s12231-013-9241-8
Sousa Júnior, J. R., Collevatti, R. G., Lins Neto, E. M. F., Peroni, N., and Albuquerque, U. P. (2018). Traditional Management Affects the Phenotypic Diversity of Fruits with Economic and Cultural Importance in the Brazilian Savanna. *Agroforest Syst.* 92, 11–21. doi:10.1007/s10457-016-0005-1
Souza, J. M., Schmidt, I. B., and Conceição, A. A. (2018). How Do Fire and Harvesting Affect the Population Dynamics of a Dominant Endemic Velloziaceae Species in campo Rupestre? *Flora* 238, 225–233. doi:10.1016/j.flora.2017.02.007
Spengler, R. N. (2021). Niche Construction Theory in Archaeology: A Critical Review. *J. Archaeol. Method Theor.* 28, 925–955. doi:10.1007/s10816-021-09528-4
Staver, A. C., Archibald, S., and Levin, S. A. (2011). The Global Extent and Determinants of savanna and forest as Alternative Biome States. *Science* 334, 230–232. doi:10.1126/science.1210465
Stier, A., de Carvalho, W. D., Rostain, S., Catzeflis, F., Claessens, O., Dewynter, M., et al. (2020). The Amazonian Savannas of French Guiana: Cultural and Social Importance, Biodiversity, and Conservation Challenges. *Trop. Conservation Sci.* 13, 194008291990047–21. doi:10.1177/1940082919900471
Terrell, J. E., Hart, J. P., Barut, S., Cellinese, N., Curet, A., Denham, T., et al. (2003). Domesticated Landscapes: The Subsistence Ecology of Plant and Animal Domestication. *J. Archaeological Method Theor.* 10, 323–368. doi:10.1023/b:jarm.0000005510.54214.57
Torres Romero, M. C., Galeano Garces, G. A., and Bernal, R. (2016). Cosecha y manejo de Copernicia tectorum (Kunth) Mart. Para uso artesanal en el caribe colombiano. *Colomb. For.* 19, 5. doi:10.14483/udistrital.jour.colomb.for.2016.1.a01
Vialou, D., Benabdelhadi, M., Feathers, J., Fontugne, M., and Vialou, A. V. (2017). Peopling South America's centre: the Late Pleistocene Site of Santa Elina. *Antiquity* 91, 865–884. doi:10.15184/aqy.2017.101
Walter, B. M. T., Carvalho, A. M. de., and Ribeiro, J. F. (2008). "O conceito de savana e de seu componente Cerrado," in *Cerrado: Ecologia e flora*. Editors S. M. Sano, S. P. de Almeida, and J. F. Ribeiro (Brasília, DF: Embrapa Informação Tecnológica), 19–45.
Welch, J. R., Brondízio, E. S., Hetrick, S. S., and Coimbra, C. E. A. (2013). Indigenous Burning as Conservation Practice: Neotropical Savanna Recovery amid Agribusiness Deforestation in Central Brazil. *PLoS One* 8, e81226. doi:10.1371/journal.pone.0081226
Welch, J. R., and Coimbra Jr., C. E. A., Jr. (2021). Indigenous Fire Ecologies, Restoration, and Territorial Sovereignty in the Brazilian Cerrado: The Case of Two Xavante Reserves. *Land use policy* 104, 104055. doi:10.1016/j.landusepol.2019.104055
Welch, J. R. (2015). Learning to hunt by Tending the Fire: Xavante Youth, Ethnoecology, and Ceremony in central Brazil. *J. Ethnobiol.* 35, 183–208. doi:10.2993/0278-0771-35.1.183
Yibarbuk, D., Whitehead, P. J., Russell-Smith, J., Jackson, D., Godjuwa, C., Fisher, A., et al. (2001). Fire Ecology and Aboriginal Land Management in central Arnhem Land, Northern australia: A Tradition of Ecosystem Management. *J. Biogeogr.* 28, 325–343. doi:10.1046/j.1365-2699.2001.00555.x

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Constructing Micro-Landscapes: Management and Selection Practices on Microbial Communities in a Traditional Fermented Beverage

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Colonche is a traditional beverage produced in Mexico by the fermentation of fruits of several cacti species. In the Meridional Central Plateau region of Mexico, where this study was conducted, it is mainly produced with fruits of *Opuntia streptacantha*; there, the producers perform spontaneous fermentation and/or fermentations through inoculums. Several factors can change the microbial community structure and dynamics through the fermentation process, but little attention has been directed to evaluate what type and extent of change the human practices have over the microbial communities. This study aims to assess the microbiota under spontaneous and inoculated fermentation techniques, the microorganisms present in the inoculums and containers, and the changes of microbiota during the process of producing colonche with different techniques. We used next-generation sequencing of the V3-V4 regions of the 16S rRNA gene and the ITS2, to characterize bacterial and fungal diversity associated with the different fermentation techniques. We identified 701 bacterial and 203 fungal amplicon sequence variants (ASVs) belonging to 173 bacterial and 187 fungal genera. The alpha and beta diversity analysis confirmed that both types of fermentation practices displayed differences in richness, diversity, and community structure. Richness of bacteria in spontaneous fermentation (^{0}D = 136 $\pm$ 0.433) was higher than in the inoculated samples (^{0}D = 128 $\pm$ 0.929), while fungal richness in the inoculated samples (^{0}D = 32 $\pm$ 0.539) was higher than in spontaneous samples (^{0}D = 19 $\pm$ 0.917). We identified bacterial groups like *Lactobacillus*, *Leuconostoc*, *Pediococcus* and the *Saccharomyces* yeast shared in ferments managed with different practices; these organisms are commonly related to the quality of the fermentation process. We identified that clay pots, where spontaneous fermentation is carried out, have an outstanding diversity of fungal and bacterial richness involved in fermentation, being valuable reservoirs of microorganisms for future fermentations. The inoculums displayed the lowest richness and diversity of bacterial and fungal communities suggesting unconscious selection on specific microbial consortia. The beta diversity analysis identified an overlap in microbial communities for both types of fermentation practices, which might reflect a shared composition of microorganisms occurring in the *Opuntia streptacantha* substrate. The variation in the spontaneous bacterial community is consistent with alpha diversity data, while fungal communities showed less differences among treatments, probably due to the high abundance and dominance of *Saccharomyces*. This information illustrates how traditional management guides selection and may drive changes in the microbial consortia to produce unique fermented beverages through specific fermentation practices. Although further studies are needed to analyze more specifically the advantages of each fermentation type over the quality of the product, our current analysis supports the role of traditional knowledge driving it and the relevance of plans for its conservation.

Keywords: microbiota, management, ferments, ethnozymology, colonche, landscape domestication

INTRODUCTION

Throughout history, human societies have developed knowledge and techniques to use a plethora of species of plants, animals, fungi and other organisms from different ecosystems to satisfy nutritional needs (Campbell-Platt, 1994; Tamang et al., 2016, 2020, 2021). Interactions between people and nature commonly include a high diversity of management practices through which people adequate organisms and other components of ecosystems to secure their livelihoods; these practices are context-dependent on local conditions, outstandingly human culture and environment (Jones et al., 1997; Odling-Smee et al., 2003; Anderson, 2005). Traditional or local knowledge commonly includes complex bodies of information on the ecological context, relationships and behavior of the elements used as food, extensive repertoires of preparation procedures, as well as about their relationships with customs, taboos, rituals, and other cultural aspects (Nabhan, 2010; Tamang, 2010; Ratcliffe et al., 2019). All these biocultural facets can be visualized through the diversity of food products and practices related to it, and provide basic notions about what is edible, where and when edible elements are available, the way these should be harvested, and how they can be improved by cooking, roasting, fermenting, or making it harmless (Lévi-Strauss, 2012; Ratcliffe et al., 2019; Tamang et al., 2020, 2021; Tsafrakidou et al., 2020; Fernández-Llamazares et al., 2021; Gadaga et al., 2021; Kennedy et al., 2021).

Fermentation practices are part of the local knowledge and food systems, directed to procure and improve human health and wellbeing, but fermented products have changed the human food supply worldwide (Harris et al., 1989; Kuhnlein and Receveur, 1996; Steinkraus, 1996; Harris, 1998; Quave and Pieroni, 2014; Svanberg, 2015; Sõukand et al., 2015; Flachs and Orkin, 2019; He et al., 2019). Fermentation can contribute to construct sustainable food systems, diversify food production, and procure safety, security and sovereignty in human communities around the world (Johns and Sthapit, 2004; Marshall and Mejia, 2011; Ojeda-Linares et al., 2021). It allows preserving and improving nutritional value of food and conferring desirable properties to the final products such as textures and sensorial properties, which are completely unlike to those of the starting materials (Smid and Hugenholtz, 2010; Smid and Kleerebezem, 2014). The microbial communities of bacteria, yeasts, and molds play a key role determining the quality of the fermented products, influencing their acidity, flavor, texture, nutritional value and other health benefits (Forssten et al., 2011; Todorov and Holzapfel, 2015; Gutiérrez-Uribe et al., 2017; El Sheikha and Hu, 2020). Changes in the microbial composition may be caused by variation in environmental factors, thus organoleptic and physicochemical characteristics of a fermented product could be modified and driven by managing fermentation environments through human practices (Escalante et al., 2016; Rebollar et al., 2017). The persons that perform and drive changes and follow the fermentation process in traditional contexts are recognized as traditional fermentation managers (Nabhan, 2010; Flachs and Orkin, 2019; Ojeda-Linares et al., 2020).

A common practice used to produce traditional ferments is the "spontaneous" fermentation, which involves microorganisms occurring in a local environment and is influenced by temperature, substrate type, techniques and tools employed, and other cultural factors that shape the composition and dynamics of the microbiota (De Vuyst and Vancanneyt, 2007; Vogelmann et al., 2009; Chaves-López et al., 2020). Due to the influence of all these factors, this type of fermentation is commonly assumed to be unpredictable, producing outcomes of inconsistent attributes; local people commonly have knowledge about how environmental and technological factors may influence the product and carry out practices to manage them, looking for decreasing the unpredictability of the resulting product. The other general practice is the use of starter cultures, which are characteristic for numerous fermented products around the world. Inoculation refreshment favors a periodically stable microbial community which provides an easy way to achieve optimal fermentations and desirable products (De Vuyst and Vancanneyt, 2007; De Vuyst et al., 2009; Brandt, 2014; Harth et al., 2016; Mukisa et al., 2017). Therefore, it is thought that this type of practice is associated with a set of selective forces favoring a specific community of microorganisms, guiding the dynamics and structure of the microbiota through the fermentation process (Vogelmann et al., 2009; Vogelmann and Hertel, 2011; Gibbons and Rinker, 2015; Liu et al., 2021).

The influence of human management over composition, structure and dynamics of microbial communities has been insufficiently analyzed, even when humans historically have developed numerous management techniques to direct, diversify and innovate the quality or to prevent the spoilage of fermented products around the world (Tamang and Fleet, 2009; Tamang et al., 2016). Ethnozymological studies have documented a wide range of activities that producers perform to adequate fermented products to their purposes; for instance, boiling the substrates, adding salt, plant, or animal products with antiseptic or flavoring roles are common practices (Quave and Pieroni, 2014; Hong et al., 2015; Sõukand et al., 2015; Pieroni et al., 2017; Álvarez-Ríos et al., 2020; Ojeda-Linares et al., 2021). Documenting the *known-how* of the management over the microbial communities in fermented products has high importance to understand the implications of human practices on the structure and dynamics of microbial communities during fermentation and to recover old human experience for innovation. In addition, this information provides elements to analyze possible processes of domestication at species and/or community levels.

Management includes a broad spectrum of practices that favor phenotypic attributes of organisms like size, flavors, colors, nutritional values, attributes to satisfy customs, rituals, ornamental, and other cultural purposes (Anderson, 2005; Casas et al., 2007). Through time, management has determined differences between wild and managed populations, the latter having higher frequencies of human-favored phenotypes. Such processes have been especially assessed in plant and animal populations where specific visible phenotypes are favored (Casas et al., 2007; Blancas et al., 2010). At ecosystem level, management practices may be directed to change species richness, diversity, and structure of communities and this is also an expression of domestication, the landscape domestication (Casas et al., 1997; Smith, 2007; Albuquerque et al., 2019; Clement et al., 2020, 2021; Franco-Moraes et al., 2021). But, although the processes involved in ecosystem management are common and widespread throughout the world, these have been less studied than domestication at species populations level and even fewer are studies documenting management and domestication at micro-landscape level.

In this study we explored the general hypothesis that the composition and structure of the microbiota involved in fermentation would differ according to management practices. We expected to find a higher microbial diversity in techniques involving spontaneous fermentation than in those using inoculums, which would be favoring reduced consortiums of microorganisms due to continuous human selection. Such differences would also influence the dynamics of change through the fermentation of communities with higher and lower diversity toward less and more predictable products, respectively. Characterizing and analyzing the type and extent of change of microbial communities according to management practices are conceptually relevant to construct and test hypotheses about how these processes and techniques lead to domestication of microorganism consortiums and, probably, of specific lineages. Also, to design innovative strategies to improve food quality. Understanding how certain management practices do help to predict how diversity, composition, and richness of microbiota can be and change, would support principles of selection and management programs of microbial communities to obtain desirable products.

Such hypothesis has been narrowly explored, particularly because testing it requires methods and study systems able to compare and measure across confidently. A traditional fermented product prepared with the same substrate and different management practices represents an optimal study system for such purpose, while using High Throughput Sequencing (HTS) techniques allow detecting or rejecting associations between microbial composition and management practices. Currently, HTS allow glimpsing the composition and structure of microbial communities in different ecosystems (Metzker, 2010; Caporaso et al., 2011) and fermenting landscapes are not the exception (Foligné and Pot, 2013; De Filippis et al., 2017; Sha et al., 2018; Astudillo-Melgar et al., 2019).

To address our hypothesis, we selected the traditional fermented beverage called colonche. Colonche is a group of traditional Mexican beverages prepared since pre-Columbian times by the fermentation of fruits of several cactus species, including several species of *Opuntia* prickly pears and columnar cacti (Ojeda-Linares et al., 2020). We conducted our study in the Meridional Central Plateau region of Mexico, where the main substrate for colonche production is *Opuntia streptacantha* fruit. For its production, prickly pear fruits are gathered in wild and cultivated populations and stored in plastic trays almost every day from August to October, when fruits are available. Local people carry out different fermentation practices, based on spontaneous or inoculated procedures. To produce colonche through spontaneous fermentation, they harvest and peel the *Opuntia* fruits *in situ*, and then place them inside a clay pot where fermentation occurs for about 12 h. In this area the colonche production is mainly performed by old men (60 ± 5 years old). The inoculated fermentation is performed by firstly boiling the fruits to concentrate their juice; then, the producers add the starter cultures from previous batches and store the fermenting juice in plastic containers for 4 h (Ojeda-Linares et al., 2020). The production of inoculated colonche in the area is mainly performed by young women (32 ± 4 years old), and the production represents a recent recovery of this beverage by the younglings. Therefore, an analysis of the microbiota associated with this fermented beverage prepared with the same substrate under different fermentation practices is possible and would allow documenting how management over the fermentation process influences the microbial communities.

Nowadays, there is a worrying erosion of local food systems, causing the disappearance of traditional food products worldwide (Pingali, 2007; Turner and Turner, 2007; Johns et al., 2013; Albert et al., 2015; Hernández-Santana and Narchi, 2018; Akinola et al., 2020). Fermented products have been poorly considered in the analysis of erosion of local food systems, even when some of them have almost disappeared. Nonetheless, a renewed interest in their production has motivated studies and actions to guarantee its permanence (Madej et al., 2014; Svanberg, 2015; Cano and Suárez, 2020; Ojeda-Linares et al., 2020, 2021). In México, it has been recorded the loss of some traditional fermented beverages, even though the main substrates are available in the nearby, but the transmission of knowledge has been lost (Ojeda-Linares et al., 2021). The vanishing of fermented products not only favors disappearing fragments of foodscapes, but also the traditional ecological knowledge over fermentation practices, and therefore the efforts that humans have historically engineered to shape microbial communities and the evolutionary processes involved in making unique products.

This study aims to describe the microbial community of colonche under different management practices and highlights the relevance of traditional knowledge to construct the micro-landscapes and, in general, to preserve unique products that are part of a local food systems. We aspire to contribute to a deeper understanding of the processes that can be involved in the selection and domestication of microbial consortia and specific lineages of the microbiota. We also aspire to contribute to the conservation of traditional knowledge over fermentation practices and the establishment of a microbial panel helpful to determine the geographical origin of the product and supports the relevance and the way of its conservation.

MATERIALS AND METHODS

Study Area and Sampling

We studied colonche samples prepared by the fermentation of *O. streptacantha* fruits. We collected nine samples from spontaneous fermentations in the village of Laguna de Guadalupe (LG) in the state of Guanajuato, México from three different producers that performs similar practices. Also, nine samples of inoculated colonche produced by three producers in Mexquitic de Carmona (MC) in the neighboring state of San Luis Potosi (**Figures 1A,E**). We in addition collected samples of residuals from two clay pots one day before producers began spontaneous colonche fermentation. These clay pots have been used for almost 80 years for colonche production and are stored indoors when fruits of *O. streptacantha* are not available. Before the fermentation starts, the producers clean them only with water (no soap is added since according to people it changes the flavor of the product; **Figure 1B**). In addition, we collected and analyzed two samples of the inoculum, which were saved from the last production season, stored in a fridge and ready to use in the following batches (**Figure 1C**) and two samples of the cooked cactus prickly pear fruit juice before fermentation in the inoculated treatment (**Figure 1D**). The cooked samples represent a treatment that producers of the locality of Mexquitic performed because it is presumed to give a longer shelf life to colonche, since it can be stored in this way before the inoculum is added.

DNA Extraction and Sequencing

Genomic DNA was extracted for all the samples with the ZR Soil Microbe DNA MiniPrep kit (Zymo Research) following the manufacturer's protocol. DNA was quantified using Qubit Fluorometric Quantitation (Thermo Fisher Scientific) and its quality was assessed on a 1% agarose gel. The obtained high-quality DNA samples were stored at −20°C util the library preparation. The libraries and targeted metagenomic sequencing were performed at ZymmoBIOMICS Service (Irvine, CA). Libraries of 16S rDNA and ITS amplicons were sequenced on the Illumina® MiSeq™ platform 2 × 300 bp paired end. For bacteria, the V3-V4 regions of the 16S rRNA were amplified as has been reported in previous works (Caporaso et al., 2011; Li and Yue, 2016). For fungi, the internal transcribed spacer (ITS) was amplified using the ITS2 primers (Yao et al., 2010; Badotti et al., 2017; Baldrian et al., 2021).

Microbiome Analysis in the Colonche Samples

The 16S rRNA and ITS amplicon sequences were processed using QIIME 2™ (Caporaso et al., 2010; Bolyen et al., 2019), version qiime2-2018.8. For all data, the DADA2 (Callahan et al., 2016) pipeline was used for quality filtering, removal of chimeric sequences, merge paired end reads and generate a table of amplicon sequence variants of each dataset (ASVs, Callahan et al., 2017). To eliminate the bases corresponding to the primers, the first 16 bases of the forward reads and 24 bases of the reverse reads of the 16S rRNA sequences were trimmed. From the ITS sequences, 22 and 24 bases of forward and reverse reads were clipped, respectively. Furthermore, to remove low-quality regions of the sequences, each read was clipped to some position where the quality decreases and was determined with the interactive quality plots of QIIME 2™ (Bolyen et al., 2019). The 16S rRNA sequences were truncated to 315 bases for forward reads and 250 bases for reverse reads, and the ITS sequences were truncated to 310 bases and 215 bases for forward and reverse reads, respectively.

Taxonomy was assigned to the representative unique sequences from each ASVs based on the Naïve Bayes classifier (Bokulich et al., 2018) and annotated according to the Greengenes 13_8 database (DeSantis et al., 2006); for the 16S rRNA data and from the ITS data the UNITE database v8.0 (Nilsson et al., 2019) was used. For each dataset, the ASVs represented by less than 10 sequences were removed in all samples, and the ASVs that were classified as plant chloroplast, mitochondria, archaea, unassigned sequences, or only assigned to *phylum* level were also eliminated. For diversity and statistical analysis, the ASVs tables of bacteria and fungi were normalized by their relative abundance (Fitzpatrick et al., 2018; Solís-García et al., 2021).

Diversity and Statistical Data Analysis

Alpha diversity was evaluated with the Hill numbers (${}^{q}D$), where the order q determines the sensitivity of the measure to the relative abundance (Chao and Chiu, 2016). ${}^{0}D$ is equivalent to the richness; the measure ${}^{1}D$ counts the ASVs proportionally to their abundances and corresponds to the effective numbers of common ASVs; the measure for ${}^{2}D$ considers the most abundant ASVs and can be interpreted as the effective number of dominant ASVs (Chao et al., 2014; Montes-Carreto et al., 2021). The comparisons of the diversity measures among colonche management practices were made under the same sample coverage and the no overlap in the 95% CI values indicates significant differences (Cumming et al., 2007). Sample coverage values, ${}^{q}D$, and their confidence intervals were calculated with the iNEXT R package 3.5.3 (Hsieh et al., 2016), using as an endpoint the maximum number of sequences in each treatment.

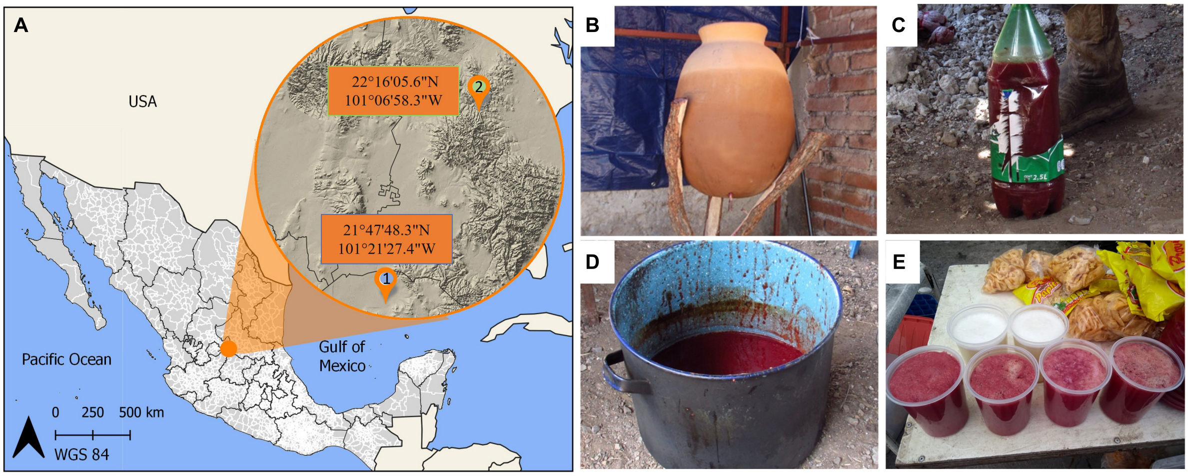

FIGURE 1 | Sampling sites and colonche samples **(A1)** the locality of Laguna de Guadalupe in Guanajuato state; **(A2)**, Mexquitic de Carmona in San Luis Potosí. **(B)** Claypots where spontaneous fermentation occurs; **(C)** Inoculum stored from the last season; **(D)** Cooked and boiled Cactus prickly pear fruits where sugars are concentrated; **(E)** Inoculated samples ready to sell in the local markets.

For beta diversity analyses, each phylogenetic tree was constructed with the ASVs of bacteria or fungi of the inoculated and spontaneous colonche management practices. The sequences alignment was made with MAFFT, the trees were inferred with FastTree and then rooted at its midpoint. The ASVs tables of bacteria and fungi log2-transformed and the dissimilarity matrices of the Unifrac weighted and unweighted distances were calculated with the phyloseq (McMurdie and Holmes, 2013) and vegan packages (Oksanen et al., 2013). The phylogenetic dissimilarities of the bacterial and fungal communities were represented with the ordination method of non-metric multidimensional scaling (NMDS) based on the Unifrac weighted and unweighted distances (Lozupone et al., 2011). To compare the structure of each community of the inoculated and spontaneous colonche management practices a permutational multivariate analysis of variance (PERMANOVA) was computed using the vegan package with 999 permutations.

Significant differences in the relative abundance of each taxon between the inoculated and spontaneous colonche management practices were evaluated through the Mann-Whitney-Wilcoxon test with an FDR correction in R v.3.5.2 software, considering as a significant values $P < 0.05$. The shared bacteria and fungi ASVs among both treatments were plotted as a Venn diagram with the VennDiagram package (Chen and Boutros, 2011).

RESULTS

Preprocessing and Taxonomic Classification

To visualize the changes in the bacterial communities between fermentation management practices we obtained pair-end sequencing of the V3-V4 region of the 16SrRNA leads to a total of 2,398,545 reads, with an average of 28,769.79 (± 33,516.46) reads per sampling, then, after filtering the ASVs table, a total of 701 in all 16S samples, belonging to 173 bacterial genera (**Supplementary Table 1**). For fungal communities by ITS sequence, a total of 1,505,383 pair-end were obtained with an average of 62,724.291 (± 23,303.49) reads for all the sampling which composed a total of 203 ASVs; then, after filtering the table with 0.01% of relative abundance, 201 ASVs were obtained, belonging to 187 yeast genera (**Supplementary Table 1**). The bacterial and fungal communities of each colonche management practices had a sample coverage of 100% suggesting that the most of the ASVs were captured (**Supplementary Figure 1A**). Also, rarefaction curves for all the samples reached the plateau indicating that the sequencing depth was sufficient to cover most of the bacterial and fungal diversity in each colonche management practices (**Supplementary Figure 1B**).

Colonche Microbiome Is Partially Consistent With the Management Hypothesis

To analyze our hypothesis, the alpha diversity was estimated using the Hill numbers (${}^{q}D$). For the ASVs of the bacterial community (**Supplementary Table 2**), the clay pots samples showed a higher richness (${}^{0}D = 543 \pm 0.121$), followed by the spontaneous samples (${}^{0}D = 136 \pm 0.433$), the inoculated samples (${}^{0}D = 128 \pm 0.929$), the cooked samples (${}^{0}D = 113.00 \pm 3.485$), and being the inoculum samples (${}^{0}D = 47 \pm 0.163$) the ones with the lowest richness (**Figure 2A**). Also, the clay pot samples were the most diverse (${}^{1}D = 131.575 \pm 1.412$, ${}^{2}D = 38.087 \pm 1.212$) compared with the other colonche management practices (**Figures 2B,C** and **Supplementary Table 2**). The diversity values of the effective number of common and dominant ASVs were significantly higher in the inoculated samples (${}^{1}D = 18.277 \pm 0.929$, ${}^{2}D = 11.507 \pm 0.04$) contrarily to the spontaneous samples (${}^{1}D = 11.081 \pm 0.049$, ${}^{2}D = 4.33 \pm 0.019$; **Figures 2B,C**). Thus, there is a reduction in richness from

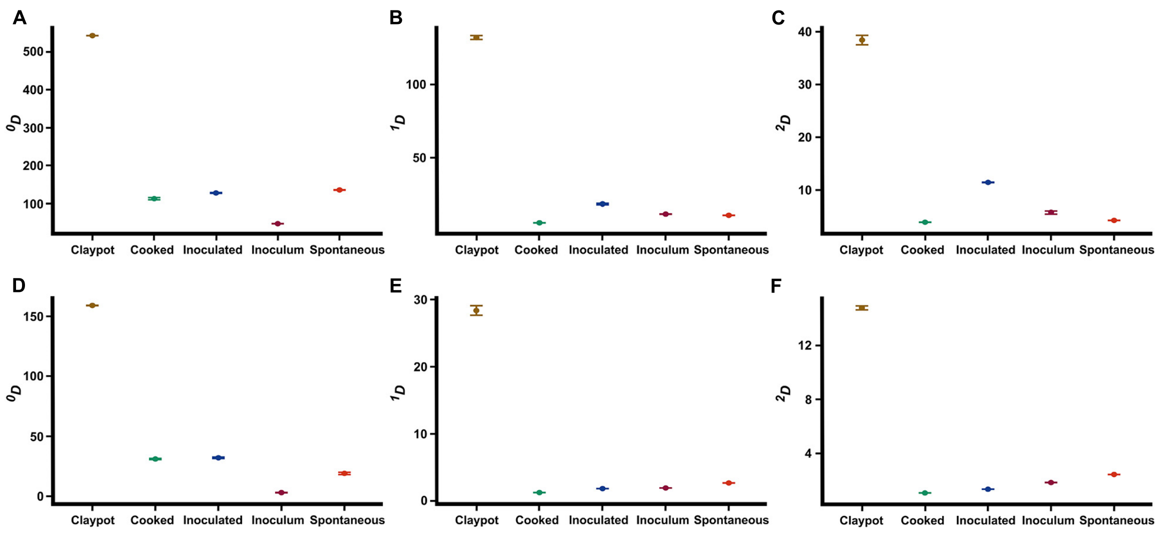

FIGURE 2 | Comparison of the richness and alpha diversity of the bacterial **(A–C)** and fungal communities **(D–F)** between the different colonche management practices estimated with the Hill numbers (^{q}D). Interval plots of richness **(A,D)**, effective number of common amplicon sequence variants (ASVs) **(B,E)**, and effective number of dominant ASVs.

spontaneous to inoculated fermentation practices in the colonche microbiome, which is consistent with our hypothesis. The richness of the ASVs of the fungal community (**Figure 2D** and **Supplementary Table 2**) showed a different pattern, the clay pots also display the highest values (^{0}D = 159 ± 0.151), followed by the inoculated samples (^{0}D = 32 ± 0.539), then the cooked samples (^{0}D = 31 ± 0.458), the spontaneous samples (^{0}D = 19 ± 0.917), and finally the inoculum with the less richness (^{0}D = 3 ± 0.151). Diversity of clay pots samples (^{1}D = 28.873 ± 0.214, ^{2}D = 14.787 ± 0.145) was higher than that of the other colonche management practices (**Figures 2E,F**). In contrast, diversity of common and dominant fungal ASVs was significantly higher in the spontaneous samples (^{1}D = 2.667 ± 0.004, ^{2}D = 2.442 ± 0.004) than in the inoculated samples (^{1}D = 1.826 ± 0.007, ^{2}D = 1.346 ± 0.004; **Figures 2E,F**).

Colonche Microbial Differences Between Spontaneous and Inoculated Fermentation Practices

To characterize the differences between spontaneous and inoculated colonche microbiome, the beta diversity of bacterial and fungal communities was represented with a NMDS using weighted and unweighted Unifrac distances (**Figure 3** and **Supplementary Figure 2**). Although phylogenetic dissimilarities between the bacterial groups in spontaneous and inoculated fermentations by the unweighted Unifrac distance allow visualizing the splitting of both bacterial communities ($p < 0.036$), there is an inoculated sample that is closer to the spontaneous samples, and the spontaneous fermented samples are more disperse and less clustered (**Figure 3A** and **Supplementary Table 3**). The weighted Unifrac distances partially allow discriminating fungal community ($p < 0.047$), it can be seen that the spontaneous bacterial communities are clustered, while the inoculated samples are more variable and there are samples that overlap with the spontaneous treatment (**Figure 3B** and **Supplementary Table 4**). Both results are supported by PERMANOVA analysis (999 permutations). Summarizing, the overlap in microbial communities for both types of fermentation practices might reflect a common shared composition of microorganisms occurring in the *Opuntia streptacantha* substrate. The variation in the spontaneous bacterial community is consistent with the data of alpha diversity, while for fungal communities there are less differences among treatments, which might reflect the high abundance and dominance of *Saccharomyces* genus, as referred to for alpha diversity (**Figure 2B**).

Colonche Microbial Genus Composition in the Different Fermentation Practices

The Microbial Community in Spontaneous Fermentation: Clay Pots and Spontaneous Colonche

Besides different diversity levels, we found that clay pots have a high richness in the composition of bacteria and fungi at the genus level (**Figure 2**). Among the most abundant bacteria genera occurring in the clay pots are: *Arthrobacter* (14.92%), *Elstera* (10.12%), *Alkanindiges* (7.72%), *Massilia* (6.92%), *Pseudomonas* (5.18%), *Nocardioides* (1.79%), *Roseomonas* (1.62%), *Rhizobium* (1.40%), *Blastococcus* (1.39%), *Achromobacter* (1.20%), *Brevundimonas* (1.15%). While for fungal community, *Penicillium* (38.15%), *Cladosporium* (9.70%), *Didymella* (9.60%), *Wickerhamomyces* (8.90%), *Naganishia*, (7.86%), *Alternaria* (6.42%), *Rhodotorula* (4.06%), *Fusarium* (3.02%), *Saitozyma* (1.62%), *Aureobasidium* (1.38%), *Vishniacozyma* (1.14%), *Cystofilobasidium* (1.01%) and although *Saccharomyces* (0.42%) ends up as the most dominant yeast in the spontaneous fermentation, its abundance is lower in the clay pots (**Figure 4**).

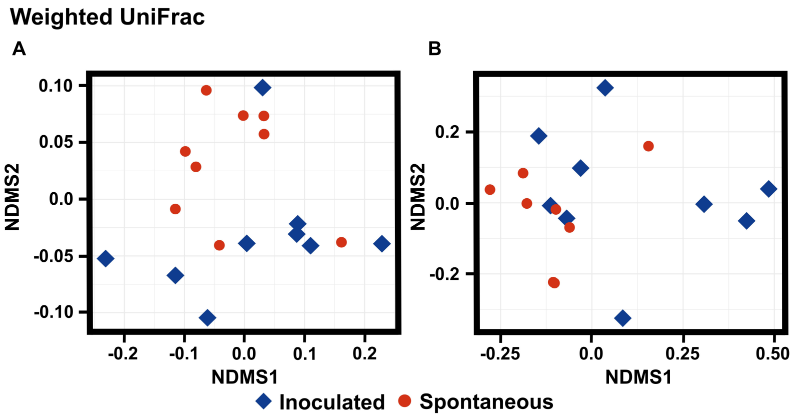

FIGURE 3 | Non-metric multidimensional scaling (NMDS) plots-based **(A)** on UniFrac weighted distance of the bacterial community structure; **(B)** an Unifrac weighted distances of the fungal community structure associated with inoculated and spontaneous fermentation practices in the colonche production.

At the end of the spontaneous fermentation process, 10 fungal ASVs (*Aureobasidium*, *Candida*, *Cladosporium*, *Pichia*, *Saccharomyces*, *Torulaspora*, *Rhodotorula*, *Wickerhamomyces*, one unidentified taxon and one not assigned fungal) are shared within the clay pots. This group is mainly involved in the final stages of the fermentation process of the spontaneous fermentation. Four groups are exclusive of the spontaneous fermented colonche (*Dekkera*, *Kazachstania*, *Kluyveromyces* and *Knufia*) and 45 are unique for clay pots. This behavior is similar in the bacterial community, in which 6 genera (*Massilia*, *Elizabethkingia*, *Clostridium*, *Bacillus*, *Alkanindiges* and one not assigned taxon) are shared with the spontaneous final product and the clay pots. For instance, 12 genera (*Weissella*, *Tanticharoenia*, *Tatumella*, *Streptococcus*, *Rheinheimera*, *Pediococcus*, *Lactococcus*, *Lactobacillus*, *Gluconacetobacter*, *Faecalibacterium*, *Dorea* and *Aeromonas*) are present in the final product of spontaneous fermentation, being particularly remarkable *Lactobacillus* and *Leuconostoc*, which are present in higher abundance (**Figure 4**). Finally, 71 ASVs are exclusive of the microbiota communities of the clay pots.

The Microbial Community in the Inoculated Fermentation: Inoculums, Cooked and Inoculated Colonche

It can be visualized that the inoculums are the samples with the lowest richness of bacteria and yeasts; for instance, we identified only 7 bacteria and 2 yeast genera, mainly dominated by multiple taxa of Lactic Acid Bacteria (LAB) as: *Lactobacillus* (24.60%), *Leuconostoc* (10.34%), *Alkanindiges* (8.65%), *Pediococcus* (6.92%), while yeasts are dominated by *Saccharomyces* (99.9%) and *Kazachstania* (0.01%). Surprisingly, there were a higher number of ASVs for the cooked samples with 32 bacteria genera (**Supplementary Table 5**) and 21 yeasts, contrasting with the final product of the inoculated fermentation, which had fewer ASVs (**Supplementary Table 6**).

As mentioned above, in the inoculated fermentation process all microbial ASVs of the inoculums are shared with the inoculated final product. Also, *Alkanindiges*, *Clostridium* *Corynebacterium*, *Gluconacetobacter*, *Lactobacillus*, *Leuconostoc*, *Massilia*, *Pediococcus*, *Sphingomonas*, *Staphylococcus*, *Weissella* and one not assigned taxon are shared between the cooked and the inoculated samples. *Dorea* and *Elstera* are the only two exclusive genera of the inoculated samples and 18 genera (*Actinomycetospora*, *Actinotelluria*, *Albidovulum*, *Arthrobacter*, *Blastococcus*, *Dietzia*, *Gaiella*, *Helcobacillus*, *Micrococcus*, *Microlunatus*, *Nocardioides*, *Oceaniovalibus*, *Ochrobactrum*, *Roseomonas*, *Solirubrobacter*, *Sporosarcina*, *Streptomyces* and *Tanticharoenia*) are exclusive of the cooked samples.

For the fungal community we registered 9 genera being commonly shared between the cooked treatment and inoculated samples (*Candida*, *Cladosporium*, *Dipodascus*, *Hanseniaspora*, *Kazachstania*, *Kluyveromyces*, *Saccharomyces*, *Torulaspora* and one unidentified taxon). The genera *Alternaria, Arthrinium, Cryptococcus, Didymella, Filobasidium, Fusarium, Mucor, Naganishia, Rhodotorula* and *Starmerella* are exclusive of cooked samples and only *Aureobasidium, Dekkera, Issatchenkia* and *Pichia* are unique for the final product of inoculated fermentation.

The Microbial Composition Between Spontaneous and Inoculated Fermentations

For bacterial communities we found that 12 ASVs are shared among the fermentation practices, like *Lactobacillus* (p < 1e-1), *Alkanindiges*, *Clostridium*, *Dorea*, *Faecalibacterium*, *Gluconacetobacter*, *Lactococcus*, *Leuconostoc* (p < 1e-1), *Pediococcus* (p < 1e-1), *Tatumella*, *Tanticharoenia*, and *Weisella* (p < 1e-1). For instance, 6 genera are exclusive to spontaneous treatment like *Aeromonas*, *Bacillus*, *Elizabethkingia*, *Massilia*, *Rheinheimera* and *Streptococcus* and 4 are exclusive of the inoculated samples (*Staphylococcus*, *Sphingomona*, *Corynebacterium*, *Elstera*) (**Figure 5A**). In the fungal communities, we identified 11 genera shared among samples under different fermentation practices: *Aureobasidium*, *Candida*, *Cladosporium*, *Dekkera* (p < 1e-1), *Hanseniaspora*, *Kazachstania* (p < 1e-6), *Kluyveromyces*, *Pichia*, *Saccharomyces*, *Torulaspora* and other unidentified taxa. The inoculated samples displayed

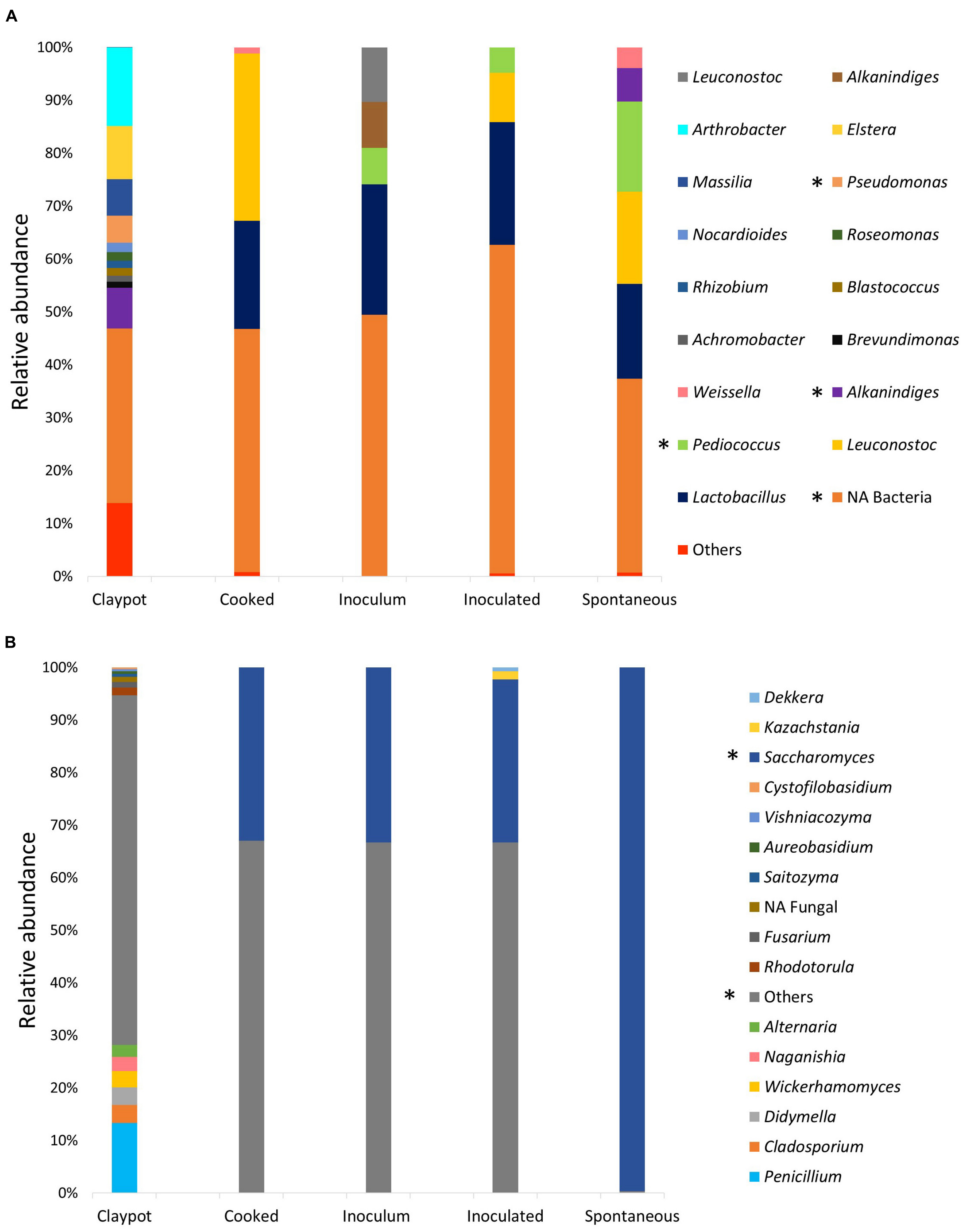

FIGURE 4 | Composition of the **(A)** Bacterial Genera composition of the community associated with the management practices and colonche production stages and, **(B)** the fungal Genera composition. Low abundance taxonomic groups (relative abundance < 1%) were reported as others. NA mean not assigned. The asterisk indicates significant differences in taxa relative abundance between management practices.

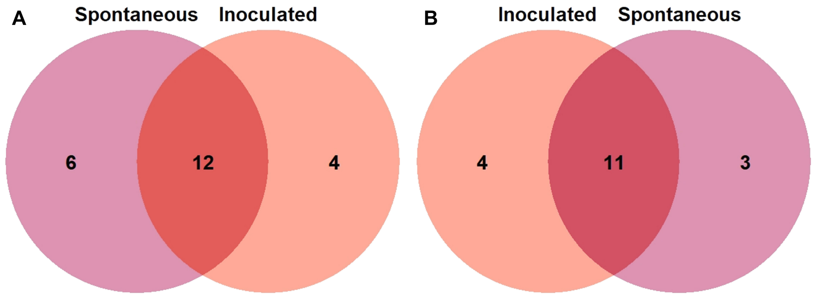

FIGURE 5 | Venn diagrams of the number of unique and shared amplicon sequence variants (ASVs) of the **(A)** bacterial and **(B)** fungal community associated with the fermentation practices of colonche samples inoculated (red) and spontaneous (purple).

4 exclusive ASVs (*Wickerhamiella*, *Issatchenkia*, *Dipodascus* and *Clavispora*), while the spontaneous fermentation samples registered 3 unique ASVs (*Wickerhamomyces*, *Knufia* and one not assigned genus) (**Figure 5B**).

DISCUSSION

Differences Between Spontaneous vs. Inoculated Fermentations

Our results confirm that spontaneous and inoculated fermentation practices significantly differ in the composition of microbial assemblages and the relative abundance of bacterial and fungal taxa in fermenting communities. These results are in concordance with most of the literature reporting that spontaneous fermentations exhibit a higher number of microbial species than inoculated products (Tamang et al., 1988; Raspor et al., 2002; Haruta et al., 2006; Domizio et al., 2007; Alves et al., 2010; Hong et al., 2015; Anagnostopoulos et al., 2020; Lu et al., 2021). These results confirm the reduction of diversity hypothesis, as can be visualized in **Figure 2**, where the lowest values of diversity for both bacteria and fungi were recorded in the inoculums and the reduction at the final composition for bacterial communities occurs in the inoculated samples. Nevertheless, this relation is not unidirectional for fungi, for which we observed small differences, contrarily to what has been previously reported (Raspor et al., 2002).

Fermentation traditionally occurs spontaneously and is initiated by a diverse community of indigenous yeasts and bacteria associated to the plants, the environment, or the fermentation facilities where it is produced (Pretorius et al., 1999; Motarjemi, 2002; Bokulich et al., 2013; Bokulich and Mills, 2013; da Silva Vale et al., 2021). In different traditional fermented beverages, the yeast genera *Hanseniaspora*, *Pichia*, *Metschnikowia*, *Candida*, *Torulaspora*, *Rhodotorula*, *Cryptococcus*, *Lachancea*, *Zygosaccharomyces* have been recorded as the most common at the initial stages of the successional process of fermentation, while strains of *Saccharomyces cerevisiae* become dominant at the last stages (Krieger-Weber et al., 2020). Although successional dynamics were not assessed in our current analysis, it could be considered that the fermentative environment as the clay pots where spontaneous fermentation occurs and the cooked samples before the inoculation, displayed a higher richness at both initial stages. This information also confirms that there is a marked dominance of the genus *Saccharomyces* at the final stages of the fermentation, and it occurs independently if it is spontaneous or inoculated fermented colonche. This can be explained because of the *Saccharomyces* capacity to quickly adapt to variable environmental conditions (Legras et al., 2018).

Our results confirm that the non-*Saccharomyces* yeast group comprises a variety of oxidative, weakly fermentative and strongly fermentative yeasts of genera like *Rhodotorula*, *Cryptococcus*, *Hanseniaspora*, *Candida*, *Pichia*, *Issatchenkia*, *Metschnikowia*, *Lachancea*, *Zygosaccharomyces*, *Starmerella*, *Torulaspora* and others (Barata et al., 2012), which are found at different frequencies at the clay pots and the cooked samples. This group has low fermentation power and are sensitive to prevailing anoxic conditions and increasing ethanol levels (Martinez et al., 2013; Quirós et al., 2014; Morales et al., 2015). Depending on the fermentative capacity and metabolic activity of the individual species, non-*Saccharomyces* yeasts are able to maintain their viability until the middle of fermentation before starting to decline (Xufre et al., 2006; Renouf et al., 2007; Andorrà et al., 2008; Zott et al., 2008, 2010; Bagheri et al., 2015; Sha et al., 2017). Nevertheless, the current results showed the dominance of *Saccharomyces* over the non-*Saccharomyces* groups in the final products of both types of fermentations. A similar observation was reported for other fermented beverages around the world (Tamang et al., 1988; Lyu et al., 2013; Yang et al., 2016; Sha et al., 2017).

In both types of fermentation, we identified constantly the *Pediococcus* genus. Some species of this genus are associated with spoilage of fermented beverages, especially beers and wines (Mokoena, 2017). It has been associated with the synthesis of excessive diacetyl, exopolysaccharides, and biogenic amines, all of which have a detrimental impact on the quality of the product (Wade et al., 2019). However, recent research has supported the contention that *Pediococcus* spp. can grow in wines considered to be microbiologically stable. In fact, the presence of *Pediococcus* spp. in wines not always lead to spoilage, and new findings have suggested potential uses for *Pediococcus* spp. to contribute to desirable characteristics of wines under certain circumstances. As *Pediococcus* was one of the most common genera identified in colonche samples, further studies through High-performance liquid chromatography (HPLC) should be addressed to characterize if the high abundance is associated with the spoilage or if it brings desirable characteristics to colonche and the distinction in the aromatic profile between fermentation practices.

The presence of yeast genera like *Wickerhamiella*, *Clavispora*, *Dipodascus* and *Issatchenkia*, has been described previously in pulque fermentation (Rocha-Arriaga et al., 2020). For instance, the differences of the fungal community between the inoculated fermentation are due to the common use of pulque to improve their fermentation or the use of the same containers for pulque production. *Torulaspora* is one of the few microorganisms previously identified in colonche samples (Ulloa and Herrera, 1978). By the current sampling we identified its presence in clay pots and in the cooked samples, which might represent the initial stages of fermentation. However, at the end of the fermentation under both types of practices low numbers of this genus were identified, and such low population density may be due to strict anaerobic conditions and low invertase activity (Visser et al., 1990; Hanl et al., 2005), mainly promoted by *Saccharomyces* species.

Kluyveromyces was also found in the colonche samples, it is a genus that has been isolated from a great variety of habitats and has been described to have high metabolic diversity and a substantial degree of intraspecific polymorphism. Therefore, several different biotechnological applications have been investigated with this yeast: production of enzymes, single-cell protein, aromatic compounds, and other applications (Varela et al., 2017). However, it cannot grow under strictly anaerobic conditions and the ethanol production is almost exclusively linked to oxygen limitation (Visser et al., 1990; van Dijken et al., 1993; Bellaver et al., 2004). In this sense, the higher abundance of *Kluyveromyces* genus in cooked and inoculated colonche samples might be due to a low alcohol content, but further studies are still needed to address the relationship between physicochemical attributes and the presence of microbial communities.

Kazachstania genus is typically encountered in the plant substrate, for instance, it is associated with grapevines and, in a low frequency, in grape must. Although it has not yet been characterized in cactus prickly pear fruits, this yeast genus provides positive aroma attributes that should be explored further. Its low presence in the final inoculated colonche product might be due to the dominance of the *Saccharomyces* which display a higher abundance in this treatment. *Rhodotorula* is also a common basidiomycete yeast that has been reported in several dairy products, it has a weak fermentative capacity, and has also been found associated with insects as vectors (Fonseca and Inácio, 2006; Kemler et al., 2017). The presence of this basidiomycete yeast might reflect the presence of insects closer to the clay pots and the low cautions in the storage of the cooked substrate. Nevertheless, this yeast was not found at the end of fermentation under both treatments, suggesting that hygienic practices are performed or inhibited during fermentation. In general, fungi held more stable ranges of diversity indexes in most of the samples analyzed, a similar pattern previously reported in beverages like pulque (Rocha-Arriaga et al., 2020).

Multiple strains of LAB from the *Lactobacillus* genus were registered in this study, *Lactobacillus* was the most abundant genus of bacteria, found abundantly (∼ 50%) in all phases of colonche fermentation except in clay pots. LAB are found in decomposing plant material and fruits, in dairy products, fermented meat and fish, cereals, beets, pickled vegetables, sourdough, silages, fermented beverages, juices, sewage and in cavities of humans and animals (König et al., 2009; Devi et al., 2013; Liu et al., 2014; Mokoena, 2017). LAB genera include *Lactobacillus, Lactococcus, Leuconostoc, Pediococcus, Streptococcus, Aerococcus, Alloiococcus, Carnobacterium, Dolosigranulum, Enterococcus, Oenococcus, Tetragenococcus, Vagococcus* and *Weissella* (Khalid, 2011), with *Lactobacillus* being the largest genus, including more than 100 species that are abundant in carbohydrate-rich substances and most of them are the most common and shared among samples of colonche in both fermentations process. It has been characterized that some LAB are used as probiotics, due to their health benefits (Ljungh and Wadstrom, 2006; De Leblanc et al., 2007; Azaïs-Braesco et al., 2010; Evivie et al., 2017). Although the main aim of this work was not to identify possible probiotics of LAB genera in colonche, we suggest that further studies in this direction may contribute to improve intestinal microbiota and human health through this beverage.

Our current study identified that 12 bacterial and 11 fungal ASVs are shared between spontaneous and inoculated colonche samples. Nevertheless, only the bacterial genera *Lactobacillus*, *Leuconostoc*, and *Pediococcus* and the *Saccharomyces* yeasts were the most abundant for both fermentation practices and appear in the inoculum and in the cooked samples. We propose as a first exploratory analysis that these 4 genera might reflect the microbial core of colonche because they appear common and abundantly in all the colonche samples. These genera are common throughout the fermentation of several fermented beverages and are closely related to food quality (Zhu et al., 2020; An et al., 2021; Ban et al., 2022). Nevertheless, further analysis as functional assignation and metaproteomics under a network approach can give insights of the functional microorganism's core and the relevance to achieve a predictable product.

The Clay Pots: Not a Starter Culture but a Practical Reservoir for Future Fermentations

The clay pots displayed some microorganism's genera associated with pathogenic activity, as are the cases of some strains of *Clostridium*, *Pseudomonas*, and some species of the genus *Pediococcus*. Nevertheless, through the fermentation stages these pathogenic strains disappear, perhaps because of the multiple strains of *Lactobacillus* in the spontaneous fermentation process. LAB have been applied in food preservation, partly due to their antimicrobial properties and because their capability to acidify the environment, making it harmless for other bacterial groups (Cizeikiene et al., 2013; Arena et al., 2018; Singh, 2018). Bacteriocins are a group of potent antimicrobial peptides produced by some microorganisms including LAB, primarily active against closely related organisms, mostly Gram-positive bacteria to gain competitive advantage for nutrients

(Parada et al., 2007; Zacharof and Lovitt, 2012; Mokoena, 2017; Timothy et al., 2021). In fermented foods, LAB display various antimicrobial activities, through production of various metabolites, including lactic acid, hydrogen peroxide, and bacteriocins. Therefore, the high presence of *Lactobacillus* might reflect the drastic changes in the composition from the clay pot samples through the final product, thus inhibiting the pathogens in the environment.

As mentioned above, clay pots displayed the highest richness of bacterial and fungal genera, including several non-*Saccharomyces* genera, some beneficial bacterial groups as LAB and some detrimental bacterial groups associated with the spoilage of the beverage. Nevertheless, some of these microorganisms contribute to subsequent microbial growth and brings a stable community, for instance, 10 fungal ASVs and 6 bacterial genera are shared between the clay pots and the spontaneous colonche. In this sense, a stable consortium as an inoculum might not be required in spontaneous fermentation due to the presence of microbial diversity in the clay pots that can promote a starter community for fermentation process. Further studies should consider including other microbial inputs, for example the cactus pear fruits that are exposed to a variety of microorganisms derived from the environment (e.g., surfaces and soil), producer's hands, and tools that can contribute to microbial communities and the quality of colonche as has been performed with cocoa fermentation (Schwan and Wheals, 2004; Lefeber et al., 2010; Figueroa-Hernández et al., 2019; Viesser et al., 2021), in which these factors contribute to the quality of the product.

The production of spontaneous colonche is mostly performed in clay pots, nevertheless, sometimes producers store the peeled cactus prickly pear fruits in plastic containers and then the fruits are placed inside the clay pots (Ojeda-Linares et al., 2020). Although we did not characterize the microbial and the physicochemical differences between the containers, it has been recorded that the material of the fermentation containers plays a significant role changing the abundance of specific genus as *Lactococcus* and *Pedioccous* and can affect pH values favoring a quicker fermentation (Liu et al., 2019). It is possible that the presence of these genera is favored by a previous storage in plastic containers and changes in the pH values might also change the dynamic in the clay pot by acidifying the medium. Though, further analysis should be performed to characterize the effect of the containers for colonche production.

The Inoculums: Insights for Unconscious Microorganisms' Selection

The producers of traditional fermented beverages select inoculums as a practical way to acquire an optimal fermentation capacity and their capability to give consistent quality and aroma compositions through the fermentation process. As documented before, the selection of inoculums is related to a community of bacteria and yeasts that improves the fermentation dynamics and is mainly characterized by a reduction of diversity (Alves et al., 2010; Anagnostopoulos et al., 2020; Lu et al., 2021). In the colonche production, *cinaiste* is the common name of the inoculum, it is stored from previous batches year after year, and our data indicate a marked dominance of *S. cerevisiae* strains and a higher number of reads compared with the rest of samples analyzed. The large inoculum of active *S. cerevisiae* cells in most cases ensures a rapid dominance of a single strain and will therefore likely reduce any impact that the natural microbiota may have if spontaneous fermentation is allowed. In addition, the inoculum shows the lowest bacterial diversity, which is consistent with a reduced richness in starter cultures, a pattern that has been previously documented for the selection of starter cultures in other traditional fermented products (Orji et al., 2003; Zorba et al., 2003; Freire et al., 2015; Fagbemigun et al., 2021; Lima et al., 2021). Our results therefore expand the documentation of the deliberate selection of microbial consortia to acquire an optimal fermented product.

Selection of microorganisms is an attempt to enhance a fermentative environment, such type of efforts to transform the environment are proposed to play an important and underappreciated role in shaping biotic communities and evolutionary processes (Jones et al., 1997; Odling-Smee et al., 2003; Anderson, 2005). In this context, the studies of management of microenvironments can make relevant contributions to analyze general processes of domestication of organisms and their environments. Morphological and physiological changes in plants and animals show evidence of domestication and provide insights of the specific human practices that produce them. Analogous changes in microorganisms are not easy to identify. In microorganisms as yeasts, features like the overexpression of metabolic routes like maltotriose and lactate, the loss of sexual reproduction and the decreasing survival in nature, have been considered significant traits to analyze domestication (Gibbons and Rinker, 2015; Gallone et al., 2016; Gibbons, 2019), but there is still a long way to explore in this direction. However, the characterization of the practices performed to produce colonche, particularly the selection of inoculums and their specific consortia, provide a signature of deliberate human management and shaping of the fermenting microenvironments.

Summarizing, our results confirm that the choice of fermentation practice and management practices as cooking the fruits or storing batches year after year influence the composition, structure, and dynamics of microbiota communities in the different stages of colonche fermentation. Coexistence of the different fermentation practices and management techniques favors the context to maintain and diversify microbial communities involved in the colonche production. As well, through the carefully reproduction of inoculums, producers promote and direct selection over microbial communities to guide the process of fermentation. The clay pots are important reservoirs of diversity, but they are not commonly considered relevant in fermentation studies. Although the most dominant bacterial and fungal ASVs were not dominant in the clay pot, its presence might highlight the importance at the beginning of the fermentation and the practices performed to clean it are also relevant to maintain the microbial community. Finally, characterizing the management practices that the producers perform to obtain specific traditional products gives insights about the knowledge that humans have to reshape biotic communities and micro-landscapes to obtain a quality product at the end of both fermentation types. Thus, it is relevant to conserve these techniques of micro-biocultural heritage, ensure its maintenance and, in some contexts, recover it in the context of the foodscape diversity (Mintz and Du Bois, 2002; Alexiades, 2003, 2009; Marshall and Mejia, 2011; Rocha et al., 2015).

CONCLUSION

The characterization of the microbial communities related to the production of a traditional fermented beverage prepared with fruits of *O. streptacantha* under spontaneous and inoculated fermentation practices, confirmed that the fermentation practices affect the species richness, diversity, and the community structure through spontaneous and inoculated fermentation practices. However, differences are slightly significant for the final products for fungal and bacterial communities, which might be the result of the increasing relative abundance of LAB and the outstanding abundance of *Saccharomyces* genus in final products of both fermentation types. The current information corroborates that there is a continuous selection on microbial communities through the elaboration and management of inoculums. This practice reduces the microbial community and, in the case studied, traditional fermenters select mostly LAB and *Saccharomyces* genera to begin their new batches of colonche year after year. Diverse microorganisms live in the container where fermentation occurs, nevertheless, trough the fermentation dynamics the diversity changes, and a stable community is reached. Although the current research was not directed to assess the differences in the colonche quality, the microbial composition at the end of the fermentation and the demand of the consumers for this product supports that both types of fermentation practices yield a good product. However, further analysis as the characterization of microbial functionalities and the physicochemical attributes might help to improve the fermentation practices. Altogether, these results provide the potential of the traditional knowledge and management over microorganisms to produce fermented beverages, thus, the importance to maintain these products, the practices and the diversity associated over the fermentation process. These results are relevant to ensure food security and safety in localities where food availability is constrained.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/, PRJNA781103.

AUTHOR CONTRIBUTIONS

CO-L conceived, designed, conducted, collected data, and wrote the manuscript. IS-G contributed to analyze the data, constructed figures, and drafted the manuscript. AC conceived, designed, advised, funded, drafted, and reviewed all versions of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.821268/full#supplementary-material

Supplementary Figure 1 | Rarefaction curves of the sample coverage for **(A)** bacterial and, **(B)** fungal community. Rarefaction curves of the observed ASVs of the **(C)** bacterial and **(D)** fungal community associated with the colonche stages and fermentation practices.

Supplementary Figure 2 | Non-metric multidimensional scaling (NMDS) plots-based **(A)** on UniFrac unweighted distance of the bacterial community structure; **(B)** and the fungal community structure associated with inoculated and spontaneous fermentation practices in the colonche production.

REFERENCES

Akinola, R., Pereira, L. M., Mabhaudhi, T., de Bruin, F. M., and Rusch, L. (2020). A review of indigenous food crops in Africa and the implications for more sustainable and healthy food systems. *Sustainability* 12:3493. doi: 10.3390/su12083493

Albert, S., Aswani, S., Fisher, P. L., and Albert, J. (2015). Keeping food on the table: human responses and changing coastal fisheries in Solomon Islands. *PLoS One* 10:e0130800. doi: 10.1371/journal.pone.0130800

Albuquerque, U. P., do Nascimento, A. L. B., da Silva, Chaves, L., Feitosa, I. S., de Moura, J. M. B., et al. (2019). A brief introduction to niche construction theory for ecologists and conservationists. *Biol. Conserv.* 237, 50–56. doi: 10.1016/j.biocon.2019.06.018

Alexiades, M. (2009). "The cultural and economic globalisation of traditional environmental knowledge systems," in *Landscape, process and power: re-evaluating traditional environmental knowledge*, ed. H. Serena (Oxford: Berghanh), 68–90.

Alexiades, M. N. (2003). Ethnobotany in the third millennium: expectations and unresolved issues. *Delpinoa* 45, 15–28.

Álvarez-Ríos, G. D., Figueredo-Urbina, C. J., and Casas, A. (2020). Physical, Chemical, and Microbiological Characteristics of Pulque: management of a Fermented Beverage in Michoacán, Mexico. *Foods* 9:361. doi: 10.3390/foods9030361

Alves, J. A., Lima, L. C. D. O., Dias, D. R., Nunes, C. A., and Schwan, R. F. (2010). Effects of spontaneous and inoculated fermentation on the volatile profile of lychee (Litchi chinensis Sonn) fermented beverages. *Int. J. Food Sci. Technol.* 45, 2358–2365. doi: 10.1111/j.1365-2621.2010.02409.x

An, F., Li, M., Zhao, Y., Zhang, Y., Mu, D., Hu, X., et al. (2021). Metatranscriptome-based investigation of flavor-producing core microbiota in different fermentation stages of Dajiang, a traditional fermented soybean paste of Northeast China. *Food Chem.* 343:128509. doi: 10.1016/j.foodchem.2020.128509

Anagnostopoulos, D. A., Kamilari, E., and Tsaltas, D. (2020). Evolution of bacterial communities, physicochemical changes and sensorial attributes of natural whole and cracked picual table olives during spontaneous and inoculated fermentation. *Front. Microbiol.* 11:1128. doi: 10.3389/fmicb.2020.01128

Anderson, M. K. (2005). *Tending the Wild*. Berkeley: University of California Press.

Andorrà, I., Landi, S., Mas, A., Guillamón, J. M., and Esteve-Zarzoso, B. (2008). Effect of oenological practices on microbial populations using culture-independent techniques. *Food Microbiol.* 25, 849–856. doi: 10.1016/j.fm.2008.05.005

Arena, M. P., Capozzi, V., Russo, P., Drider, D., and Fiocco, D. (2018). Immunobiosis and probiosis: antimicrobial activity of lactic acid bacteria with a focus on their antiviral and antifungal properties. *Appl. Microbiol. Biotechnol.* 102, 9949–9958. doi: 10.1007/s00253-018-9403-9

Astudillo-Melgar, F., Ochoa-Leyva, A., Utrilla, J., and Huerta-Beristain, G. (2019). Bacterial diversity and population dynamics during the fermentation of palm wine from Guerrero Mexico. *Front. Microbiol.* 10:531. doi: 10.3389/fmicb.2019.00531

Azaïs-Braesco, V., Bresson, J. L., Guarner, F., and Corthier, G. (2010). Not all lactic acid bacteria are probiotics,…but some are. *Br. J. Nutr.* 103, 1079–1081. doi: 10.1017/S0007114510000723

Badotti, F., de Oliveira, F. S., Garcia, C. F., Vaz, A. B. M., Fonseca, P. L. C., Nahum, L. A., et al. (2017). Effectiveness of ITS and sub-regions as DNA barcode markers for the identification of Basidiomycota (Fungi). *BMC Microbiol.* 17:42. doi: 10.1186/s12866-017-0958-x

Bagheri, B., Bauer, F. F., and Setati, M. E. (2015). The diversity and dynamics of indigenous yeast communities in grape must from vineyards employing different agronomic practices and their influence on wine fermentation. *South Afr. J. Enol. Vitic.* 36, 243–251.

Baldrian, P., Větrovský, T., Lepinay, C., and Kohout, P. (2021). High-throughput sequencing view on the magnitude of global fungal diversity. *Fungal Divers.* 1, 1–9. doi: 10.1007/s13225-021-00472-y

Ban, S., Chen, L., Fu, S., and Xu, Y. (2022). Modelling and predicting population of core fungi through processing parameters in spontaneous starter (Daqu) fermentation. *Int. J. Food Microbiol.* 363:109493. doi: 10.1016/j.ijfoodmicro.2021.109493

Barata, A., Malfeito-Ferreira, M., and Loureiro, V. (2012). The microbial ecology of wine grape berries. *Int. J. Food Microbiol.* 153, 243–259. doi: 10.1016/j.ijfoodmicro.2011.11.025

Bellaver, L. H., de Carvalho, N. M. B., Abrahão-Neto, J., and Gombert, A. K. (2004). Ethanol formation and enzyme activities around glucose-6-phosphate in Kluyveromyces marxianus CBS 6556 exposed to glucose or lactose excess. *FEMS Yeast Res.* 4, 691–698. doi: 10.1016/j.femsyr.2004.01.004

Blancas, J., Casas, A., Rangel-Landa, S., Moreno-Calles, A., Torres, I., Pérez-Negrón, E., et al. (2010). Plant Management in the Tehuacán-Cuicatlán Valley, Mexico 1. *Econ. Bot.* 64, 287–302. doi: 10.1007/s12231-010-9133-0

Bokulich, N. A., and Mills, D. A. (2013). Facility-specific "house" microbiome drives microbial landscapes of artisan cheesemaking plants. *Appl. Environ. Microbiol.* 79, 5214–5223. doi: 10.1128/AEM.00934-13

Bokulich, N. A., Kaehler, B. D., Rideout, J. R., Dillon, M., Bolyen, E., Knight, R., et al. (2018). Optimizing taxonomic classification of marker-gene amplicon sequences with QIIME 2's q2-feature-classifier plugin. *Microbiome* 6:90. doi: 10.1186/s40168-018-0470-z

Bokulich, N. A., Ohta, M., Richardson, P. M., and Mills, D. A. (2013). Monitoring seasonal changes in winery-resident microbiota. *PLoS One* 8:e66437. doi: 10.1371/journal.pone.0066437

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., et al. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat. Biotechnol.* 37, 852–857. doi: 10.1038/s41587-019-0209-9

Brandt, M. J. (2014). Starter cultures for cereal based foods. *Food Microbiol.* 37, 41–43. doi: 10.1016/j.fm.2013.06.007

Callahan, B. J., McMurdie, P. J., and Holmes, S. P. (2017). Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *ISME J.* 11, 2639–2643. doi: 10.1038/ismej.2017.119

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., and Holmes, S. P. (2016). DADA2: high-resolution sample inference from Illumina amplicon data. *Nat. Methods* 13, 581–583. doi: 10.1038/nmeth.3869

Campbell-Platt, G. (1994). Fermented foods: a world perspective. *Food Res. Int.* 27, 253–257. doi: 10.1016/0963-9969(94)90093-0

Cano, A. N. H., and Suárez, M. E. (2020). Ethnobiology of algarroba beer, the ancestral fermented beverage of the Wichí people of the Gran Chaco I: a detailed recipe and a thorough analysis of the process. *J. Ethn. Food.* 7:4.

Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., et al. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* 7, 335–336. doi: 10.1038/nmeth.f.303

Caporaso, J. G., Lauber, C. L., Walters, W. A., Berg-Lyons, D., Lozupone, C. A., Turnbaugh, P. J., et al. (2011). Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *Proc. Natl. Acad. Sci. U. S. A.* 108, 4516–4522. doi: 10.1073/pnas.1000080107

Casas, A., Caballero, J., Mapes, C., and Zárate, S. (1997). Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Bol. Soc. Bot. México* 61, 31–47. doi: 10.17129/botsci.1537

Casas, A., Otero-Arnaiz, A., Pérez-Negrón, E., and Valiente-Banuet, A. (2007). In situ management and domestication of plants in Mesoamerica. *Ann. Bot.* 100, 1101–1115. doi: 10.1093/aob/mcm126

Chao, A., and Chiu, C. H. (2016). "Species richness: estimation and comparison," in *Wiley StatsRef: Statistics Reference Online*, eds N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri, and J. L. Teugels (Chichester: John Wiley & Sons, Ltd), 1–26. doi: 10.1002/9781118445112.stat03432.pub2

Chao, A., Chiu, C. H., and Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annu. Rev. Ecol. Evol. Syst.* 45, 297–324. doi: 10.1146/annurev-ecolsys-120213-091540

Chaves-López, C., Rossi, C., Maggio, F., Paparella, A., and Serio, A. (2020). Changes occurring in spontaneous maize fermentation: an overview. *Fermentation* 6:36. doi: 10.3390/fermentation6010036

Chen, H., and Boutros, P. C. (2011). VennDiagram: a package for the generation of highly-customizable Venn and Euler diagrams in R. *BMC Bioinformatics* 12:35. doi: 10.1186/1471-2105-12-35

Cizeikiene, D., Juodeikiene, G., Paskevicius, A., and Bartkiene, E. (2013). Antimicrobial activity of lactic acid bacteria against pathogenic and spoilage microorganism isolated from food and their control in wheat bread. *Food Control* 31, 539–545. doi: 10.1016/j.foodcont.2012.12.004

Clement, C. R., Casas, A., Parra-Rondinel, F. A., Levis, C., Peroni, N., Hanazaki, N., et al. (2021). Disentangling domestication from food production systems in the neotropics. *Quaternary* 4:4. doi: 10.3390/quat4010004

Clement, C. R., Levis, C., Franco-Moraes, J., and Junqueira, A. B. (2020). "Domesticated nature: the culturally constructed niche of humanity," in *Participatory biodiversity conservation Concepts, Experiences, and Perspectives*, ed. C. Baldauf (Cham: Springer), 35–51. doi: 10.1007/978-3-030-41686-7_3

Cumming, G., Fidler, F., and Vaux, D. L. (2007). Error bars in experimental biology. *J. Cell Biol.* 177, 7–11. doi: 10.1083/jcb.200611141 da Silva Vale, A., de Melo Pereira, G. V., de Carvalho Neto, D. P., Sorto, R. D., Goés-Neto, A., Kato, R., et al. (2021). Facility-specific 'house'microbiome ensures the maintenance of functional microbial communities into coffee beans fermentation: implications for source tracking. *Environ. Microbiol. Rep.* 13, 470–481. doi: 10.1111/1758-2229.12921

De Filippis, F., Parente, E., and Ercolini, D. (2017). Metagenomics insights into food fermentations. *Microb. Biotechnol.* 10, 91–102. doi: 10.1111/1751-7915.12421

De Leblanc, A. D. M., Matar, C., and Perdigón, G. (2007). The application of probiotics in cancer. *Br. J. Nutr.* 98, S105–S110. doi: 10.1017/S0007114507839602

De Vuyst, L., and Vancanneyt, M. (2007). Biodiversity and identification of sourdough lactic acid bacteria. *Food Microbiol.* 24, 120–127. doi: 10.1016/j.fm.2006.07.005

De Vuyst, L., Vrancken, G., Ravyts, F., Rimaux, T., and Weckx, S. (2009). Biodiversity, ecological determinants, and metabolic exploitation of sourdough microbiota. *Food Microbiol.* 26, 666–675. doi: 10.1016/j.fm.2009.07.012

DeSantis, T. Z., Hugenholtz, P., Larsen, N., Rojas, M., Brodie, E. L., Keller, K., et al. (2006). Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Appl. Environ. Microbiol.* 72, 5069–5072. doi: 10.1128/AEM.03006-05

Devi, M., Rebecca, L. J., and Sumathy, S. (2013). Bactericidal activity of the lactic acid bacteria *Lactobacillus delbreukii*. *J. Chem. Pharm. Res.* 5, 176–180.

Domizio, P., Lencioni, L., Ciani, M., Di Blasi, S., Pontremolesi, C. D., and Sabatelli, M. P. (2007). Spontaneous and inoculated yeast populations dynamics and their effect on organoleptic characters of Vinsanto wine under different process conditions. *Int. J. Food Microbiol.* 115, 281–289. doi: 10.1016/j.ijfoodmicro.2006.10.052

El Sheikha, A. F., and Hu, D. M. (2020). Molecular techniques reveal more secrets of fermented foods. *Crit. Rev. Food Sci. Nutr.* 60, 11–32. doi: 10.1080/10408398.2018.1506906

Escalante, A., López Soto, D. R., Velázquez Gutiérrez, J. E., Giles-Gómez, M., Bolívar, F., and López-Munguía, A. (2016). Pulque, a traditional Mexican alcoholic fermented beverage: historical, microbiological, and technical aspects. *Front. Microbiol.* 7:1026. doi: 10.3389/fmicb.2016.01026

Evivie, S. E., Huo, G. C., Igene, J. O., and Bian, X. (2017). Some current applications, limitations and future perspectives of lactic acid bacteria as probiotics. *Food Nutr. Res.* 61:1318034. doi: 10.1080/16546628.2017.1318034

Fagbemigun, O., Rösch, N., and Sung, C. G. (2021). Nutritional and sensory qualities of indigenous and starter culture fermented milk from Nigeria. *Int. J. Sci. Technol.* 9, 7–9.

Fernández-Llamazares, Á, Lepofsky, D., Lertzman, K., Armstrong, C. G., Brondizio, E. S., Gavin, M. C., et al. (2021). Scientists' Warning to Humanity on Threats to Indigenous and Local Knowledge Systems. *J. Ethnobiol.* 41, 144–169. doi: 10.2993/0278-0771-41.2.144

Figueroa-Hernández, C., Mota-Gutierrez, J., Ferrocino, I., Hernández-Estrada, Z. J., González-Ríos, O., Cocolin, L., et al. (2019). The challenges and perspectives of the selection of starter cultures for fermented cocoa beans. *Int. J. Food Microbiol.* 301, 41–50. doi: 10.1016/j.ijfoodmicro.2019.05.002

Fitzpatrick, C. R., Copeland, J., Wang, P. W., Guttman, D. S., Kotanen, P. M., and Johnson, M. T. (2018). Assembly and ecological function of the root microbiome across angiosperm plant species. *Proc. Natl. Acad. Sci. U. S. A.* 115, E1157–E1165. doi: 10.1073/pnas.1717617115

Flachs, A., and Orkin, J. D. (2019). Fermentation and the ethnobiology of microbial entanglement. *Ethnobiol. Lett.* 10, 35–39. https://www.jstor.org/stable/26910053

Foligné, B., and Pot, B. (2013). Probiotics from research to market: the possibilities, risks and challenges. *Curr. Opin. Microbiol.* 16, 284–292. doi: 10.1016/j.mib.2013.06.008

Fonseca, A., and Inácio, J. (2006). "Phylloplane yeasts," in *Biodiversity and ecophysiology of yeasts*, eds G. Péter and C. Rosa (Berlin: Springer), 263–301. doi: 10.1007/3-540-30985-3_13

Forssten, S. D., Sindelar, C. W., and Ouwehand, A. C. (2011). Probiotics from an industrial perspective. *Anaerobe* 17, 410–413. doi: 10.1016/j.anaerobe.2011.04.014

Franco-Moraes, J., Clement, C. R., de Oliveira, J. C., and de Oliveira, A. A. (2021). A framework for identifying and integrating sociocultural and environmental elements of indigenous peoples' and local communities' landscape transformations. *Perspect. Ecol. Conserv.* 19, 143–152. doi: 10.1016/J.PECON.2021.02.008

Freire, A. L., Ramos, C. L., and Schwan, R. F. (2015). Microbiological and chemical parameters during cassava based-substrate fermentation using potential starter cultures of lactic acid bacteria and yeast. *Food Res. Int.* 76, 787–795. doi: 10.1016/j.foodres.2015.07.041

Gadaga, T. H., Lehohla, M., and Ntuli, V. (2021). Traditional fermented foods of Lesotho. *J. Microbiol. Biotechnol. Food Sci.* 2021, 2387–2391.

Gallone, B., Steensels, J., Prahl, T., Soriaga, L., Saels, V., Herrera-Malaver, B., et al. (2016). Domestication and divergence of Saccharomyces cerevisiae beer yeasts. *Cell* 166, 1397–1410. doi: 10.1016/j.cell.2016.08.020

Gibbons, J. G. (2019). How to Train Your Fungus. *mBio* 10, e02445–19. doi: 10.1128/mBio.03031-19

Gibbons, J. G., and Rinker, D. C. (2015). The genomics of microbial domestication in the fermented food environment. *Curr. Opin. Genet. Dev.* 35, 1–8. doi: 10.1016/j.gde.2015.07.003

Gutiérrez-Uribe, J. A., Figueroa, L. M., Martín-del-Campo, S. T., and Escalante, A. (2017). "Pulque," in *Fermented Foods in Health and Disease Prevention*, eds J. Frias, C. Martinez-Villaluenga, and E. Peñas (Cambridge: Academic Press), 543–556. doi: 10.1016/B978-0-12-802309-9.00023-6

Hanl, L., Sommer, P., and Arneborg, N. (2005). The effect of decreasing oxygen feed rates on growth and metabolism of Torulaspora delbrueckii. *Appl. Microbiol. Biotechnol.* 67, 113–118. doi: 10.1007/s00253-004-1695-2

Harris, L. J. (1998). "The microbiology of vegetable fermentations," in *Microbiology of fermented foods* (Boston: Springer), 45–72. doi: 10.1007/978-1-4613-0309-1_2

Harris, L. J., Daeschel, M. A., Stiles, M. E., and Klaenhammer, T. R. (1989). Antimicrobial Activity of Lactic Acid Bacteria Against Listeria monocytogenes. *J. Food Prot.* 52, 384–387. doi: 10.4315/0362-028X-52.6.384

Harth, H., Van Kerrebroeck, S., and De Vuyst, L. (2016). Community dynamics and metabolite target analysis of spontaneous, backslopped barley sourdough fermentations under laboratory and bakery conditions. *Int. J. Food Microbiol.* 228, 22–32. doi: 10.1016/j.ijfoodmicro.2016.04.011

Haruta, S., Ueno, S., Egawa, I., Hashiguchi, K., Fujii, A., Nagano, M., et al. (2006). Succession of bacterial and fungal communities during a traditional pot fermentation of rice vinegar assessed by PCR-mediated denaturing gradient gel electrophoresis. *Int. J. Food Microbiol.* 109, 79–87. doi: 10.1016/j.ijfoodmicro.2006.01.015

He, J., Zhang, R., Lei, Q., Chen, G., Li, K., Ahmed, S., et al. (2019). Diversity, knowledge, and valuation of plants used as fermentation starters for traditional glutinous rice wine by Dong communities in Southeast Guizhou, China. *J. Ethnobiol. Ethnomed.* 15:20. doi: 10.1186/s13002-019-0299-y

Hernández-Santana, G., and Narchi, N. E. (2018). "The seri traditional food system: cultural heritage, dietary change, and the (Re) awakening of dietary resilience among coastal hunter-gatherers in the Mexican Northwest," in *In Coastal Heritage and Cultural Resilience*, ed. L. L. Price (Cham: Springer), 135–182. doi: 10.1007/978-3-319-99025-5_7

Hong, L., Zhuo, J., Lei, Q., Zhou, J., Ahmed, S., Wang, C., et al. (2015). Ethnobotany of wild plants used for starting fermented beverages in Shui communities of southwest China. *J. Ethnobiol. Ethnomed.* 11:42. doi: 10.1186/s13002-015-0028-0

Hsieh, T. C., Ma, K. H., and Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). *Methods Ecol. Evol.* 7, 1451–1456. doi: 10.1111/2041-210X.12613

Johns, T., and Sthapit, B. R. (2004). Biocultural diversity in the sustainability of developing-country food systems. *Food Nutr. Bull.* 25, 143–155. doi: 10.1177/156482650402500207

Johns, T., Powell, B., Maundu, P., and Eyzaguirre, P. B. (2013). Agricultural biodiversity as a link between traditional food systems and contemporary development, social integrity and ecological health. *J. Sci. Food Agric.* 93, 3433–3442. doi: 10.1002/jsfa.6351

Jones, C. G., Lawton, J. H., and Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957. doi: 10.1890/0012-96581997078[1946:PANEOO]2.0.CO;2

Kemler, M., Witfeld, F., and Yurkov, A. (2017). "Phylloplane yeasts in temperate climates," in *Yeasts in Natural Ecosystems: Diversity*, eds P. Buzzini, M. A. Lachance, and A. M. Yurkov (Cham: Springer), 171–197. doi: 10.1007/978-3-319-62683-3_6

Kennedy, G., Kanter, R., Chotiboriboon, S., Covic, N., Delormier, T., Longvah, T., et al. (2021). Traditional and Indigenous Fruits and Vegetables for Food System Transformation. *Curr. Dev. Nutr.* 5:nzab092. doi: 10.1093/cdn/nzab092

Khalid, K. (2011). An overview of lactic acid bacteria. *Int. J. Biosci.* 1, 1–13.

König, H., Unden, G., and Fröhlich, J. (2009). *Biology of Microorganisms on Grapes, in Must and in Wine*. Heidelberg: Springer, 3–30. doi: 10.1007/978-3-319-60021-5

Krieger-Weber, S., Heras, J. M., and Suarez, C. (2020). *Lactobacillus plantarum*, a new biological tool to control malolactic fermentation: a review and an outlook. *Beverages* 6:23. doi: 10.3390/beverages6020023

Kuhnlein, H. V., and Receveur, O. (1996). Dietary change and traditional food systems of indigenous peoples. *Annu. Rev. Nutr.* 16, 417–442. doi: 10.1146/annurev.nu.16.070196.002221

Lefeber, T., Janssens, M., Camu, N., and De Vuyst, L. (2010). Kinetic analysis of strains of lactic acid bacteria and *acetic acid bacteria* in cocoa pulp simulation media toward development of a starter culture for cocoa bean fermentation. *Appl. Environ. Microbiol.* 76, 7708–7716. doi: 10.1128/AEM.01206-10

Legras, J. L., Galeote, V., Bigey, F., Camarasa, C., Marsit, S., Nidelet, T., et al. (2018). Adaptation of *S. cerevisiae* to fermented food environments reveals remarkable genome plasticity and the footprints of domestication. *Mol. Biol. Evol.* 35, 1712–1727. doi: 10.1093/molbev/msy066

Lévi-Strauss, C. (2012). "The culinary triangle," in *Food and Culture*, eds C. Counihan and P. Van Esterik (Oxfordshire: Routledge), 54–61.

Li, X., and Yue, X. (2016). Analysis of the microbiota in naturally fermented cabbage of Northeastern part of China by high-throughput sequencing of the V3-V4 regions of the 16S rRNA gene. *Int. J. Agric. Biol.* 18, 1153–1158. doi: 10.17957/IJAB/15.0219

Lima, C. O. D. C., Vaz, A. B., De Castro, G. M., Lobo, F., Solar, R., Rodrigues, C., et al. (2021). Integrating microbial metagenomics and physicochemical parameters and a new perspective on starter culture for fine cocoa fermentation. *Food Microbiol.* 93:103608. doi: 10.1016/j.fm.2020.103608

Liu, D., Legras, J. L., Zhang, P., Chen, D., and Howell, K. (2021). Diversity and dynamics of fungi during spontaneous fermentations and association with unique aroma profiles in wine. *Int. J. Food Microbiol.* 338:108983. doi: 10.1016/j.ijfoodmicro.2020.108983

Liu, L., She, X., Qian, Y., Li, Y., Tao, Y., Che, Z., et al. (2019). Effect of different fermenting containers on the deterioration of Sichuan pickle. *LWT* 111, 829–836. doi: 10.1016/j.lwt.2019.05.024

Liu, W., Pang, H., Zhang, H., and Cai, Y. (2014). "Biodiversity of lactic acid bacteria," in *Lactic Acid Bacteria*, eds H. Zhang and Y. Cai (Dordrecht: Springer), 103–203. doi: 10.1007/978-94-017-8841-0_2

Ljungh, A., and Wadstrom, T. (2006). Lactic acid bacteria as probiotics. *Curr. Issues Intest. Microbiol.* 7, 73–90.

Lozupone, C., Lladser, M. E., Knights, D., Stombaugh, J., and Knight, R. (2011). UniFrac: an effective distance metric for microbial community comparison. *ISME J.* 5, 169–172. doi: 10.1038/ismej.2010.133

Lu, Y., Guan, X., Li, R., Wang, J., Liu, Y., Ma, Y., et al. (2021). Comparative study of microbial communities and volatile profiles during the inoculated and spontaneous fermentation of persimmon wine. *Process Biochem.* 100, 49–58. doi: 10.1016/j.procbio.2020.09.023

Lyu, C., Chen, C., Ge, F., Liu, D., Zhao, S., and Chen, D. (2013). A preliminary metagenomic study of puer tea during pile fermentation. *J. Sci. Food Agric.* 93, 3165–3174. doi: 10.1002/jsfa.6149

Madej, T., Pirożnikow, E., Dumanowski, J., and Łuczaj, Ł (2014). Juniper beer in Poland: the story of the revival of a traditional beverage. *J. Ethnobiol.* 34, 84–103. doi: 10.2993/0278-0771-34.1.84

Marshall, E., and Mejia, D. (2011). *Traditional Fermented Food and Beverages for Improved Livelihoods*. Rome: FAO, 21.

Martinez, F. A. C., Balciunas, E. M., Salgado, J. M., Gonzalez, J. M. D., Converti, A., and de Souza Oliveira, R. P. (2013). Lactic acid properties, applications and production: a review. *Trends Food Sci. Technol.* 30, 70–83. doi: 10.1016/j.tifs.2012.11.007

McMurdie, P. J., and Holmes, S. (2013). phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS One* 8:e61217. doi: 10.1371/journal.pone.0061217

Metzker, M. L. (2010). Sequencing technologies: the next generation. *Nat. Rev. Genet.* 11, 31–46. doi: 10.1038/nrg2626

Mintz, S. W., and Du Bois, C. M. (2002). The anthropology of food and eating. *Annu. Rev. Anthropol.* 31, 99–119. doi: 10.1146/annurev.anthro.32.032702.131011

Mokoena, M. P. (2017). Lactic acid bacteria and their bacteriocins: classification, biosynthesis and applications against uropathogens: a mini-review. *Molecules* 22:1255. doi: 10.3390/molecules22081255

Montes-Carreto, L. M., Aguirre-Noyola, J. L., Solís-García, I. A., Ortega, J., Martinez-Romero, E., and Guerrero, J. A. (2021). Diverse methanogens, bacteria and tannase genes in the feces of the endangered volcano rabbit (Romerolagus diazi). *PeerJ* 9:e11942. doi: 10.7717/peerj.11942

Morales, P., Rojas, V., Quirós, M., and Gonzalez, R. (2015). The impact of oxygen on the final alcohol content of wine fermented by a mixed starter culture. *Appl. Microbiol. Biotechnol.* 99, 3993–4003. doi: 10.1007/s00253-014-6321-3

Motarjemi, Y. (2002). Impact of small scale fermentation technology on food safety in developing countries. *Int. J. Food Microbiol.* 75, 213–229. doi: 10.1016/S0168-1605(01)00709-7

Mukisa, I. M., Ntaate, D., and Byakika, S. (2017). Application of starter cultures in the production of Enturire–a traditional sorghum-based alcoholic beverage. *Food Sci. Nutr.* 5, 609–616. doi: 10.1002/fsn3.438

Nabhan, G. P. (2010). Ethnobiology for a diverse world: microbial ethnobiology and the loss of distinctive food cultures. *J. Ethnobiol.* 30, 181–183. doi: 10.2993/0278-0771-30.2.181

Nilsson, R. H., Larsson, K. H., Taylor, A. F. S., Bengtsson-Palme, J., Jeppesen, T. S., Schigel, D., et al. (2019). The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Res.* 47, D259–D264. doi: 10.1093/nar/gky1022

Odling-Smee, F. J., Laland, K. N., and Feldman, W. (2003). *Niche construction. Monographs in Population Biology*. Princeton: Princeton University Press, 37. doi: 10.1353/pbm.2003.0003

Ojeda-Linares, C. I., Vallejo, M., Lappe-Oliveras, P., and Casas, A. (2020). Traditional management of microorganisms in fermented beverages from cactus fruits in Mexico: an ethnobiological approach. *J. Ethnobiol. Ethnomed.* 16:1. doi: 10.1186/s13002-019-0351-y

Ojeda-Linares, C., Álvarez-Ríos, G. D., Figueredo-Urbina, C. J., Islas, L. A., Lappe-Oliveras, P., Nabhan, G. P., et al. (2021). Traditional fermented beverages of Mexico: a biocultural unseen foodscape. *Foods* 10:2390. doi: 10.3390/foods10102390

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., et al. (2013). Package 'vegan'. *Commun. Ecol. Package Ver.* 2, 1–295. http://cran.r-project.org/

Orji, M. U., Mbata, T. I., Aniche, G. N., and Ahonkhai, I. (2003). The use of starter cultures to produce 'Pito', a Nigerian fermented alcoholic beverage. *World J. Microbiol. Biotechnol.* 19, 733–736. doi: 10.1023/A:1025172506965

Parada, J. L., Caron, C. R., Medeiros, A. B. P., and Soccol, C. R. (2007). Bacteriocins from lactic acid bacteria: purification, properties and use as biopreservatives. *Braz. Arch. Biol. Technol.* 50, 512–542. doi: 10.1590/S1516-89132007000300018

Pieroni, A., Sõukand, R., Quave, C. L., Hajdari, A., and Mustafa, B. (2017). Traditional food uses of wild plants among the Gorani of South Kosovo. *Appetite* 108, 83–92. doi: 10.1016/j.appet.2016.09.024

Pingali, P. (2007). Westernization of Asian diets and the transformation of food systems: implications for research and policy. *Food Policy* 32, 281–298. doi: 10.1016/j.foodpol.2006.08.001

Pretorius, I. S., Van der Westhuizen, T. J., and Augustyn, O. P. H. (1999). Yeast biodiversity in vineyards and wineries and its importance to the South African wine industry. A review. *South Afr. J. Enol. Vitic.* 20, 61–70. doi: 10.21548/20-2-2234

Quave, C. L., and Pieroni, A. (2014). Fermented foods for food security and food sovereignty in the Balkans: a case study of the Gorani people of Northeastern Albania. *J. Ethnobiol.* 34, 28–43. doi: 10.2993/0278-0771-34.1.28

Quirós, M., Rojas, V., Gonzalez, R., and Morales, P. (2014). Selection of non-Saccharomyces yeast strains for reducing alcohol levels in wine by sugar respiration. *Int. J. Food Microbiol.* 181, 85–91. doi: 10.1016/j.ijfoodmicro.2014.04.024

Raspor, P., Cus, F., Jemec, K. P., Zagorc, T., Cadez, N., and Nemanic, J. (2002). Yeast population dynamics in spontaneous and inoculated alcoholic fermentations of Zametovka must. *Food Technol. Biotechnol.* 40, 95–102. http://www.ftb.com.hr

Ratcliffe, E., Baxter, W. L., and Martin, N. (2019). Consumption rituals relating to food and drink: a review and research agenda. *Appetite* 134, 86–93. doi: 10.1016/j.appet.2018.12.021

Rebollar, E. A., Sandoval-Castellanos, E., Roessler, K., Gaut, B. S., Alcaraz, L. D., Benítez, M., et al. (2017). Seasonal changes in a maize-based polyculture of central Mexico reshape the co-occurrence networks of soil bacterial communities. *Front. Microbiol.* 8:2478. doi: 10.3389/fmicb.2017.02478

Renouf, V., Claisse, O., and Lonvaud-Funel, A. (2007). Inventory and monitoring of wine microbial consortia. *Appl. Microbiol. Biotechnol.* 75, 149–164. doi: 10.1007/s00253-006-0798-3

Rocha, J. A., Boscolo, O. H., and Fernandes, L. R. R. D. M. V. (2015). Ethnobotany: a instrument for valorisation and identification of potential for the protection of traditional knowledge. *Interações* 16, 67–74. doi: 10.1590/151870122015105

Rocha-Arriaga, C., Espinal-Centeno, A., Martinez-Sánchez, S., Caballero-Pérez, J., Alcaraz, L. D., and Cruz-Ramírez, A. (2020). Deep microbial community profiling along the fermentation process of pulque, a biocultural resource of Mexico. *Microbiol. Res.* 241:126593. doi: 10.1016/j.micres.2020.126593

Schwan, R. F., and Wheals, A. E. (2004). The microbiology of cocoa fermentation and its role in chocolate quality. *Crit. Rev. Food Sci. Nutr.* 44, 205–221. doi: 10.1080/10408690490464104

Sha, S. P., Jani, K., Sharma, A., Anupma, A., Pradhan, P., Shouche, Y., et al. (2017). Analysis of bacterial and fungal communities in Marcha and Thiat, traditionally prepared amylolytic starters of India. *Sci. Rep.* 7:10967. doi: 10.1038/s41598-017-11609-y

Sha, S. P., Suryavanshi, M. V., Jani, K., Sharma, A., Shouche, Y. S., and Tamang, J. P. (2018). Diversity of yeasts and molds by culture-dependent and culture-independent methods for mycobiome surveillance of traditionally prepared dried starters for the production of Indian alcoholic beverages. *Front. Microbiol.* 9:2237. doi: 10.3389/fmicb.2018.02237

Singh, V. P. (2018). Recent approaches in food bio-preservation-a review. *Open Vet. J.* 8, 104–111. doi: 10.4314/ovj.v8i1.16

Smid, E. J., and Hugenholtz, J. (2010). Functional genomics for food fermentation processes. *Annu. Rev. Food Sci. Technol.* 1, 497–519. doi: 10.1146/annurev.food.102308.124143

Smid, E. J., and Kleerebezem, M. (2014). Production of aroma compounds in lactic fermentations. *Annu. Rev. Food Sci. Technol.* 5, 313–326. doi: 10.1146/annurev-food-030713-092339

Smith, B. D. (2007). Niche construction and the behavioral context of plant and animal domestication. *Evol. Anthropol.* 16, 188–199. doi: 10.1002/evan.20135

Solís-García, I. A., Ceballos-Luna, O., Cortazar-Murillo, E. M., Desgarennes, D., Garay-Serrano, E., Patiño-Conde, V., et al. (2021). Phytophthora root rot modifies the composition of the avocado rhizosphere microbiome and increases the abundance of opportunistic fungal pathogens. *Front. Microbiol.* 11:3484. doi: 10.3389/fmicb.2020.574110

Sõukand, R., Pieroni, A., Biró, M., Dénes, A., Dogan, Y., Hajdari, A., et al. (2015). An ethnobotanical perspective on traditional fermented plant foods and beverages in Eastern Europe. *J. Ethnopharmacol.* 170, 284–296. doi: 10.1016/j.jep.2015.05.018

Steinkraus, K. H. (1996). *Handbook of Indigenous Fermented Food*, 2nd Edn. New York: Marcel Dekker, Inc.

Svanberg, I. (2015). Ræstur fiskur: air-dried fermented fish the Faroese way. *J. Ethnobiol. Ethnomed.* 11:76. doi: 10.1186/s13002-015-0064-9

Tamang, J. P. (2010). "Diversity of fermented beverages," in *Fermented Foods and Beverages of the World*, eds J. P. Tamang and K. Kailasapathy (New York: CRC Press), 85–125. doi: 10.1007/s00253-016-7941-6

Tamang, J. P., Cotter, P. D., Endo, A., Han, N. S., Kort, R., Liu, S. Q., et al. (2020). Fermented foods in a global age: east meets West. *Compr. Rev. Food Sci. Food Saf.* 19, 184–217. doi: 10.1111/1541-4337.12520

Tamang, J. P., Jeyaram, K., Rai, A. K., and Mukherjee, P. K. (2021). Diversity of beneficial microorganisms and their functionalities in community-specific ethnic fermented foods of the Eastern Himalayas. *Food Res. Int.* 148:110633. doi: 10.1016/j.foodres.2021.110633

Tamang, J. P., Sarkar, P. K., and Hesseltine, C. W. (1988). Traditional fermented foods and beverages of Darjeeling and Sikkim–a review. *J. Sci. Food Agric.* 44, 375–385. doi: 10.1002/jsfa.2740440410

Tamang, J. P., Watanabe, K., and Holzapfel, W. H. (2016). Review: diversity of microorganisms in global fermented foods and beverages. *Front. Microbiol.* 7:377. doi: 10.1007/BF00437031

Tamang, J. P.,and Fleet, G. H. (2009). "Yeasts diversity in fermented foods and beverages," in *Yeasts Biotechnology: Diversity and Applications*, eds T. Satyanarayana and G. Kunze (New York: Springer), 169–198. doi: 10.1007/978-1-4020-8292-4_9

Timothy, B., Iliyasu, A. H., and Anvikar, A. R. (2021). Bacteriocins of lactic acid bacteria and their industrial application. *Curr. Top. Lact. Acid Bact. Probiotics* 7, 1–13. doi: 10.35732/ctlabp.2021.7.1.1

Todorov, S. D., and Holzapfel, W. H. (2015). "Traditional cereal fermented foods as sources of functional microorganisms," in *Advances in fermented foods and beverages*, ed. W. Holzapfel (Sawston: Woodhead Publishing), 123–153. doi: 10.1016/B978-1-78242-015-6.00006-2

Tsafrakidou, P., Michaelidou, A. M., and Biliaderis, G. C. (2020). Fermented cereal-based products: nutritional aspects, possible impact on gut microbiota and health implications. *Foods* 9:734. doi: 10.3390/foods9060734

Turner, N. J., and Turner, K. L. (2007). Traditional food systems, erosion and renewal in Northwestern North America. *Indian J. Tradit. Knowl.* 6, 57–68. http://hdl.handle.net/123456789/828

Ulloa, M., and Herrera, T. (1978). Torulopsis taboadae, una nueva especie de levadura aislada del colonche de Zacatecas. México. *Sci. Fungorum* 12, 5–12.

van Dijken, J. P., Weusthuis, R. A., and Pronk, J. T. (1993). Kinetics of growth and sugar consumption in yeasts. *Antonie van leeuwenhoek* 63, 343–352. doi: 10.1007/BF00871229

Varela, J. A., Gethins, L., Stanton, C., Ross, P., and Morrissey, J. P. (2017). "Applications of Kluyveromyces marxianus in Biotechnology," in *Yeast diversity in human welfare*, eds T. Satyanarayana and G. Kunze (Singapore: Springer), 439–453. doi: 10.1007/978-981-10-2621-8_17

Viesser, J. A., de Melo Pereira, G. V., de Carvalho Neto, D. P., Favero, G. R., de Carvalho, J. C., Goés-Neto, A., et al. (2021). Global cocoa fermentation microbiome: revealing new taxa and microbial functions by next generation sequencing technologies. *World J. Microbiol. Biotechnol.* 37:118. doi: 10.1007/s11274-021-03079-2

Visser, W., Scheffers, W. A., Batenburg-van, der Vegte, W. H., and van Dijken, J. P. (1990). Oxygen requirements of yeasts. *Appl. Environ. Microbiol.* 56, 3785–3792. doi: 10.1128/aem.56.12.3785-3792.1990

Vogelmann, S. A., and Hertel, C. (2011). Impact of ecological factors on the stability of microbial associations in sourdough fermentation. *Food Microbiol.* 28, 583–589. doi: 10.1016/j.fm.2010.11.010

Vogelmann, S. A., Seitter, M., Singer, U., Brandt, M. J., and Hertel, C. (2009). Adaptability of lactic acid bacteria and yeasts to sourdoughs prepared from cereals, pseudocereals and cassava and use of competitive strains as starters. *Int. J. Food Microbiol.* 130, 205–212. doi: 10.1016/j.ijfoodmicro.2009.01.020

Wade, M. E., Strickland, M. T., Osborne, J. P., and Edwards, C. G. (2019). Role of Pediococcus in winemaking. *Aust. J. Grape Wine Res.* 25, 7–24. doi: 10.1111/ajgw.12366

Xufre, A., Albergaria, H., Inácio, J., Spencer-Martins, I., and Gírio, F. (2006). Application of fluorescence in situ hybridisation (FISH) to the analysis of yeast population dynamics in winery and laboratory grape must fermentations. *Int. J. Food Microbiol.* 108, 376–384. doi: 10.1016/j.ijfoodmicro.2006.01.025

Yang, L., Yang, H. L., Tu, Z. C., and Wang, X. L. (2016). High-throughput sequencing of microbial community diversity and dynamics during douchi fermentation. *PLoS One* 11:e0168166. doi: 10.1371/journal.pone.0168166

Yao, H., Song, J., Liu, C., Luo, K., Han, J., Li, Y., et al. (2010). Use of ITS2 region as the universal DNA barcode for plants and animals. *PLoS One* 5:e13102. doi: 10.1371/journal.pone.0013102

Zacharof, M. P., and Lovitt, R. W. (2012). Bacteriocins produced by lactic acid bacteria a review article. *Apcbee Procedia* 2, 50–56. doi: 10.1016/j.apcbee.2012.06.010

Zhu, M. Z., Li, N., Zhou, F., Ouyang, J., Lu, D. M., Xu, W., et al. (2020). Microbial bioconversion of the chemical components in dark tea. *Food Chem.* 312:126043. doi: 10.1016/j.foodchem.2019.126043

Zorba, M., Hancioglu, O., Genc, M., Karapinar, M., and Ova, G. (2003). The use of starter cultures in the fermentation of boza, a traditional Turkish beverage. *Process Biochem.* 38, 1405–1411. doi: 10.1016/S0032-9592(03)00033-5

Zott, K., Claisse, O., Lucas, P., Coulon, J., Lonvaud-Funel, A., and Masneuf-Pomarede, I. (2010). Characterization of the yeast ecosystem in grape must and wine using real-time PCR. *Food Microbiol.* 27, 559–567. doi: 10.1016/j.fm.2010.01.006

Zott, K., Miot-Sertier, C., Claisse, O., Lonvaud-Funel, A., and Masneuf-Pomarede, I. (2008). Dynamics and diversity of non-Saccharomyces yeasts during the early stages in winemaking. *Int. J. Food Microbiol.* 125, 197–203. doi: 10.1016/j.ijfoodmicro.2008.04.001

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Ecological Knowledge and Management of Fauna Among the *Mexicatl* of the Sierra Negra, México: An Interpretive Approach

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Generally motivated by the relevance of animals in human subsistence, the management of fauna has taken different shapes throughout the world. This study aims to analyse a typology of management forms, exploring their relationship with the motivation to maintain coexistence and use of fauna and mitigate negative human-fauna interactions by the *Mexicatl* (Nahua) people in Central Mexico. We generally expected to find a broad spectrum of management types in a gradient of interactions intensity. This is because we hypothesised that the more meaningful these interactions due to the magnitude of benefit or damage, philias, or phobias among other positive or negative perceptions, and ecological aspects and management viability, the more actions and practices might be motivated to maintain or mitigate them. We conducted a qualitative research based on interpretivist approaches, mixing qualitative and quantitative analyses, to register the *Mexicatl* names of fauna present in the area and recognised by locals and to analyse the influence of local ecological knowledge (LEK) and natural history as perceived by people on the use, conflicts, and management practices regarding local fauna. In order to gather such information, in 2018 and 2019 we generated 356 free lists of fauna and 20 sessions of group interviews about the presence of animals in the area, the *Mexicatl* name, information on distribution, diet, use, management, and other facts. We used visual stimuli with children and young people from schools of basic and intermediate levels in five rural communities and the municipal head of Coyomeapan, Puebla. We also generated free lists and in-depth interviews with 18 persons older than 16 years. People recognised 114 animal items, the most salient being 11 domestic and 14 wild animals including deer, medium and small mammals, snakes, and birds. For both domestic and wild fauna, people reported 18 use categories and three types of damage (crop losses, predation of domestic animals, and damages to health). LEK interacted with traditional celebrations, religious beliefs, land tenure, and migration to define preferences and management types of fauna. Bushmeat demand, especially for *Mazama temama* and *Cuniculus paca,* was related to a perception of healthy nutrition properties. Management actions included husbandry of domestic animals, extraction of wild animals for supply, or to avoid damages, captivity, tolerance to damage, protection of seeds and domestic animals threatened by wild fauna, regulations for extraction of wild fauna, and agreements to prevent conflicts. Mixed quantitative and qualitative approaches allowed the interpretation of the human-fauna interactions related to subsistence, coexistence, and the high relevance of LEK, perceptions, religious beliefs, ecosystem, socio-demographic factors, and animal behaviour and habits, which are crucial factors that influence the shaping of management practices. Local management strategies of fauna were diverse and contribute to biocultural conservation and theoretical construction on domestication.

Keywords: ethnozoology, wildlife, worldview, local ecological knowledge, animals management, traditional ecological knowledge, humans-animals coexistence, subsistence

INTRODUCTION

Management actions are concrete expressions of worldviews of human individuals or societies. It involves decisions on elements and/or processes of ecosystems at several scales to use, conserve, and/or restore them (Casas et al., 2016). Management of fauna populations may involve decisions on animals' ecological partners, such as host plants, diet elements, or abiotic elements of their habitat (Ojasti, 2000; Zeder, 2015) to ease obtention, ensure the availability of animals (Zeder, 2015), or to deliberately reduce their populations (Ojasti, 2000; Sinclair et al., 2006).

Fauna management actions are based on the several corpuses of place-based, local empirical knowledge that accumulated, evolved through time, and incorporated Western scientific and conservation biology principles (Sánchez, 1999). Local ecological knowledge (LEK) (or traditional ecological knowledge *sensu* Berkes, 2008) is adaptive information (i.e., knowledge, beliefs, values, symbols, techniques, and practices) about the interactions of living beings, including humans, with others and their environment that is transmitted through generations (Berkes, 2008). Local management may, or may not, be enough to allow the viability of fauna populations and their habitats, especially when external pressures (i.e., global, national) cause the deterioration of quality of life and environment, and the collapse of local institutions (Ostrom et al., 1999; Agatha, 2016), including the mechanisms of LEK adaptation and transmission (Fernández-Llamazares and Reyes-García, 2016). However, research on local management practices that likely do it, including technology, decision making (Ostrom et al., 1999), and the favourable social institutions and conditions that allow this management to occur, should enlighten conservation strategies (Casas et al., 2016).

Fauna plays complex roles in human life. People engage in affective or even religious relations with animals. They recognise their intrinsic value or consider them in their ecological dimension. However, humans also appreciate fauna in a utilitarian sense or relate it to factors of damage. Animals have provided food, medicine, company as pets, ornaments, traction, transport, materials to manufacture tools or shelter, entertainment, amulets, and symbols of status, religion, belonging to a group (Nóbrega-Alves, 2012; Nóbrega-Alves and Albuquerque, 2018), or offering in ceremonies (López-Austin, 1999; Willerslev and Vitebsky, 2014; Santos-Fita et al., 2015). Animals may also be bioindicators about changes in weather (Rivero-Romero et al., 2016; Nóbrega-Alves and Duarte-Barboza, 2018) and human health (Nóbrega-Alves and Albuquerque, 2018). In addition, animals, trained or not, can help to obtain other animals in hunting or fishing (Santos-Fita et al., 2012; Pinto et al., 2018). Nevertheless, fauna may also transmit diseases, compete with humans for food, or be poisonous and harmful, which can sometimes result in human lethal actions towards fauna populations (Marchini, 2014).

Negative interactions between humans and wildlife occur when requirements and behaviour of the latter have negative impacts on human agenda, or vice versa (Madden, 2004). Human conflict can also arise when groups of people disagree regarding the animals' management (Marchini, 2014). For instance, while some persons or human groups involved in the management of a socio-ecological system consider that they receive a benefit due to the presence of an animal, others may consider it as harmful (Ceausu et al., 2018). But both conflicts and conditions to achieve human-fauna coexistence may be managed (Madden, 2004), and attending to them has become a main challenge for biodiversity conservation.

Coexistence is mediated through ecological, cultural, economic, and social dimensions. Therefore, it cannot be universally defined (Knox et al., 2020). However, this concept has been proposed (Madden, 2004) to integrate the management of human-wildlife and human-human reaction to conflicts in a way that ensures the long-term viability of populations of both humans and wildlife. Coexistence considers the ability to share a landscape in space and/or time, the human tolerance towards the damages caused by wildlife (Lute and Carter, 2020), the learning and changes in behaviour from both wildlife and humans, and the presence and legitimacy of social institutions, including formal and informal rules that regulate reaction to conflicts (Carter and Linell, 2016).

The purpose of our research was to analyse how LEK, human perceptions of fauna, and ecological aspects and habits of animals interact to shape the types of management practices by the *Mexicatl* people towards wild and domestic fauna, for satisfying subsistence needs and human-fauna coexistence. We analysed these aspects in a context in which people live close to forests and heavily depend on biotic and agricultural resources to live and continually make decisions towards fauna on their daily life. We aimed to answer the following questions: (1) Which wild and domestic animals are relevant to people in their human-influenced and wild environments? (2) Which needs use animals for satisfaction? Which animals are used to satisfy these needs?; (3) Which animals cause damages? What specific damage(s) do they cause? (4) How do people manage animals? (5) Which management choices, based on LEK, allow the human-fauna coexistence? and (6) How do human-fauna interactions differ among villages located in different ecosystems?

We generally expected that LEK plays a major role in the management practices engaged to ensure the availability of useful fauna and to mitigate human-fauna negative interactions or human-human conflicts that could arise in relation to animals. In addition, other factors related to ecological aspects, behaviour, and habits of animals influence how the interactions and management are.

MATERIALS AND METHODS

Study Area

The municipality of Coyomeapan is located in the portion of the Sierra Madre Occidental known as Sierra Negra in the state of Puebla, México. It is part of the area of influence of the Tehuacán-Cuicatlán Biosphere Reserve (Secretaría de Medio Ambiente y Recursos Naturales-Comisión Nacional de ÁĄreas Naturales Protegidas [SEMARNAT- CONANP], 2013). We conducted our work in Santa María Coyomeapan, an urban nucleus with 1,288 people (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020) and in four *Mexicatl* rural communities. The village of Aticpac, with 160 inhabitants (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020), is located in the transition between semi-evergreen tropical forest, cloud forest, and pine forest. The village is settled in an area locally known as "Tierra Caliente" (TC), which includes the villages of Ahuatla, Caxalli, and Ixtlahuac with 554, 216, and 431 inhabitants, respectively (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020), are located in the pine forest area, which in this manuscript will be referred to as "Sierra." People's subsistence mainly relies on the agroecosystem called *milpa* which includes maize, beans, and several species of edible weedy plants called *"quelites"* (Blancas et al., 2013). In the Sierra, crops also include apple, fava beans, chile canario (*Capsicum pubescens* Ruiz and Pav) and avocado, while in the TC, crops include sugarcane, banana, coffee, and tepejilote (*Chamaedorea tepejilote* Liebm.). Domestic animals raised include sheep (*Ovis aries* L.), goats (*Capra hircus* L.), pigs (*Sus scrofa* L.), chickens (*Gallus gallus* L.), and turkeys (*Meleagris gallopavo* L.). Familiar remittances from abroad are a considerable source of income; small commerce and low intensity tourism also occur. Trade of products from the different ecosystem regions is carried out in the plaza of Santa María Coyomeapan every Thursday and Sunday. Zoological and ethnozoological literature is scarce for the area, but previous work reported the presence of the American deer (*Mazama temama* Kerr) (Pérez-Solano et al., 2012), herpetofauna (Canseco and Gutiérrez, 2010; Linares-Rosas et al., 2021), and use reports of 13 mammals, snakes, and immature stages of Saturniidae and Hepialidae Lepidoptera (Zarazúa-Carbajal et al., 2020; Linares-Rosas et al., 2021; **Figure 1**).

Research Design

Our work incorporates insights from the grounded theory (Strauss and Corbin, 1998), ethnosciences (Argueta et al., 2012; Casas et al., 2016; Nóbrega-Alves and Albuquerque, 2018; Albuquerque et al., 2020), and fauna management (Ojasti, 2000; Sinclair et al., 2006; Zeder, 2006, 2015; Carter and Linell, 2016; Zarazúa, 2016; Ceausu et al., 2018; Zarazúa-Carbajal et al., 2020). We conducted exploratory qualitative research that allowed us to adopt an interpretive perspective from which the construction of multiple realities through social interaction is recognised. In addition, it allowed to show that the investigation was influenced by the researcher's own interpretations (Maxwell, 2013; Castillo et al., 2020). The information was generated through cultural domain and semi-structured interview techniques (Newing et al., 2011) and through direct observation of items and events. We included people of different profiles (women, men, specialised hunters, children, and teenagers) who use and manage animals and could show variation in their perspectives about fauna management to increase the internal validity of the analysis (Drury et al., 2011). Although the general approach is qualitative, we used both quantitative and qualitative analyses of the information.

Semi-Structured Interviews and Observation

From April 2018 to July 2019, we conducted workshops with 356 students aged 8–17 years old in groups of 15–40 students each in three elementary schools, two secondary schools, and one high school. Also, we carried out individual in-depth interviews with adults (>16 years old). Each workshop and interview started with a presentation of our research team that included the purposes of the project. We requested permission to take notes and/or audio recordings before each session. In workshops, we asked the students to write down, individually, a free list of the animals present in the community. Free lists included wild and domestic fauna items. We continued with a visual stimulus instrument consisting, in the projection, of photographs of animal species previously reported in the Tehuacán-Cuicatlán and the Sierra Negra regions. We asked the following about each animal: if it occurs in the area, its *Mexicatl* name, information on distribution, diet, use, management, and free additional facts. We conducted 11 workshops about mammals, four about domestic fauna, three about herpetofauna, two about insects, and one about birds (**Supplementary Additional Table 1** in Additional File 1). In each session, we carried out games (30–180 min each, depending on the interest of the group) in which we asked open questions about the damages an animal may cause.

Interviews with adults were carried out with 14 women and four men of 18 households from Ahuatla, Caxalli, and Aticpac (nine from the Sierra, and nine from the TC). They

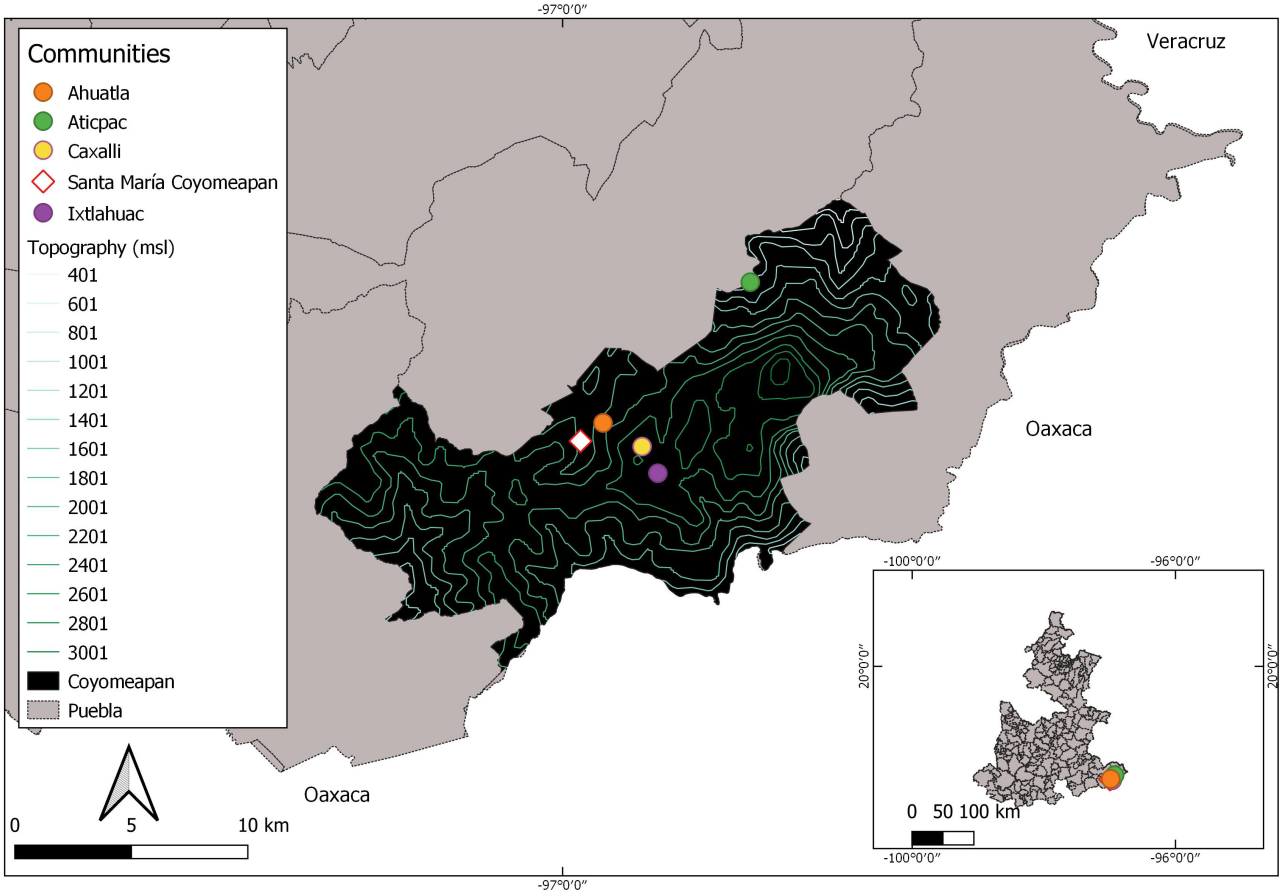

FIGURE 1 | Study Area. Rural communities are displayed as circles and the municipal seat as a square. Aticpac is classified as "Tierra Caliente" (TC) while Ahuatla, Caxalli, and Ixtláhuac as "Sierra." The Cerro del Tzintzintepetl (Tzintzintepetl Hill) is located in the highest elevation area between Aticpac and the Sierra communities. Figure elaborated in Quantum Geographic Information System (QGIS) (Open Source Geospatial foundation [OsGeo], 2020). with layers available from Geoportal Comisión Nacional para la Biodiversidad (CONABIO, 1998; Ávila-Blomberg and Moreno-Díaz, 2008; Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2018).

recognised themselves as *Mexicatl* and were bilingual *Mexicatl*–Spanish speakers, native from their villages or living there for at least 15 years. Their main economic activities are agriculture and animal husbandry, but some of them have complementary occupations. We started asking an oral free list of the wild animals present in the community, prioritising mentions of wild animals that would be more difficult to be directly observed by visitors compared with domestic animals. Afterwards, we performed a semi-structured in-depth interview, with open questions about nomenclature, distribution, diet, use, conflicts, and management (**Supplementary Additional Table 2** in Additional File 1). We added questions to deepen information or when new subjects arose. Printed photographs of the animals or its display on a laptop screen were used to relate an animal to its taxonomic identity and to stimulate conversations. Additional information related to fauna management that arose from direct observation (i.e., demonstrations of management practices by people, hunting evidence such as skins or skulls) or informal conversations was registered in pictures and field diaries and used as a complementary source of data. When cited as sources of information throughout this manuscript, interviews to adult people are labelled as follows: (a) Sierra: D6, D7/8/9, D10, D11, D12, D13/28, D14, D25, D16, D18; and (b) TC: D5/23, D19, D20, D21, D22, D24, D25, D26, D27, while information from workshops with students is labelled D41 for the secondary school of the municipal head, D42 for the high school the municipal head, and D43 for Mariana Zarazúa (MZ) field diaries.

Data Analysis

Free Lists

Items were listed in Spanish and/or *Mexicatl*. Before the analysis, all items were homogenised in their written nomenclature to avoid synonyms. Male, female, and young animals of a given species were considered as one item (i.e., rooster, hen and chicken; male and female turkey). However, we maintained the distinction between creole turkey and farm turkey, butterfly and their immature stages, and between frog and tadpole. All free lists' analyses were performed using R 3.6.3 R software (2020) and R studio (2021).

We calculated the frequency of mention of each item, its average order of mention, and the Smith salience index, calculated as follows: $S = \left(\Sigma \frac{L-Rj+1}{L}\right) N$; where "L" is the length of the list, "R*j*" is the rank of item *j* in the list, and "N" is the number of lists (Smith and Borgatti, 1997) in accordance with da Silva et al. (2019). An item was considered salient if its Smith salience index value was above the average value for the group and if the probability that the value turned out by chance was less than 5% ($p < 0.05$). To calculate this probability per group, lists from 1,000 random populations with the same number of items and informants as the group were simulated using the Monte Carlo method (da Silva et al., 2019). To perform the analysis, we grouped the lists following age and provenance of people. At the first level, we grouped the students' overall lists (n = 356). Then, we grouped students' lists in eight sets according to their community of origin and school grade (elementary, 8–12 years old; secondary, 12–15 years old; and high school, 15–17 years old) to register the matches of the salient items among these eight sets. Free lists from adults were analysed by overall grouping ($n = 16$) on the first level and as two sets (TC and Sierra, 8 free lists each) on the second level.

We compared the total inventory of wild fauna items among age groups (adults, high school, secondary school, and elementary school students) and regions (Sierra, TC, municipal head) according to the presence/absence of data with an analysis of similarities (ANOSIM) using Jaccard distances ("anosim" function, package vegan, Rsoftware) (Oksanen et al., 2020). In a similar way, we compared the inventory of wild fauna salient items among age groups (adults vs. secondary school).

Salience, Use, and Conflict Reports

We built contingency tables with the counts of the listed items (students and adults separately), categorising variables according to the salience (salient or not salient), use (yes or not), and whether they cause damage (yes or not). We tested the independence between these variables with the Fisher's exact test (fisher.test function, R software).

Analysis of Natural History, Use, Conflict, and Management Typology

Audios and notes were transcribed, and the text was codified (Strauss and Corbin, 1998; Maxwell, 2013) by using the software ATLAS.ti 8 (2021). Codes were grouped into categories (Maxwell, 2013; **Table 1**) and organised into a typology and a general scheme of fauna use and management.

RESULTS

Free List Inventory, Frequency, Order, and Salience Analyses

Students' Free List

An inventory of 108 animal items was registered in 356 lists. Wild mammals represented 26.78% of the items followed by arthropods at 24.11%, birds at 19.96%, reptiles at 8.93%, amphibia at 3.57%, snail, and fish (one item each). All domestic animals

TABLE 1 | Organisational categories and references of theoretical frames used for analysing the information generated in this research.

Category[a]	Definition (Number and percentage of mentions)[b]	References
Natural history (O)	Codes and categories relating to diet, life cycles, distribution or ecological interactions of used/managed fauna	NA
Fauna use (O)	Codes and categories describing use typology (155 mentions for 70 animals; 100%)	López-Austin, 1999; Nóbrega-Alves, 2012; Willerslev and Vitebsky, 2014; Santos-Fita et al., 2015; Rivero-Romero et al., 2016; Nóbrega-Alves and Albuquerque, 2018; Nóbrega-Alves and Duarte-Barboza, 2018; Pinto et al., 2018.
Food (T)	Meat, eggs, milk or other parts and products of an animal, except honey, are eaten (26%)	
Ornamental/ Exhibition (T)	The living animal, taxidermies, or parts of the animal's body such as skin or bone remains are displayed as an ornament or status symbol (18%)	
Medicine (T)	The animal or parts of the animal are used to treat illnesses or aid birth labour (14%)	
Pet (T)	The animal is kept alive as animal companion (7%)	
Tool (T)	Parts of the animal such as bones, shields, antlers, or products such as wax are used as an instrument to facilitate human work (6%).	
Commercialisation (T)	People obtain an income after selling the animal to a second user (6%)	
Recreational (T)	An animal or its parts are used for recreation (4%)	
Amulet (T)	An animal or its parts are worn, kept, or displayed for protection against illness, or for attract good fortune (4%)	
Bioindicator (T)	Animals that indicate changes in weather, through behaviour and/or other phenotypical traits (3.3%)	
Traction/transport (T)	An animal is used to carry weight, people or as a draught animal (2%)	
Gift/offering (T)	Animals used as food or a special gift for someone in dairy life or to the godparents "padrinos" in social celebrations such as weddings, or ritual ceremonies "vestir al difunto" (dress a deceased person), among others (turkey) (2%)	
Honey (T)	Use of the honey, generally with edible or medicinal purposes (1.3%)	

(Continued)

TABLE 1 | (Continued)

Category[a]	Definition (Number and percentage of mentions)[b]	References
Fertiliser (T)	Use of the animal faeces to improve growth and productiveness of the plants (1.3%)	
Pest control (T)	Use of the animal to reduce the presence of damaging insects or mice (1.3%)	
Souvenir (T)	Part of the animal is kept as a reminder of a place or event (1.3%)	
Surveillance (T)	The animal is kept for announcing the presence of someone in the house or to drive away damaging fauna (1.3%)	
Animal health (T)	Animals are used to treat or prevent animal illness (1.3%)	
Aid in hunting (T)	Animals are used to facilitate the hunt (0.65%)	
Fibres (T)	Use of the shelter of the animal for obtaining raw material to manufacture strings, clothing or others (0.65%)	
Damage caused by fauna (O)	Codes and categories describing damages caused by fauna to crops, domestic animals or human health (41 mentions for 36 animals; 100%)	Marchini, 2014
Crop damage (T)	Crop losses because the animals (wild or domestic) predate part of the plants, either foliage, roots, flowers, fruits, or seeds; it also includes behaviours such as plant removing while looking for insects (61%)	
Predation of domestic animals (T)	Animals kill or feed on domestic animals, causing death, wounds, or illness. These are mostly wild animals, but free ranging dogs are also included (24%)	
Damage to human health (T)	These include disease (i.e., rabies) transmission, ophidian accident, and stings or bites of animals considered as poisonous (14.6%)	
Damage to merchandise (T)	This was the case only for the stole of eggs from a small grocery store by *Bassariscus* sp. (<1%)	
Fauna management (O)	Codes and categories describing actions towards fauna, host plants or habitat, intended to use, conserve, restore, perform land planning, reduce damages caused by fauna or achieve coexistence.	Ostrom et al., 1999; Ojasti, 2000; Sinclair et al., 2006; Zeder, 2006, 2015; Casas et al., 2016; Carter and Linell, 2016; Zarazúa-Carbajal et al., 2020
Supply (T)	Practices for obtaining animals in order to use them. Includes: Hunting, wild fauna captivity, gathering, feeding of domestic animals, health of domestic animals, reproduction of domestic animals, cares towards domestic animals.	
Extraction for prevention (T)	Fauna extraction to prevent damages to other items or processes. Includes: Hunting, poisoning	
Prevention (T)	Damage prevention that does not involve fauna extraction. Includes: Cares towards domestic animals, drive away, crop protection	
Assume the loss (T)	Withdrawal from economic activities or tolerance to the damages caused by fauna, because damage prevention is not effective. Includes: Tolerance to damage, abandonment of an activity.	
Human conflict prevention (T)	Agreements between people to prevent or remediate human conflicts caused by fauna management. Includes: agreements about grazing, gathering, hunting, retribution for stallion.	
Conservation (T)	Regulations to fauna extraction. Includes: Agreements, rules, personal attitudes that could imply regulations to fauna extraction.	

(Continued)

[a]*O, organisational categories (general subjects of research, used for ordering the information and defined before the interviews) T, theoretical categories (allow to situate the information in an abstract framework; they are defined by the researcher, often arising from theoretical background) (Maxwell, 2013). NA, does not apply.*
[b]*Number of mentions for use and damage was calculated as the summatory of the number of categories mentioned for each animal, by all interviewed adults (n = 18). A given animal could have been mentioned by the same person for more than one use or damage category.*

(mammals and birds) represented the 15.75% In addition, this technique allowed the registry of two items that we did not expect within the animal cultural domain, the "chane" and the "duende" (two of several spiritual beings recognised by people as present in forests, sometimes tricky, specially to children), although its frequency was low (n = 2 each). The 24 items that were determined as salient included 11 domestic and 13 wild animals (eight mammals, two reptiles, two birds, and one butterfly). Although not salient, the items, namely, frog, racoon, and bee, also had Smith values above the mean (**Table 2**). **Table 3** shows a summary of the lists by school groups.

Adult People's Free Lists

A total of 48 wild items were listed by adults. Mammals represented the seven most salient items (squirrel, deer, rabbit, white-nosed coati, racoon, opossum, and armadillo) and 45.8% of the listed items. Reptiles and birds represented 20.83% in each of the listed items and arthropods the 10.41%. Although not salient, the items snake, peccary, paca, skunk, and dove had Smith index values above the mean (**Table 4** and **Supplementary Additional File 2**).

We did not find significant differences in the general wild animal inventory between age groups (adults vs. high school vs. secondary school vs. elementary school $R = 0.1364$, $p = 0.171$) or provenance (Sierra vs. Tierra Caliente vs. Municipal seat $R = 0.1798$, $p = 0.133$) for wild animal salient items between age groups (adults vs. secondary school $R = 0.75$, $p = 0.333$).

Salience, Use, and Conflict Reports

We rejected the independent null hypothesis between a higher salience and use reports for both students and adults (respectively, p-value < 0.05; p-value $= 0.01$). We also rejected

TABLE 2 | Smith salience index, mean position, and frequency of wild and domestic animal items in 356 students' free lists, with *p*-values.

Item in English	Item in Spanish[a]	Salience (Smith Index)	Salience *p*-value	Mean position	Mean position *p*-value	Frequency	Frequency *p*-value
rabbit	**conejo**	**0.584**	0	**5.1538**	0	**286**	0
dog	**perro**	**0.5039**	0	**5.3202**	0.0001	**253**	0
hen	**gallina**	**0.485**	0	**7.2028**	0.0246	**281**	0
cat	**gato**	**0.4725**	0	**6.4598**	0.002	**261**	0
snake	**serpiente**	**0.3874**	0	**7.083**	0.0173	**229**	0
squirrel	**ardilla**	**0.3641**	0	7.7293	0.0896	**229**	0
turkey	**guajolote**	**0.3459**	0	7.5743	0.0619	**202**	0
bird	**pájaro**	**0.3137**	0	7.6763	0.0796	**207**	0
deer	**venado**	**0.313**	0	7.4565	0.0464	**184**	0
horse	**caballo**	**0.2484**	0	8.1494	0.1984	**154**	0
lamb	**borrego**	**0.2168**	0	9.7267	0.1842	**161**	0
pig	**cerdo**	**0.2134**	0	9.6139	0.2189	**158**	0
mouse	**ratón**	**0.2028**	0	9.872	0.147	**164**	0
donkey	**burro**	**0.1896**	0	8.976	0.4676	**125**	0
cow	**vaca**	**0.1834**	0	11.6621	0.0023	**145**	0
armadillo	**armadillo**	**0.1698**	0	9.487	0.2617	**115**	0
lizard	**lagartija**	**0.1663**	0	9.9697	0.1262	**132**	0
eagle	**águila**	**0.1518**	0	9.2703	0.34	**111**	0
duck	**pato**	**0.1442**	0	8.8696	0.487	**92**	0
opossum	**tlacuache**	**0.1385**	0	**10.5849**	0.0369	**106**	0
goat	**chivo**	**0.1355**	0	**10.5926**	0.0362	**108**	0
butterfly	**mariposa**	**0.1189**	0	**11.6204**	0.0024	**108**	0
coyote	**coyote**	**0.1108**	0.0003	**6.9016**	0.0101	**61**	0.0151
gray fox	**zorra**	**0.1072**	0.0005	9.5946	0.2247	**74**	0
frog	rana	0.0864	0.0683	10.0968	0.1	**62**	0.0105
racoon	mapache	0.0732	0.3573	9.4038	0.2906	52	0.2001
bee	abeja	0.0724	0.3856	**13.4**	0	**70**	0.0002
fish	pez	0.0676	0.4438	**10.8148**	0.0209	54	0.1279
vulture	zopilote	0.0672	0.4305	**10.86**	0.0189	50	0.2988
spider	araña	0.0635	0.3025	9.9615	0.127	52	0.2001
ant	hormiga	0.0564	0.1157	13.2545	0	55	0.1002
hawk	gavilán	0.0531	0.0625	**10.5952**	0.0361	42	0.2854
gopher	tuza	**0.0475**	0.0173	**11.3256**	0.0053	43	0.3438
peccary	jabalí	**0.0433**	0.0056	9.1538	0.3892	**26**	0.0003
owl	búho	**0.0417**	0.0033	9.5	0.2583	**30**	0.0042
fly	mosca	**0.0403**	0.0023	10.0667	0.1057	**30**	0.0042
worm	gusano	**0.039**	0.0014	**12.9512**	0	41	0.2323
hummingbird	colibrí	**0.0347**	0.0002	**11.0435**	0.0117	**23**	0.0001
toad	sapo	**0.0314**	0	**11.9231**	0.0009	**26**	0.0003
skunk	zorrillo	**0.0306**	0	**15.7667**	0	**30**	0.0042
cricket	grillo	**0.0294**	0	10.3182	0.0645	**22**	0.0001
dove	paloma	**0.0283**	0	**12.7727**	0	**22**	0.0001
bat	murciélago	**0.0266**	0	**14.8485**	0	**33**	0.0181
woodpecker	pájaro carpintero	**0.0261**	0	**10.9412**	0.0152	**17**	0
owl	tecolote	**0.0223**	0	**11.6364**	0.0024	**22**	0.0001
wolf	lobo	**0.0218**	0	9.4667	0.2675	**15**	0
turtle	tortuga	**0.0208**	0	10	0.1207	**12**	0
earthworm	lombriz	**0.017**	0	**14.1875**	0	**16**	0
white nosed coati	tejón	**0.0167**	0	**11.9231**	0.0009	**13**	0
mole	topo	**0.0152**	0	10.2727	0.0711	**11**	0

(Continued)

TABLE 2 | (Continued)

Item in English	Item in Spanish[a]	Salience (Smith Index)	Salience *p*-value	Mean position	Mean position *p*-value	Frequency	Frequency *p*-value
ring tailed cat	*chicna*	**0.014**	0	9.1	0.4128	**10**	0
tadpole	renacuajo	**0.0137**	0	**11.1**	0.0102	**10**	0
grasshopper	chapulín	**0.0126**	0	**13.7**	0	**10**	0
mount cat	gato montés	**0.0113**	0	**5.4**	0.0001	**5**	0
snail	caracol	**0.0108**	0	**15.7**	0	**10**	0
Mexican alligator lizard	kuwishi	**0.0105**	0	**6.1667**	0.0007	**6**	0
iguana	iguana	**0.0093**	0	**11**	0.0135	**14**	0
rat	rata	**0.0091**	0	7.6667	0.0785	**6**	0
lice	piojo	**0.0089**	0	**15**	0	**9**	0
mosquito	mosco	**0.0079**	0	**13.7**	0	**10**	0
scorpion	alacrán	**0.0076**	0	**16.9**	0	**10**	0
poxokuili	*poxokuili*	**0.0069**	0	**13**	0	**5**	0
wessel	onza	**0.0068**	0	**12.1667**	0.0005	**6**	0
mule	mula	**0.0065**	0	8.75	0.4355	**4**	0
wasp	avispa	**0.0058**	0	15.8333	0	**6**	0
rattlesnake	cascabel	**0.0054**	0	**13.6**	0	**5**	0
tarantula	tarántula	**0.0054**	0	**2**	0	**2**	0
woodlouse	cochinilla	**0.0052**	0	**13.2**	0	**5**	0
paca	tepezcuintle	**0.005**	0	**7**	0.0138	**4**	0
raven	cuervo	**0.0049**	0	**12.6667**	0	**3**	0
margay	tigrillo	**0.0044**	0	8	0.1565	**2**	0
peacock	pavo real	**0.0041**	0	**12.6**	0.0001	**5**	0
canary	canario	**0.0034**	0	**15**	0	**3**	0
monkey	mono	**0.0033**	0	10	0.1207	**3**	0
centipedes	cienpiés	**0.0032**	0	**18**	0	**4**	0
cockroach	cucaracha	**0.0032**	0	**14.3333**	0	**3**	0
caterpillar	*xigala*	**0.003**	0	8.5	0.3321	**2**	0
farm turkey	pavo	**0.0028**	0	**14.25**	0	**4**	0
sparrow	gorrión	**0.0025**	0	**15.3333**	0	**3**	0
Coral snake	coralillo	**0.0024**	0	**11.6667**	0.0023	**3**	0
quail	codorniz	**0.0023**	0	9.5	0.2583	**2**	0
porcupine	puercoespín	**0.0023**	0	9	0.4613	**2**	0
insect	insecto	**0.0022**	0	**15.5**	0	**2**	0
beetle	escarabajo	**0.0021**	0	**18**	0	**2**	0
fierce	*tekuani*	**0.0021**	0	**11.25**	0.0066	**4**	0
caterpillar	oruga	**0.0019**	0	**17**	0	**3**	0
hare	liebre	**0.0017**	0	10	0.1207	**2**	0
cardinal bird	pájaro cardenal	**0.0017**	0	**6**	0.0003	**1**	0
grasshopper	saltamonte	**0.0016**	0	**7**	0.0138	**1**	0
palanca snake	palanca	**0.0015**	0	9	0.4613	**1**	0
mockingbird	zenzontle	**0.0015**	0	**15.5**	0	**2**	0
dragon fly	libelula	**0.0013**	0	**15.5**	0	**2**	0
jaguar	jaguar	**0.0012**	0	9	0.4613	**2**	0
horn pitviper	*nagascoatl*	**0.0012**	0	11	0.0135	**1**	0
aquatic snake	víbora de agua	**0.0012**	0	9	0.4613	**1**	0
axolotl	ajolote	**0.001**	0	**17.5**	0	**2**	0
parakeet	perico	**0.001**	0	**18**	0	**2**	0
hawk	halcón	**0.0008**	0	**16**	0	**1**	0
flea	pulga	**0.0008**	0	**20.3333**	0	**3**	0
chane	*chane*	**0.0005**	0	**23**	0	**2**	0
kinkajou	*biok*	**0.0004**	0	**15**	0	**1**	0

(Continued)

TABLE 2 | (Continued)

Item in English	Item in Spanish[a]	Salience (Smith Index)	Salience *p*-value	Mean position	Mean position *p*-value	Frequency	Frequency *p*-value
Stick worm	gusano de palo	**0.0004**	0	**23.5**	0	**2**	0
dove	pichón	**0.0004**	0	**22**	0	**1**	0
"capanila" bird	pájaro capanila	**0.0003**	0	**16**	0	**1**	0
dwarf	duende	**0.0002**	0	**24**	0	**2**	0
goose	ganso	**0.0002**	0	**27**	0	**1**	0
anteater	oso hormiguero	**0.0002**	0	**18**	0	**1**	0
moth	polilla	**0.0001**	0	**21**	0	**1**	0

Animal items listed: 108, Mean of Smith97 index: 0.069, Mean of Frequency: 46.20. Salient items and significative values (p < 0.05) are shown in bold letters.
[a]Mexicatl names are instead provided for some animals (italics).

TABLE 3 | Number of lists and items for each school group.

	High school Santa Maria	Secondary school Santa Maria	High school Ahuatla[b]	Secondary school Ahuatla[b]	Primary school Ahuatla	Secondary school Ixtlahuac	Primary school Caxalli	Schools Aticpac
Zone classification	Municipal seat[a]	Municipal seat[a]	Sierra Low	Sierra Low	Sierra Low	Sierra High	Sierra High	Tierra Caliente[c]
Number of lists	60	188	15	27	16	16	18	16
Total number of items	69	100	51	56	40	34	33	53
Number of salient items	17	23	11	10	10	7	4	11
Mean of Smith salience (lowest – higher value)	0.103 (0.001–0.669)	0.078 (0.000–0.611)	0.147 (0.003–0.623)	0.130 (0.001–0.568)	0.175 (0.002–0.555)	0.159 (0.006–0.757)	0.207 (0.012–0.558)	0.164 (0.003–0.695)
Mean of Frequency (lowest- higher value)	11.449 (1–55)	27.59 (1–156)	4.137 (1–14)	6.571 (1–21)	5.225 (1–12)	4.617 (1–14)	6.934 (1–11)	4.943 (1–14)

[a]Including rural barrios Segunda sección and Cuarta sección; [b]selected from municipal head secondary and high school; and [c]10 students from elementary school, 3 from secondary school and 3 from the municipal head high school. Outputs available in Supplementary Additional File 2.

the independent null hypothesis between a higher salience and damage reports for students (*p*-value < 0.05), but not for adults. A high percentage of the listed animals was not reported to have any use or did not cause any damage (**Table 5**).

Recognised Diet, Distribution, Seasonality, and Life Cycles

Diet

Most birds and mammals were reported to feed on sources related to anthropogenic activities such as crops, secondary vegetation, or domestic animals. However, trees identified as sources of food for birds and mammals in the lowlands of TC were black "*zapotl*" [*Diospyros nigra* (JF Gmel.) Perrier], "*amatl*" (*Ficus* sp.), and "*yoloxochitl*" (*Magnolia* sp.), while in the highlands, "*xometl*" (*Sambucus mexicana* C. Presl ex DC), pinecones (*Pinus* spp.), and acorns (*Quercus* spp.) were mentioned. White tailed deer was reported to feed on "*apashmama*" (*Lopezia racemosa* Cav.) and "*teterisia*" (*Monnina xalapensis* Kunth) leaves, butterflies, bees, stingless bees, hummingbirds, and bats were recognised as flower visitors that feed on nectar and pollen. On the other hand, bats were also identified as blood suckers, frugivorous, and insectivorous. Dogs and cats were reported to feed mainly on wild fauna and on human leftovers (**Supplementary Additional File 3**).

Environmental Units of Presence and Distribution of Fauna

We found similar trends across age groups in the identification of environmental units associated to presence and distribution of fauna. Three categories of distribution were identified: (1) general environmental units, including mount (the most frequent response in all age groups), field, water bodies, homes, and milpas standing among other crops such as banana, apple, peach, and pea; (2) specific elements of the environment, namely trees (the most frequent response in all age groups), stones, herbs, soil, under the stones, underground, dry trees, rotten trees, canyon, and trails, among others; and (3) spatial units, namely, TC and Tzintzintepetl Hill. TC was related to mammals, snakes, birds and arthropods. Tzintzintepetl Hill was related to wild animals in general and fantastic fauna (eg., an animal that produces gold). The main difference between generations was that spatial units were not reported by children from elementary schools, but were mentioned in workshops of secondary-high school and in interviews with adults (**Supplementary Additional File 6**).

TABLE 4 | Smith salience index, mean position, and frequency of wild animal items in 16 adults' free lists, with *p*-values.

Item in English	Item in Spanish[a]	Salience (Smith Index)	Salience *p*-value	Mean position	Mean position *p*-value	Frequency	Frequency *p*-value
squirrel	**ardilla**	**0.612**	0	3.8571	0.1551	**14**	0
deer	**venado**	**0.6048**	0	2.9167	0.0723	**12**	0
rabbit	**conejo**	**0.4575**	0	4.7273	0.2597	**11**	0
white nosed coati	**tejón**	**0.3952**	0.0001	2.875	0.0723	**8**	0.0064
racoon	**mapache**	**0.3665**	0.0005	5.3333	0.3332	**9**	0.0009
opossum	**tlacuache**	**0.2933**	0.0068	3.3333	0.1093	6	0.0853
armadillo	**armadillo**	**0.2617**	0.0195	6.7143	0.534	**7**	0.0274
snake	víbora	0.212	0.0716	6.875	0.4511	**8**	0.0064
peccary	jabalí	0.1629	0.2049	8.2	0.2839	5	0.2063
paca	tepezcuintle	0.136	0.3254	9.8333	0.1492	6	0.0853
skunk	zorrillo	0.1335	0.3386	5.5	0.3737	4	0.4103
dove	paloma	0.1251	0.3817	7	0.4511	5	0.2063
ring tailed cat	*chicna*	0.1056	0.4941	7.3333	0.3948	3	0.5897
gray fox	zorra	0.1027	0.4755	4	0.1982	2	0.3295
bird	pájaro	0.0997	0.456	6.5	0.5148	4	0.4103
quail	*koyotcho*	0.0943	0.4192	6	0.457	4	0.4103
bat	murciélago	0.0936	0.4132	5.5	0.3737	2	0.3295
wessel	onza	0.0786	0.3233	7.5	0.3777	2	0.3295
margay	tigrillo	0.0625	0.2323	8.5	0.2614	2	0.3295
scorpion	alacrán	0.0595	0.2015	4.5	0.2435	2	0.3295
rattlesnake	cascabel	0.0583	0.1951	9	0.2236	2	0.3295
coyote	coyote	0.0574	0.1891	9	0.2236	2	0.3295
hummingbird	colibrí	0.0529	0.1637	3	0.104	1	0.114
turtle	tortuga	0.0481	0.1397	4	0.1982	1	0.114
hawx	*kuixi*	0.0469	0.1338	5	0.3197	1	0.114
lizard	lagartija	0.0441	0.1198	11.6667	0.0657	3	0.5897
woodpecker	p carpintero	0.0439	0.1193	12.5	0.0482	2	0.3295
owl	tecolote	0.0404	0.1026	7	0.4511	1	0.114
frog	rana	0.0341	0.0798	11	0.0977	1	0.114
black widow	viuda negra	0.0312	0.0677	4	0.1982	1	0.114
anteater	oso hormiguero	0.0288	0.0607	8	0.3247	1	0.114
iguana	iguana	0.0284	0.0595	**13**	0.0416	1	0.114
mouse	ratón	0.0267	0.0534	**14.5**	0.0201	2	0.3295
mazahuatl snake	*mazahuatl*	0.0257	0.051	11	0.0977	1	0.114
kinkajou	*biok*	0.0256	0.0505	**14**	0.0257	1	0.114
pheasant	faisán	**0.0246**	0.0476	8.5	0.2614	2	0.3295
eagle	águila	**0.024**	0.0455	9	0.2236	1	0.114
coral snake	coralillo	**0.0221**	0.0421	12	0.0641	1	0.114
agouti	*kowtuza*	**0.0208**	0.0366	9	0.2236	1	0.114
tonalquetzi bird	*tonalquetzi*	**0.0192**	0.0316	10	0.1481	1	0.114
tepotzo snake	*tepotzo*	**0.0184**	0.0312	**13**	0.0416	1	0.114
ahuatl snake	*ahuatl*	**0.0147**	0.0223	**14**	0.0257	1	0.114
rat	rata	**0.0142**	0.02	**18**	0.0053	1	0.114
cricket	grillo	**0.0114**	0.0163	**19**	0.0039	1	0.114
gopher	tuza	**0.01**	0.0133	**12.5**	0.0482	2	0.329
cockroach	cucaracha	**0.0085**	0.0076	**20**	0.0028	1	0.114
Mexican alligator lizard	*kuwishi*	**0.0078**	0.0065	**15**	0.0182	1	0.114
fly	mosca	**0.0048**	0.0014	**13**	0.0416	1	0.114

Animal items listed: 48, Mean of Smith97 index: 0.109, Mean of Frequency: 3.167 Salient items and significative values ($p < 0.05$) are shown in bold letters.
[a]*Mexicatl names are instead provided for some animals (italics).*

TABLE 5 | Contingency tables with the count of items with use and damage reports included in free lists.

Group of freelists	Variable	Use (proportion in brackets)			Damage (proportion in brackets)		
Students	**Salience**	**no**	**yes**	**total**	**no**	**yes**	**total**
(108 items)	no	62 (0.57)	22 (0.20)	84 (0.77)	62 (0.57)	22 (0.20)	84 (0.77)
	yes	3 (0.02)	21 (0.19)	24 (0.22)	10 (0.09)	14 (0.12)	24 (0.21)
	Total	65 (0.59)	43 (0.39)	108	72 (0.66)	36 (0.32)	108
Adults	Salience	no	yes	total	no	yes	total
(48 items)	no	22 (0.45)	19 (0.39)	41 (0.85)	19 (0.39)	22 (0.45)	41 (0.85)
	yes	0	7 (0.15)	7 (0.15)	1 (0.02)	6 (0.13)	7 (0.15)
	Total	22 (0.45)	26 (0.54)	48	20 (0.42)	28 (0.58)	48

Insects (*Okuilitzin*)

"Hoja santa" or *"nextokuili"* (Coleoptera: Melolonthidae) (D27 TC) is an animal that becomes the plant "*tlanekpakilitl,*" *Piper auritum* Kunth, after it burrows underground (D20 TC, D21 TC, D23, TC). The similarity of the inflorescence of the plant to a white worm is interpreted by participants as a vestige of this transformation (D23 TC).

"Kuetla" is the immature stage of the butterfly *Arsenura armida* Cramer (**Figure 2**). Three instars were recognised. In the first one, caterpillars have "horns" and are small and dark. As they grow, they lose their horns and become fatty. When they are ready to be eaten, they are fatty, with green, orange, and dark stripes. They can be found in groups of over a hundred in the higher section of a single trunk of a *Heliocarpus appendiculatus* Turcz tree. They lay in the trunk during the day, but feed on leaves at night. People said that when *kuetlas* fall from trees, they are eaten by snakes. Therefore, people must be aware and mindful when approaching a *Heliocarpus* tree to collect *"kuetla."* Some women expressed their phobia towards these larvae. They are found in groups, which are called "little herds" or "*setlamoxotzintli*" in Mexicatl (Nahuatl) (D23 TC). *Kuetlas* availability occurs mainly in July but also on October.

A life cycle involving Hepialidae, Saturniidae, Cicacidae, and Melolonthidae was proposed in TC, where these insect groups co-occur. The "*chajkchama,*" "*chajchamokuili,*" or true *"poxokuili"* larvae (immature Hepialidae) live inside the "*chajkchamakowitl*" tree (*Lippia myriocephala* Schltdl. And Cham.) for 2 or 3 months. Since woodpeckers predate them, they are usually only found in the lower sections of trees (D43 TC). Then, the "*chajkchama*" enters a stage in which "it loses its hands" (corresponding to the pupa, called "*mosawa*"), and afterwards becomes a butterfly (**Figure 2**). Then, the butterfly will only live for around a month and lays its eggs in a different tree (*H. appendiculatus*). These eggs become the *poxokuili or "kuetla"* (immature stages of *A. armida*). Afterwards, these *kuetla* fall down, burrow in the soil, and become a cicadas (Cicacidae) "*xikilixi,*" which is seen aboveground for 3 or 4 months during the warm season. Some people have heard that this cycle further continues—that Cicacidae become "*nextokuili*" (Melolonthidae) and *Piper auritum*. It is because of such cycles of metamorphosis linking one insect to another that *Lippia myriocephala*'s bark and *Piper auritum* leaves and stems have nice, beautiful, and similar smells (D23 TC, D43 TC).

Reptiles

Snakes (kuwatl). In the Sierra region the main kind of snakes recognised by people were the rattlesnakes "*tehuankuwatl*" (*Crotalus* spp.), the aquatic snakes "*ahuatl*" (*Thamnophis* sp.), and the horned vipers "*akaskuwatl*" (*Ophryacus* spp.). According to locals, rattlesnakes are abundant and fearful. They run away or hide inside the earth in the presence of people. Therefore, snake bites are rare events. Snakes are often seen near fallen trees (D14

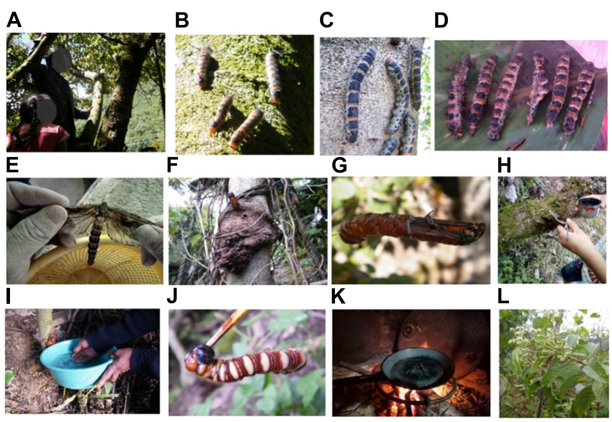

FIGURE 2 | *Kuetlas*, also called *poxokuili*, are collected from *H. appendiculatus* in the secondary vegetation and then relocated in a *H. appendiculatus* tree into the family home to be maintained under surveillance. **(A)** A girl and his grandfather supervise that a small group "manadita" recently collected climbs up the selected tree. At this stage, *kuetlas* had horns **(B)**, but the procedure can be also done with more mature *kuetlas* such as in **(C)**. **(D)** *Kuetlas* roasted by the girl's grand-grandmother are ready to be eaten as a snack. *Hepialidae gathering*. After identification as "the mother," an adult was released by a man in TC, with the intention of assuring the presence of this animal **(E)**. If the house or "little sponge" in host trees is intact, the worm must be present. Otherwise, the sponge will have holes or the molt left in the change from pupa to adult can be seen **(F,G)**. A girl in TC **(H)** and a woman in Sierra **(I)** show how to take out a "worm" from *Lippia myriocephala* and *Fraxinus* sp. **(J)** using water to drown it and, afterwards, using a spine to extract it when its head comes out. It must be done in silence since worms are very aware of the presence of predators. If they notice that a person is nearby, they will not come out. **(K)** Worms are fried with salt and eaten as a snack. **(L)** *L. myriocephala*.

S). Meanwhile, aquatic snakes are perceived to be abundant in rivers and springs, mainly during April and May (D11 S, D12 S). Their abundance in the Sierra is the reason why the village "Ahuatla" has its name (D8 S) (although "*ahuatl*" can also have other meanings such as "thorn" or "oak"). They are also fearful and do not bite. According to participants, they "just see you and jump into the water" (D12 S). In contrast, the horned pit vipers are considered to be fearless and wait for people or even approach closer instead of running away (D8 S, D12 S). However, encounters with this snake may have a symbolic value (D13 S). A man is said to have killed one, and to his surprise, inside the snake were nine smaller ones – its offspring. This meant that this kind of snake does not lay eggs, as locals have thought before "it is like a rabbit, not like a bird" (D8 S).

Because the offspring were different sizes, he thought that some of them were more mature than others and, therefore, were meant to born at different times (D8 S). The man wondered how many at a time and how often. Coral snakes, called "*eskuwatl,*" were also reported in the Sierra, but were more often associated to TC (D11 S), where there is a much higher abundance and variety of snakes are recognised. However, species richness in the Sierra was recognised to be underestimated as a participant said, "there are more snakes, but we do not know how to identify them because we do not know them" (D16 S). Lizards *"kuwishi"* (*Abronia* spp.) are believed to be "the mother of the rattlesnake" which may explain why they are considered as poisonous and even feared (D13 S).

Mammals

Small mammals like squirrels, rabbits, and opossums are commonly seen near villages or in crop fields. In the Sierra, two kinds of squirrels are recognised by people: one arboreal which has red hair "*chichilmoto*" (*Sciurus aureogaster* F.Cuvier) and one of the same sizes, but grey, that inhabits within holes in the rocks and is called "*tlalmoto.*" In TC, a third type, called "*tepaxi*" or "*tepaxitsi,*" which is smaller and feeds on nuts was recognised. Rabbits are commonly seen in the field (D10 S, D8 S). They are born within a hole in the ground, during which the female removes its hair and places them inside the hole to shelter her cubs. If she comes out, she covers the hole with ground to avoid predation by weasel (*Mustela frenata* Lichtenstein) (D8 S).

Opossums are active at night (D10 S) and the data gathered mainly came from people that had direct experiences killing these animals.

"Once we killed one, and after the sunrise its cubs were around the body, they were nine, without hair, the size of a new-born kitty [. . .] it carries them on its bag" (D11 S).

"my husband once found one of them with their cubs, he says it has a little hole in its belly, but it is not actually a hole, it is a little bag and there is where babies are. Why don't these babies fall? Well, I don't know, he says, they are just stuck in there" (D12:19 S).

Other animals are more frequently seen in forests and are seasonally associated to crop fields, such as racoons and skunks (D8 S, D23 TC). The racoon is reported to be associated with places full of trees (D 11 S) which it climbs (D 23 TC) and, similarly, to *Nasua narica* L. and *Pecari tacaju* L., it can be seen either alone (solitaries are called "*seltwa*") or in groups (called "*mieke*" or "*miektli*") (D23 TC). Also, it is recognised to store its food as a participant said, "My husband's uncle once told him that they went to find firewood and tried to pull a dry stick from a tree, and when they were pulling it, a lot of maize fell down, because inside, they store their food" (D18:66 S). Two kinds of skunks are recognised: the *cadena* skunk (bigger, with one big with spot in the back; *Mephitis macroura* Lichtenstein) and the *caparote* skunk (smaller, black with small white spots in the body; *Spilogale putorius* L.). They are nocturnal (D23 TC) and their presence is desirable in Sierra cornfields since they feed on Melolonthidae larvae that plague maize roots (D8 S).

Armadillo is easily recognised by its shield as a participant mentioned, "if you touch it, it gets inside and rolls" (D11 S), and because it leaves a trace of little holes in the soil (D11 S, D23 TC). It lives under the soil or rocks, and once it has burrowed into the soil, it is not possible to take it out even by pulling the tail (D12 S). They have been seen with 3 cubs (D23 TC).

Deer is the biggest mammal recognised as common in the area. Based on the shape and size of their antlers, different kinds of white tailed deers (*Odocoileus virginianus* Zimmerman) are recognised by people in the Sierra. The "*chilliwa*" has antlers shaped like a basket in accordance to its namesake, "*chiwi,*" means basket. It is smaller than the "*tlegalatzi,*" which is named after their resemblance to the shape of a wooden pole. There is also the "*xokotewitswa,*" which is a big deer, but with small antlers that end in a small sphere that resemble a "*tejocote*" (*Crataegus mexicana* DC) fruit (D8 S). However, the white tailed deers that have been recently seen near villages in the Sierra region have small antlers (D11). The size of the antlers is also the criterion used by some people, mainly the young, to differentiate males (bigger antlers) from females (D26 TC). "*Temotzi*" (*M. temama*) is distinguished as a small and reddish deer, which only lives in TC (D8 S, D22 TC). The loss of the antlers of the deer is recognised. However, there is no consensus on how often it happens. One man of the Sierra argued that "People say that the antlers fall down. They say every year, but I don't think so (. . .) they look really sturdy (...) they are never seen on the ground, where these fall, then? (. . .) Antlers fall, but maybe after 10 years" (D7:16 S). In contrast, a hunter in TC stated that all deers throw away their antlers every year on San Andrés Day (D43:3 TC), celebrated on November 30. The behaviour of brushing up the antlers against trees has been observed in November (D7 S), the mating around mid-November, and young deer, aged about 1 month, whose skin is covered with white spots are seen around June. Therefore, pregnancy is calculated to last about 6 months (D7 S). Deers were differentiated from other mammals because they lack vessel "*xixiwa*" (D8). They are known to make their own paths or use human paths to move across vegetation (D8 S, D20 TC).

Paca (*Cuniculus paca* L.) is nocturnal, and although it is not often seen by most people, its feeding sites are identified in TC because it leaves the peel of the fruits, such as lime or avocado. It has two frontal teeth, and cubs are born (1 or 2) between May and June. It burrows in the rocks and caves. While most people call it just "*tepezcuintle,*" one man distinguished two kinds. The

TABLE 6 | Trends in animal's abundance and their causes, as reported in adults' interviews.

Animal	Zone	Previous abundance (Before 35–50 years)	Trend in abundance (In the last 35–50 years)	Cause	Reference to sources	Number of persons that mentioned it
Insects						
Lepidoptera						
Giant silk worm "kuetlas"(*Arsenura armida*)	TC	nd	Decreased	ND	D27	1
Poxokuiles(*Arsenura polyodonta)*	Municipal seat	High	Decreased	Shifts in rain patterns	D43	2
Diptera						
Flies	Sierra	Low	Increased	Use of "gallinaza" as fertiliser[a]	D16	1
Birds						
Cuculidae						
Roadrunner(*Geococcyx velox*)	Sierra	Low	Disappeared	Hunting and dogs	D7	1
Phasianidae						
Creole chicken(*Gallus gallus*)	Sierra	High	Decreased	Arrival of chickens "from the city"	D11	1
Farm chicken(*Gallus gallus*)	Sierra	Low	Increased	Egg laying periodicity and fatten speed	D11	1
Mammals						
Didelphidae						
Opossum(*Didelphis* spp.)	Sierra	High	Decreased	Fire	D10	1
Dasypodidae						
Armadillo(*D. novemcinctus*)	Sierra	High	Decreased	Fire	D10, D16	2
Armadillo(*D. novemcinctus*)	TC	nd	Increased	Human consumption has decreased	D25	1
Canidae						
Coyote(*Canis latrans*)	Sierra	High	Dissapeared	Fire	D7, D11, D13, D15	4
Coyote(*Canis latrans*)	Sierra	High	Dissapeared	Hunting	D7	1
Felidae						
Tigrillo(*Leopardus* sp.)	TC	nd	Decreased	Hunting	D21	1
Leporidae						
Rabbit(*Sylvilagus* sp.)	Sierra	High	Decreased	Fire	D10, D11	2
Cervidae						
Deer(*O. virginianus*)	Sierra	High	Decreased	Fire and logging	D10, D11, D16	3
Deer(*M. temama*)	TC	nd	Decreased	Hunting	D25	1
Sciuridae						
Squirrel(*S. aureogaster*)	Sierra	High	Decreased	Fire	D10, D11	2
Squirrel(*S. aureogaster*)	TC	High	Decreased	ND	D19	1
Cuniculidae						
Paca(*C. paca*)	TC	High	ND	ND	D23	1
Animals in general	TC	High	Decreased	Fire	D27	1

[a] *"Gallinaza" is a poultry excreta-based fertiliser bought from the chicken farms established in Tehuacán. This fertiliser is considered by some of the interviewed persons as "soil contamination," and it is acknowledged that it creates dependency despite how it helps to increase crop productivity, at least in the short term. The adoption of this practice was facilitated after the temporal migration of men to work in agricultural fields in Tehuacán.*

bigger has big cheeks and is called "*tekomawa,*" while the smaller "*kowtetekiwsi*" has no cheeks (D23 TC).

Mammals that are not often seen are felids, namely, porcupine and kinkajou. Small felids identified in pictures as *Leopardus wiedii* Schinz are recognised as small beasts called "*tekuantsin*" which are common in TC, especially near the *Pinus* spp. forests where there are a lot of squirrels. However, it is not easy to find them because they avoid humans. Bigger felids, such as *Leopardus pardalis* L., are recognised as big beasts called "*wey tekuani.*" They are hunter animals but are locally scarce (D23 TC). Although the kinkajou is well recognised by its call, even mimicked by children (**Supplementary Additional File 4**), it is often identified in pictures as a monkey. Porcupines are recognised to spend all their life just lying on top of trees in TC, hypnotising small animals as mentioned by a participant, "It has a kind of magnet for attracting them, who knows how it does for putting these animals to sleep." Its reproduction data are unknown (D23 TC).

Causes of Fauna Extirpation

Hunting and fires in the limits of Coyomeapan and Zoquitlán were recognised as the main causes of fauna decrease and extirpation (**Table 6**). Great fires were dated before 1970 and between 1970 and 1990. The official fire record (Comision Nacional Forestal, CONAFOR, Puebla) shows a great fire in 1998 (at least 1,000 ha affected). During 2018, we

FIGURE 3 | Animals managed and used. **(A)** A captured rabbit (*Sylvilagus* sp.) is held in captivity in Sierra; **(B)** lambs are forced to use a bottle in their mouth to prevent conflicts caused by grazing in inappropriate places; **(C)** a duck grooms a puppy in Sierra. These birds are kept in homes to prevent illness in other domestic animals; **(D)** Chaparra, a specialised hunter dog in TC; **(E)** Turkeys are considered to be rude, but highly appreciated as edible and gifts in celebrations; **(F)** A meal with *Poxokuili* (*Arsenura polyodonta* Jordan) bought in the municipal head plaza prepared in "salsa" and a soup. These *poxokuili* are collected from *Ceiba* sp. tree in Chimalhuaca, a nearby village, and are annually available around August, depending on the rainfall. Men collect them and women prepare and sell them; **(G)** An armadillo carcase exhibited in TC, **(H)** *Sciurus aureogaster* skin exhibited in TC; **(I)** Furniture with *Mazama temama* legs as pieces; **(J)** *C. paca* skull kept in exhibition in a home in TC after being eaten; **(K)** bull horns exhibited in a home in Sierra, **(L)** *Didelphis* sp. hand kept as a souvenir in Sierra; **(M)** *Actias truncatipenis* (Sonthonnax, 1899) and other butterflies are kept as a souvenir in the Sierra; Some yellow butterflies are used by children as temporal tattoos; Toucan's bills are exhibited and used in traditional medicine in TC **(N,O)**; **(P)** Snakes that are perceived as poisonous are drowned and kept in sugarcane alcohol as part of the first-aid kit in homes in Sierra and TC; **(Q)** The dorsal gland of a peccary is kept in sugarcane alcohol to attend labour complications in TC; **(R)** While the outer part of immature Hepialidae are edible, the inside is used to treat herpes labialis; **(S)** Vespidae-*Leucaena* sp. galls are sold in municipal seat plaza as a snack. **(T)** *Arsenura polyodonta* are individually prepared with the quelite known as "*pipitza*" [*Porophyllum tagetoides* De Candolle (DC)].

observed the beginning of a 15-day long fire in the limits of Coyomeapan and Zoquitlán. According to people, this fire caused the burning of wild and domestic animals. Sharing of testimonies and pictures of these animal remains (testimonies D43) contribute to explain why fire is identified as a major factor that causes fauna extirpation. We observed that people living in communities closer to pine forest quickly responded in volunteer brigades to dig ditches and prevent the advance of fire.

Use Typology

Eighteen use categories were reported for domestic and wild fauna by students, and 13 of these were also reported by adults (**Table 1** and **Figures 3**, **4A**). **Table 7** includes data on consumption events along a year while **Table 8** includes data on local prices of traded fauna (frequencies of mention for each animal are available in the **Supplementary Additional File 3**). A specialised hunting dog can cost above 3,000 Mexican pesos. Since it is considered hard to find, in case of non-solved conflicts, killing dogs that belong to another hunter is a local form of revenge.

Between the Sierra and TC, we found redundancy in the presence of most animals. However, use reports differed between Sierra and TC. This was the case of the medicinal use of opossum "*tlakua*" (*Didelphis* spp.) to induce labour in Sierra (D10 S, D11 S, D12 S) instead of porcupine "*wistlakua,*" meaning literally opossum with thorns (*Sphiggurus* sp.) (D23 TC), the dorsal gland of peccary (D21 TC), and the penis of *M. temama* (D43) which are used in TC.

Preference Information

Among edible animals, preferences and selection for a particular phenotype or species are trade-offs between size, taste, smell, colour, behaviour, quality of meat, fattening speed, and, in the case of birds, egg laying reliability. It is desirable to own both sexes of a domestic animal, otherwise, people must borrow stallion from neighbours (10 S). Fattening speed overcomes colour of turkeys (D10 S, D14 S). Taste of creole hens is preferred over taste of farm hens brought from the city, but the latter fatten faster than creoles and are reliable laying hens whose white eggs can be easily sold (D11 S). In general, hen eggs overcome turkey eggs as edible. However, turkey eggs are preferred for healing in "limpias" (D10 S), a ritual performed to prevent, diagnose, or heal several illnesses.

Animal behaviour also determines preferences. Turkeys, for instance, peck people, escape very often (D18S, D19S), get ill easier, and require more care for being fed compared to other poultry (D10 S, D13 S, D18 S, D41). However, female turkeys are excellent hatchers for eggs of both hen and turkey (D10 S). Moreover, both male and female turkey are important as a gift to the godparents in social celebrations such as weddings or in the anniversary of someone's death (D6 S, D41). Regarding smell, lamb meat is preferred over the goat meat because the latter is considered to smell badly (D41). Meats of rabbit and squirrel are preferred over that of racoon, since the latter has a smell called "*xoquilla,*" like a raw egg (D25 TC).

Paca stands among wild animals as a special food. People considered it as "freaking awesome" (D23:66 TC), sacred, a special gift to someone (D41), an animal that is killed because

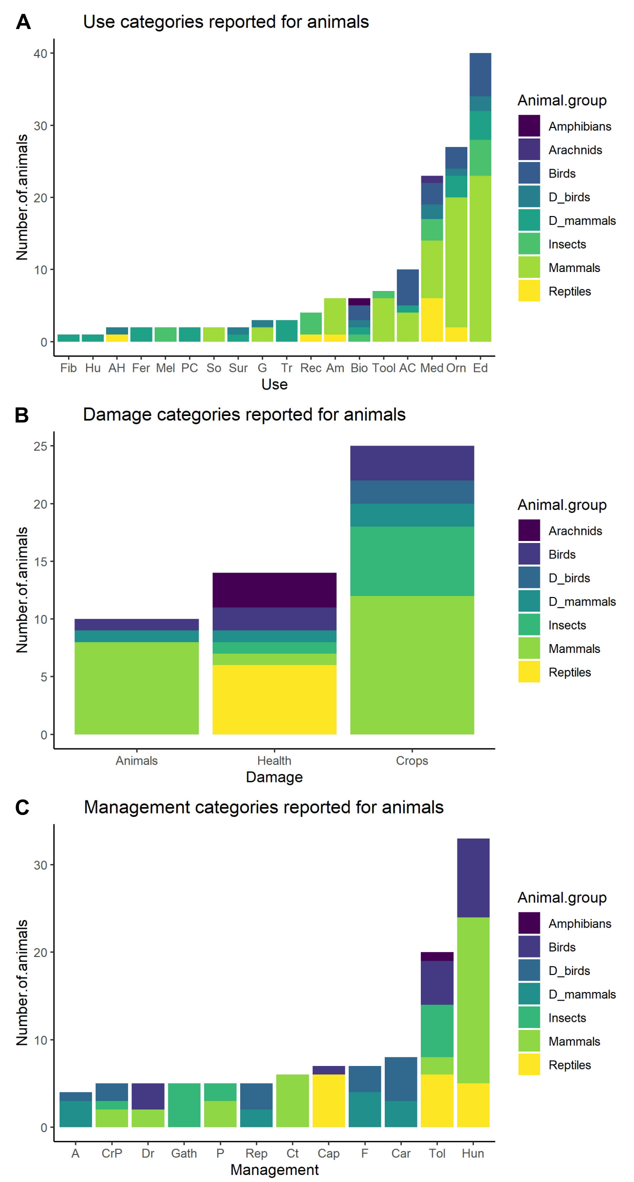

FIGURE 4 | Distribution of use, conflict, and management categories for animal group. **(A)** Use categories: Edible (Ed), Ornamental/exhibition (Orn), and Medicinal (Med) categories. Those with more reports were mainly represented by wild animal items. However, seven categories were only reported for domestic animals. AC, animal companion; Bio, bioindicator; Am, amulet; Rec, recreational; Tr, traction/transport; G, gift/offering; Sur, surveillance; So, souvenir; PC, pest control; Mel, honey production; Fer, fertiliser; AH, animal health; Hu, aid in hunting; Fib, Fibers. **(B)** Damage categories: both wild and domestic animals were related to damage. **(C)** Management categories. Tol, Tolerance; P, poison; CrP, crop protection; Gath, gathering; Cap, capture (obtaining snakes and birds, but not killing them to get them); Ct, captivity (keeping the animal alive at home); Hun, hunting; Dr, drive away; Rep, reproduction; Car, cares; F, feeding; A, agreements. Elaborated in R software (Rudis et al., 2020; Garnier et al., 2021; Wickham et al., 2021).

it is a delicacy (D20 TC), and has healthy meat, available throughout the year (D23 TC). It lives in TC, but is also consumed in the Sierra as a memorable event (D12 S, D16 S). Nevertheless, a few people said they preferred the taste of other bushmeat. Deer, squirrel, white-nosed coati, armadillo, and the quail "*koyotcho*" are among the considered tastier animals (D10 S, D11 S, D16 S, D19 TC, D20 TC, D21 TC, D24 TC, D25 TC, D26 TC, D27 TC).

An animal's diet also shapes people's preferences on its meat. *M. temama* meat is considered tasty and fresh because this animal "has a fine diet, based in wild fruits and plants from the *acahual*" (secondary vegetation). In contrast, the white-tailed deer is considered drier because it "feeds on dry leaves from the highlands" (D43). Similarly, some people perceive that eating armadillo is dangerous because they think these animals feed on coral snakes (D11 S, D20 TC).

People's age can influence food preferences. Most adults prefer the taste of the edible immature stages of *A. armida "kuetla"* compared to the "*chajkchama*" (Hepialidae), although the latter is more appreciated by children (D21 TC, D22 TC, D25 TC). The fact that these Hepialidae can be found at low height in the trees makes them easily accessible to be gathered by children, in contrast to other kinds of Lepidoptera in the area. Adults think that young people have experimented on changes in their preferences due to migration processes. For example, they do not like dotted eggs because of the colour (D10 S), or have abandoned local, healthy food that people used to eat more often in the past, including greens "*quilitl*" and bushmeat (D10 S).

Typology of Damages

The four kinds of damages caused by 36 animals (41 mentions) were damage to crops, predation of domestic animals, damage to human health, and damage to merchandise (**Table 1** and **Figure 4B**) (Frequency available in **Supplementary Additional File 3**).

We identified differences in animals recognised as damaging between the Sierra and TC. This results in different attitudes towards the animal and the decisions to eliminate it in one region, but to accept it in other. For example, the Coleoptera larvae, known as "*xahuistli*" or *"nextokuili,"* are not appreciated in the Sierra since they feed on maize root. Therefore, crop rotation should be practiced. Otherwise, the milpa will be plagued (D8:14,15,17 S). Differently, in TC these larvae are appreciated because they are considered related to the life cycle of a valued green: *Piper auritum* (D20:103 TC, D21:81 TC, D27:30 TC, D43:8).

Participants said that the location of milpas influences the magnitude of damage that animals can cause. For instance, in TC, people that have their milpas high and close to the mount (mature vegetation) are those more affected by white-nosed coati and peccary (D26 TC, D27 TC).

Regarding snake bites, TC snakes were in general recognised as more dangerous than those in the Sierra and bites were reported to occur in first place on feet and in second place on people's hands, while working in the field or gathering firewood (D8 S, D12 S, D13 S, D14 S, D21 TC, D25 TC). In the case of Elapidae, the consequence is that "blood comes out from every pore in the body" and in just one case a man lost part of his hand, even after attention in the hospital (D8 S, D13 S, D25 TC). In the case of horned pit vipers, the consequence is swelling and deep

TABLE 7 | Consumption events and accessibility reported for edible animals in adult interviews.

Animal	Consumption events in a year	Zone	Number of adult informants	Reference	Accessibility	Reference
Insects						
Hymenoptera, Apidae						
Stingless bee honey (Meliponini)	<1	TC	1	D20	Hard to get.	D20
Lepidoptera, Saturniidae						
Kuetlas (*Arsenura armida*)	seasonally (July, October)	TC	2	D21, D26	Trade-offs: located near, but hard to find and climbing or tools are needed.	D20, D25
Lepidoptera, Hepialidae						
Chajchama (Hepialidae)	Mainly seasonally (February-March)	TC	1	D27	Trade-offs: easy to get, scarce during most of the year.	D21, D25
Birds						
Tinamidae						
Quail (*Crypturellus* sp.)	1 (during bean season)	TC	2	D20, D26	Easy to get.	D20
Phasianidae						
Chicken meat (*Gallus gallus*)	6	TC	1	D19	NA	
Turkey meat (*Meleagris gallopavo*)	Celebrations	TC	1	D20	Hard to raise.	
Turkey meat (*Meleagris gallopavo*)	Celebrations	S	1	D6	Hard to raise.	D18, D19, D10, D13, D18
Mammals						
Didelphidae						
Opossum (*Didelphis* sp.)	6	S	1	D18	NA	
Opossum (*Didelphis* sp.)	<1	S	1	D16		
Dasypodidae						
Armadillo (*Dasypus novemcinctus*)	1	S	1	D12	Hard to get.	D12
Armadillo (*Dasypus novemcinctus*)	<1	S	1	D16		
Leporidae						
Rabbit (*Sylvilagus* sp.)	<1	S	1	D16	Easy to get.	D12
Procyonidae						
White nosed coati (*Nasua narica*)	1–2 (during milpa season)	TC	2	D24, D26	NA	
White nosed coati (*Nasua narica*)	3 (during milpa season)	TC	1	D19		
Racoon(*Procyon lotor*)	3 (during milpa season)	TC	1	D20	NA	
Racoon(*Procyon lotor*)	<1	S	1	D16		
Cervidae						
Deer(*Mazama temama*)	1–2	TC	3	D24, D20, D26	The most difficult to get, "about 150 individuals present."	D26, D23
Tayassuidae						
Pecary(*Pecari tajacu*)	1–2	TC	3	D19, D23, D26		
Sciuridae						
Squirrel(*Sciurus aureogaster*)	30 (during milpa season)	TC	1	D22	The most easy to get.	D26
Squirrel(*S. aureogaster*)	1–3	TC	3	D19, D24, D26		
Squirrel(*S. aureogaster*)	1	S	1	D11	Hard to get.	D11
Squirrel(*S. aureogaster*)	<1	S	1	D16		
Geomyidae						
Gopher (*Orthogeomys* sp.)	<1	TC	1	D23	NA	
Erizonthidae						
Porcupine (*Spigghurus mexicanus*)	<1	TC	1	D23	NA	D23
Cuniculidae						
Paca(*Cuniculus paca*)	4–15 (individuals killed)	TC	1	D23	Trade-offs: Plenty of individuals and always available but far from town	D23, D20
Paca(*C. paca*)	1–2	TC	2	D19, D20		
Paca(*C. paca*)	<1	S	2	D16, D12		

This information comes from semi-structured interviews, but does not come from a survey with statistical validity.

TABLE 8 | Price of animals locally sold.

Taxonomic identity	Sell unity	Rank of price in Mexican pesos	Perceived price	Reference	Number of adult informants	Price in USD for 1 kg
Insects						
Hymenoptera, Vespidae						
Polonxocos (Vespidae-*Leucaena* guts)	150 gr	5		D43 municipal head plaza	3	1.65
Lepidoptera, Saturniidae						
Poxokuiles (Arsenura polyodonta)	10 individuals (prepared)	10–20	Expensive	D43 municipal head plaza, D12 S	3	5–10
Kuetlas(Arsenura armida)	10 individuals (prepared)	10–15	Expensive	D21 TC, D20 TC, D25 TC	3	5–8
Reptiles						
Snakes (Ophidia)	sugar cane glass	20		D11 S		–
Birds						
Phasianidae						
Hen *(Gallus gallus)*	individual (alive)	100–150		D41 municipal head (May 23, 2019), D15 S		–
Creole hen *(Gallus gallus)*	piece	2.50–3		D16 S, D18 S	2	2.5
Male creole turkey *(Meleagris gallopavo)*	individual (alive) (5–8 kg)	500–800	Expensive	D41 municipal head (February 13, 2019; May 23, 2019), D18 S, D25 TC	2	–
Female creole turkey*(Meleagris gallopavo)*	individual (alive) (3.5 kg)	200–300		D11 S, D12 S	2	–
Male and female creole turkey *(Meleagris gallopavo)*	kg	80–100		D41 municipal head (May 23, 2019), D11 S, D12 S, D15 S, D18 S, D25 TC	5	4–5
Juvenile farm turkey*(Meleagris gallopavo)*	individual (alive)	35		D12 S	1	–
Mammals						
Didelphidae						
Opossum *(Didelphis* spp.)	tail	10		D12 S	1	–
Leporidae						
Rabbit*(Sylvilagus* sp.)	1/2 kg (prepared)	150	Expensive	D16 S	1	15
Mephitidae						
Skunk (ND)	individual	2000–10000	Expensive	D41 municipal head (February 15, 2019), D23 TC	1	–
Procyonidae						
White nosed coati*(Nasua narica)*	kg	60		D19 TC	1	3
Cervidae						
Deer*(Mazama temama)*	kg	70		D26 TC	1	3.51
Equidae						
Horse*(Equus caballus)*	individual (alive)	>7000	Expensive	D41 municipal head (May 28, 2019)		–
Donkey*(Equus asinus)*	individual (alive)	9000	Expensive	D41 municipal head (May 23, 2019)		–
Bovidae						
Lamb*(Ovis aries)*	individual (alive) (15–40 kg)	800–2000		D12 S, D15 S	2	2.5
Lamb*(Ovis aries)*	kg (alive)	50		D15 S, D16 S, D18 S	3	2.5
Goat*(Capra hircus)*	kg	50		D12 S	1	2.5
Tayassuidae						
Peccary*(Pecari tajacu)*	kg	80		D41 municipal head (February 15, 2019)		4
Sciuridae						
Squirrel*(Sciurus aureogaster)*	individual	15		D19 TC	1	1.65
Cuniculidae						
Paca*(Cuniculus paca)*	kg	80–500	Expensive	D41 municipal head (February 15, 2019), D19 TC, D21 TC, D23 TC	3	4–25

This information comes from semi-structured interviews, does not come from a survey with statistical validity.

pain, and in the case of *Crotalus* spp. sometimes even nothing (D8 S). To attend snake bites, it is considered enough drinking a "medicine" prepared with snakes and sugarcane alcohol, but a few people have also visited the clinic (D8 S, D12 S, D13 S, D14 S, D21 TC, D25 TC).

Fauna Management Typology and General Scheme

Definitions of each management category is provided below, indicating the theoretical category they belong to **Table 1** and **Figure 4C**, the fieldwork sources from which they emerged (interviews, workshops, field diary), examples, and, in some cases, further information about the interactions with other categories. Based on these interactions, we have proposed a descriptive scheme of fauna management (**Figure 5**):

Hunting

Definition: Vertebrates' extraction in a planned or opportunistic way using weapons, traps or, dogs. *Category:* Supply and extractive prevention. *Sources:* 16 adult informants: D7 S, D8 S, D9 S, D10 S, D11 S, D12 S, D13 S, D16 S, D18 S, D19 TC, D20 TC, D21 TC, D23 TC, D24 TC, D25 TC, D26 TC; school groups: D41, D42, field diary (testimonies) D43. *Examples for supply:* Fire guns, sticks or machetes are used to obtain medium sized mammals such as armadillo (D12 S, D16 S). Small birds are usually killed with slingshots (D16 S) but big sized birds that walk such as quails used to be obtained with a snare (D8 S) and more recently, with rifles (D20 TC). Gophers, rabbits and white-nosed coatis can be also obtained through traps. Dogs are involved in the hunt of deer, rabbit, armadillo and racoon but not in the hunting of paca or skunk. *Examples for extractive prevention:* Snakes (D12 S) and *kuwishi* (*Abronia* sp.) because they are considered poisonous. *Tekolotl* and *xiastli* (owls) because they are considered bad or witches. To prevent damage to domestic animals, people kill *tlakua* (opossum) which is considered "a bad animal, although its tail is good" (D11 S), or the coyote which is considered by most people to be extirpated. In the case of *tlalmoto* (squirrel), burrows are set in fire. Extraction of animals is also mediated through cats for rodent control, preventing predation on stored maize seeds. *Interactions with other categories:* Hunting strategies vary according to the animal natural history. For example, in TC, it is known that *temazate* deer feeds on the leaves of chili "*chiltepetl"* and follows paths in vegetation. Therefore, the hunter can wait for him. Other animals, such as white nosed coati or peccary, are waited in the milpas and hunted when they come to feed, especially in the maize season around October. Differently, the paca must be waited at night close to its feeding place, and a site to spy is built high in the trees, so the hunter can avoid been detected. Snakes are captured manually and kept alive until they are used to prepare an antivenom with sugarcane alcohol. However, they may be killed soon.

Wild Fauna Captivity

Definition: To control the feeding and mobility of an animal *ex situ*. *Category:* Supply. *Sources:* 11 adult informants: D5 S, D7 S, D8 S, D11 S, D12 S, D14 S, D16 S, D20 TC, D23 TC, D25 TC, D27 TC; school groups: D41, D42; field diary: D43. *Examples:* The animals kept in captivity for at least a year were rabbits (direct observation D43) and squirrels. Other animals which are brought to homes and die soon include agouti (*Dasyprocta* sp.), peccary and *temazate* deer (*M. temama*). Interviewed people identified the feeding as the main factor to captivity success. *Interactions with other categories:* The animal will die unless its diet is well known, or if it accepts a diet based on maize without getting ill, finding by itself part of its own food. In the case of peccary, their sharp teeth were the reason of deciding not continuing with captivity. Reproduction in captivity of wild fauna was not documented.

Gathering

Definition: Taking small animals through manual collecting or by tools, sometimes manipulating biotic elements such as host plants. *Category:* Supply. *Sources:* 8 adult informants: D12 S, D15 S, D20 TC, D21 TC, D22 TC, D25 TC, D26 TC, D27 TC; school groups: D41; field diary: D43. *Examples:* Gathering was documented for immature stages of lepidoptera (direct observation D43). In TC and in Sierra, people tolerate host trees (D27 TC) of immature stages of Hepialidae (*Lippia myriocephala* in TC or *Fraxinus* sp. in Sierra) to keep availability of these animals, which are extracted, mainly by children, using water and a spine. In TC, the immature stages of *A. armida*, called "*kuetlas,*" are collected from *jonote* (*H. appendiculatus*) trees by adults, mainly men, who use a bamboo stick from ground level, climb, or even log the tree to take the *"kuetlas"* more easily. Some people collect them from trees growing in secondary vegetation and then take them to their homes to keep them in a selected *H. appendiculatus* tree until they are ready to be eaten. This relocation requires an active surveillance of the animals to assure that they are eating well, they are safe from predators, and no other people is removing them. Stingless bee honeycombs are also collected. This implies the use of smoke or soapy water to drive bees away (D41). *Interactions with other categories:* see Agreements.

Feeding of Domestic Animals

Definition: People's choices on the kinds and sources of food offered to an animal, including choices on grazing land. *Category:* Supply. *Sources:* 14 adult informants: D8 S, D10 S, D11 S, D12 S, D14 S, D15 S, D18 S, D19 TC, D20 TC, D21 TC, D22 TC, D24 TC, D25 TC, D27 TC; school groups: D41. *Examples:* Almost all domestic animals are fed on maize grain or tortillas. However, turkeys feed on nixtamal (maize cooked in limewater) and as juveniles, the nixtamal should be enriched with *quelites* (*Cucurbita ficifolia* Bouché or "chilacayota" leaves, among others) (D10 S, D11 S, D18 S). Women sing to the juvenile turkeys (direct observation D43, audio examples available in **Supplementary Additional File 4**) and feed them in their mouth to make them easier to eat. In contrast, chickens that come from farms must be fed with commercial food until they get used to maize. Dogs and cats hunt small wild animals by themselves. Dogs are also fed with leftovers, duck eggs, or leftovers of killed animals as gophers. People maintain lambs, goats, horses, and donkeys locked at night and take them to graze the whole day. *Interactions with other categories:* A person who owns land takes his/her animals to

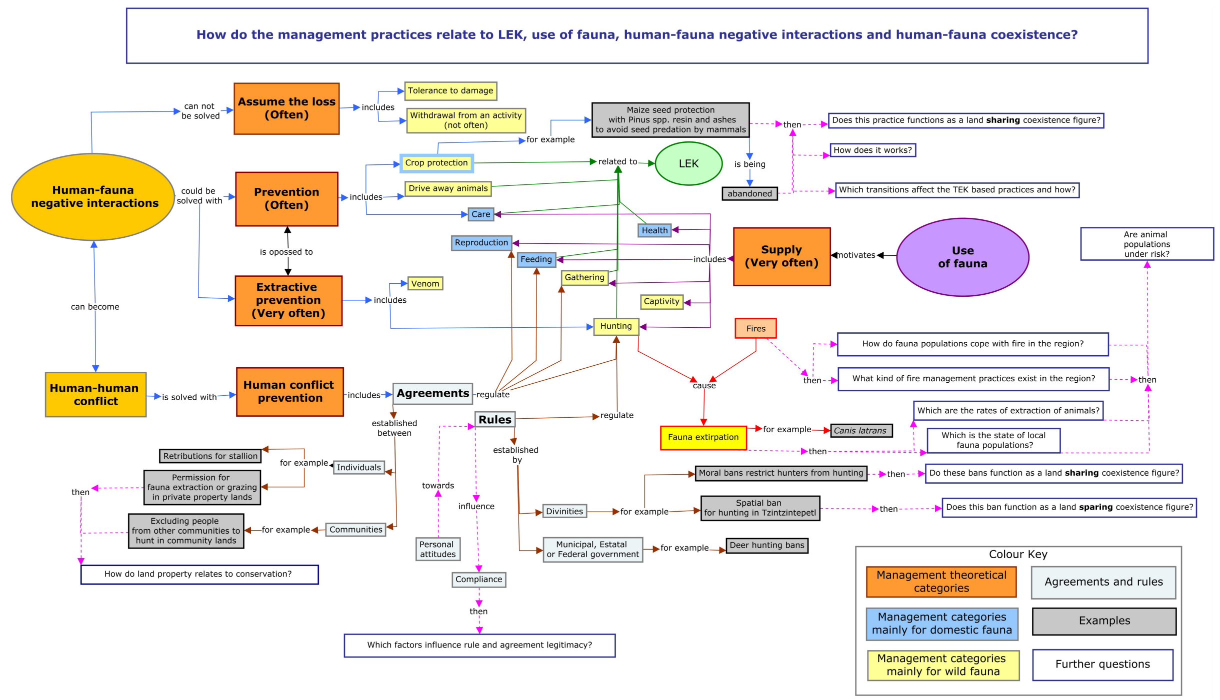

FIGURE 5 | General management scheme linking categories, examples, and further questions. Five management categories are shown. In the left side are those that respond to management of negative interactions between humans and fauna and human-human conflicts: assume the loss, prevention, extractive prevention, and human conflict prevention. The right side shows the supply which is motivated by the use of animals. Each of these five management categories include substantive categories which are non-exclusive. Yellow boxes show categories mainly related to wild fauna, while blue boxes show categories related mainly to domestic fauna. Crop protection contains both colours since it is related to both wild and domestic fauna. In the centre of the figure, local ecological knowledge (LEK) is related to several management practices for the prevention of damages to supply. Agreements are set to prevent human conflicts related to fauna supply decisions such as wild fauna extraction and domestic fauna reproduction. Rules also regulate hunting. Hunting and fires (orange boxes) have been recognised by interviewed persons as the main causes of fauna extirpation. Examples and further questions that arose in the process are included. This figure was elaborated with Cmap (https://cmap.ihmc.us/). A simplified version of this figure is available in **Supplementary Additional File 5**.

graze there, but others must have personal agreements with the landowners, or take the animals to graze to the mount.

Health of Domestic Animals

Definition: Animal illnesses recognised by people and their treatments. *Category:* Supply. *Sources:* 12 adult informants: D10 S, D11 S, D12 S, D14 S, D15 S, D16 S, D18 S, D21 TC, D22 TC, D24 TC, D25 TC, D26 TC; school groups: D41, D42; field diary D43. *Examples:* When they become ill, chickens and turkeys are fed with tomatoes or aloe (direct observation D43) and their underwing is smeared with tomato or sugarcane alcohol. To treat snake bites, horses are smeared with snake sugarcane alcohol and, in cases of birth complications, people provide an infusion of opossum tail. Prevention practices include vaccines and keeping ducks in homes to protect poultry and turkeys from getting ill. People place red threads to juvenile turkeys, lambs, and goats (direct observation D43) to avoid the "envy" (damage or illness caused by someone's negative emotions). The interest in finding the way to keep the domestic animals healthy is reflected in the experimental incorporation of information coming from different sources, including products announced in TV such as human antihistaminic pills, but also in the will of the people of participating in this research and interchange information with others about how to take care of their animals (D11 S).

Reproduction of Domestic Animals

Definition: People choices on sexual partners for animals, artificial selection criteria and care to ensure offspring survival. *Category:* Supply. *Sources:* 7 adult informants: D6 S, D10 S, D11 S, D12 S, D13 S, D14 S, D15 S; school groups: D41, D42. *Examples:* In turkeys, artificial selection does not seem to be rigorous. Females are cross breed with the male that is available, either because a friend lent it or because the female escaped to find a male by herself. If there were several available males, people would let the female choose, or would allow the fastest male to fertilise her. Some people invest great effort to grow the new-born turkeys. For example, by putting them inside a box with electric bulbs to maintain the heat, while others just cover them at night with a cloth, so the strong ones will survive (D10 S). In the case of hens, besides the meat, an element of selection are eggs. Women select from a hen the eggs of their preference (white, red, or yellow) and give them to another hen to hatch them, so they maintain a variety that will be for direct consumption or to sell. *Interaction with other categories:* see Agreements.

Cares Towards Domestic Animals

Definition: Protection of animals for their wellbeing, from escape, predation by wild fauna or exclusion from crops. *Category:* Supply and damage prevention. *Sources:* 8 adult informants: D10 S, D11 S, D13 S, D14 S, D16 S, D18 S, D19 TC, D21 TC; school groups: D41; field diary D43. *Examples for supply:* Women must be aware of turkeys (even chase them to bring them back) since they often escape. If the eggs of the hens locked inside the yard are fragile, sand is introduced so the hens can eat the small stones (D 41). The lambs must be sheared so they can be comfortable in the heat season even though their wool is not used or sold anymore. Their tails are cut when they are cubs, so they will grow more and will not get dirty. In the case of the few bulls in the localities, it must be avoided to take them to the mount because their legs broke easily and must be watched to avoid robbery from outsiders (D42). *Examples for damage prevention:* Often, locking the domestic animals within a cage or yard is enough to avoid predation by wild fauna, however, there is a trade-off between having them locked and their health since they "become sad" (meaning they get weak or ill). Consequently, they are maintained for great part of the day as free rangers. People try to keep the yard close to their homes since reducing this distance also reduces losses by predation. On the other hand, cages are also useful to avoid the chickens and turkeys to take out the plants that have been recently sown.

Drive Away

Definition: Scaring animals with noise or visual clues. *Category:* Damage prevention. *Sources:* 9 adult informants: D8 S, D11 S, D12 S, D13 S, D18 S, D20 TC, D22 TC, D25 TC, D27 TC; school groups: D41, D42. *Examples:* To avoid predation, the dog is locked within the cage or yard together with the chickens and turkeys. Since electric light arrived at the region ca. 15 years ago, the events of hematophagous bats feeding on domestic animals have decreased, therefore people place electric bulbs in the yards. This practice also dissuades the "*k'zoma*" (*Mustela frenata*) to get close. If the hens or turkeys cry, a prey bird must be close, so people scare the juvenile chickens with noises, so they hide to protect themselves. In TC, leaves of malango or *"awewejcho"* (*Colocasia esculenta* (L.) Schott) are put inside the gopher's burrows to cause irritation, so they will go away. To drive away the animals from crop fields, visual signs are used, especially scarecrows, constructed with cloths, or pieces of plastic.

Crop Protection

Definition: Direct protection of crops from animal predation with local technology. *Category:* Damage prevention. *Sources:* 3 adult informants; D13 S, D20 TC, D26 TC; school groups: D41; field diary D43. *Examples:* Put ash or lamb excreta around plants to drive away the gopher (D41). Corn seeds are protected from mammal seed predation, with ash and *Pinus* sp. resin (direct observation D43). This preparation implies the extraction of *Pinus* sp. chips and two *Agave americana* L. leaves, as well as the use of small dry branches enough to maintain a small fire for 1 h (**Figure 6**). *Interaction with other categories:* This practice is much less common than it was thirty years ago, and in words of one woman "we do not even know why it has been abandoned" (D43). Knowledge about how to perform this technique is transmitted from generation to generation as part of the wisdom inherited from the ancestors.

Poison

Definition: Commercial products that cause the death of animals and are applied in their food. *Category:* Extractive prevention. *Sources:* 3 adult informants: D12 S, D16 S, D25 TC; school groups: D41, D42. *Examples:* In the case of *"mapachi"* (racoon), poison is placed directly in corn; for the squirrel, it is placed in an avocado that is introduced in its burrow; for the gopher, the poison is mixed with corn dough and small balls of this mixture is placed in the seeding fields. Poisons are sold in the community, but their provenance is unknown.

Tolerance

Definition: People assume the damage because there is nothing that can be done. *Category:* Assume the loss. *Sources:* 3 adult informants; D8 S, D12 S, D13 S. *Examples:* This is the case of birds that eat the crops, after learning that the drive away strategies are not a threat. It is also the case of encounters with snakes (D13 S).

Abandonment of an Activity

Definition: Stop performing an economic activity because of the damages caused by fauna. *Category:* Assume the loss. *Sources:* One adult informant: D11 S. *Examples:* This was the case in which *Bassariscus* sp. fed on the eggs that were to be sold at a grocery store, so the owner gave up after several tries and stopped to sell the eggs because she had another source of income.

Agreements

Definition: Negotiations among people intended to prevent or reduce problems. *Category:* Human conflict prevention, conservation. *Sources:* 6 adult informants: D5 S, D8 S, D9 S, D13 S, D18 S, D21 TC, D25 TC; school groups: D41, D42; field diary testimonies and direct observation D43. *Examples and interactions with other categories:* These are mainly related to human conflicts involved in hunting, gathering, grazing and domestic animal reproduction. For conservation, agreements can involve land ordering and closure for preservation in the form of a legend, such as the recognition of the Tzintzintepetl Hill as a kind of fauna source, a place of great abundance of animals in which it is prohibited to hunt, otherwise the hunter would attract bad luck (D5 S, D41). Outside this area, agreements for regulating the access to resources in communal lands, i.e., any agreement of closure (calendar, age, sex) towards deer or other animals, were not registered. However, according to the customs, people do not go hunting in communities where they do not belong, and they do not accept hunters from other communities. Strong penalisation is applied to whom violate the rule (D8 S, D9 S).

There seems to be no regulation of the extraction of edible Lepidoptera in communal lands. However, there are personal agreements with private landowners to extract them (D21 TC, D25 TC). We did not register restrictions to grazing animals in communal lands, but action is taken to keep them from causing damage (D18 S). For lambs, they make masks with plastic bottles, or maintain them tied. For horses, their owner asks permit from a landowner before tying the horse in his

FIGURE 6 | Prevention of corn seed predation by mammals. **(A)** *Pinus* sp. Chips are extracted (ca. 1 kg) and placed in a clay pot. A clay molcajete is also shown (left). **(B)** The clay molcajete is placed in a hole below the earth and covered with two *Agave americana* leaves with a hole in the middle. **(C)** The chips inside the pot are placed on the top and sealed to the *A. americana* leaves with fresh clay. **(D)** The system is covered with branches and a fire is kept alive for 1 h before the sunset. After extinguishing the fire, the system is left to work all night. **(E)** The next morning, the resin can be collected from the molcajete. **(F,G)** The resins and ashes are spread over the seeds and mixed. **(H)** the seeds are ready to be sown or stored.

property (direct observation D43). If an animal causes damage, its owner must pay it.

In the case of animal reproduction, a personal agreement is taken to retribute the person who lent the male. In the case of turkeys, the retribution can be one new-born turkey; in the case of pigs, a symbolic economic retribution is well received (D13 S, D41, D42).

Rules

Definition: Regulations imposed from the outside, such as the federal, state, municipal, local or religious authorities. *Category:* Conservation. *Sources:* 5 adult informants: D5 S, D7 S, D9 S, D43 TC; school groups D41; field diary (testimonies) D43. *Examples and interactions with other categories:* According to people, a rule has been established by the municipal authority 12–15 years ago, forbidding deer hunting (D9 S), but deer hunting is practiced. Another recognised rule is the national army's request to register the possession of fire guns of any kind (D5 S). To reduce potential misunderstandings with military authorities, some people registered their guns and follow their hunting activity as usual, but others were dissuaded to hunt or are discrete about it (D7 S, D43).

Hunters recognised the need to ask for permission to divine authorities, specifically to San Andrés, before going hunting to the mount (D43 TC). Also, to avoid the "mal aire" (the illness caused by a damaging wind or spirit, that penetrates into the body of a person or an animal), a hunter must pray and ask permit to the owners of the animals. They also need to be aware of the signs they send to inform him on whether it is possible to go hunting. In addition, the hunter should not bring any money, otherwise animals will not appear (D43 TC). However, extraction of small birds and mammals with a slingshot, performed mainly by children and with edible purposes, seems to have open access (D41).

Attitudes

Definition: Personal ways of feeling or thinking about a situation (related to management practices), including a rule or an agreement, and which may reflect a behaviour. *Category:* Conservation. *Sources:* 4 adult informants: D7 S, D10 S, D11 S, D23 TC; field diary (testimonies and direct observation) D43. *Examples:* We observed that adults of Hepialidae moths were identified, and people took care of them to assure the following year there would be enough "worms" (direct observation D43, July 2019). Several people had personal regards towards avoiding the unregulated logging and mistreating animals, they expect that with these actions the forest will remain alive, and the water cycles will remain functional (D10 S, D11 S). The respect to rules and agreements may be also a question of attitude (D7 S, D23 TC, D43). Something similar happens with the act of killing animals associated to bad luck like owls or foxes: some people fear that if they kill the animal, they will also die, while others consider this as a misguided belief (D7 S).

DISCUSSION

Common Ground With Previous Research and Future Perspectives

As expected, LEK of people plays a major role in shaping management practices together with other concrete elements of the worldview, such as the relevance of a given animal for a celebration (i.e., turkey) (van't Hooft and Flores-Farfán, 2012). People often specified to us when their management practices came from the knowledge inherited from their "grandparents" or ancestors. However, as documented in other regions, LEK is complemented (Giovannini et al., 2011) or replaced (Rangel-Landa et al., 2016) through the incorporation of non-local knowledge and practices, some of which can contribute to solve specific needs, while others can result in human, animal, and ecological damage (Olubukola et al., 2020). Taking an interpretive perspective has provided valuable elements for approaching to local fauna husbandry, extraction, coexistence, and conservation practices and for conceptualising socio-ecological questions and pathways related to them (Drury et al., 2011; Newing et al., 2011; Castillo et al., 2020).

Fauna management involves changes through time, as worldview and LEK processes do (López-Austin, 1999; Berkes, 2008). In some cases, the legitimacy of ancient practices and regulations may become endangered due to changes in land tenure and use, work and agriculture dynamics, and/or the arrival of certain religious groups or military presence (González-Jácome, 2004; Santos-Fita et al., 2012; Flores-Armillas et al., 2020b). In this scenario, the incorporation of ecological approaches at population or community scale to biocultural conservation efforts do not provide a solution but can contribute to inform adaptive processes to reduce risk on animal populations. For example, since the use and management of Lepidoptera involve decisions on their host trees (Ramos-Elorduy et al., 2008; Escamilla-Prado et al., 2012; Molina-Nery et al., 2017), research efforts have been made to incorporate natural history, population and community ecology, and active propagation and cultivation of host plants to manage the edible Hepialidae (Hernández-Atlahua, 2015; Oltehua-Tzitzihua, 2016; Molina-Nery et al., 2017).

The main strength of our free listing work is that it shows the relative importance of mammals and snakes among a broad spectrum of animals relevant to people, from which only some elements have reports of use or damage. However, we sacrificed a detailed inventory within each recognised group of animals (Quinland, 2005; Meireles et al., 2021). Such an approach has been followed for herpetofauna in TC (Linares-Rosas et al., 2021), increasing the biocultural inventory for this group and is recommended as a further step for other animal Classes. Zoological inventories with a biocultural approach will not only contribute to confirm taxonomic identification but deepen human-fauna interactions beyond an utilitarian dimension.

While some human-fauna interactions can be highly predictable across an animal's distribution range, local singularities can take place. Our results are consistent with previous reports of extraction of mammals and birds in the Neotropics (Ojasti, 2000) and Lepidoptera in Mexico (Aldasoro-Maya and Gómez, 2016). At the same time, it is possible to distinguish local singularities between different ecosystems within the study area. For example, the fact that several mammals are used for attending births in TC is consistent with the spectrum of species reported in other regions of Mexico (Alonso-Castro, 2014). However, in the Sierra, only opossums are used with this purpose. Solitary and collective hunting expeditions, and waiting and using the aid of dogs to find and get animals are similar to other Neotropical Forest areas (Santos-Fita et al., 2012; de Paula et al., 2018). The sights and extraction of *C. paca* has been reported to be higher during dry season by people in Tabasco, México (Gallina et al., 2012) and in the Brazilian Cerrado (de Paula et al., 2018). This discrepancy with the permanent availability of paca reported in our results, could be explained if hunters travel to nearby areas to search paca throughout the year (Valsecchi et al., 2014). Gathering of Saturniidae and the Hepialidae genera *Phassus* sp. and *Schausiana* sp. (Lepidoptera) is similar to that reported for other regions from central to southern México, such as those in the Nahua and Tlahuica areas (Ramos-Elorduy et al., 2008; Escamilla-Prado et al., 2012; Gómez et al., 2015; Aldasoro-Maya and Gómez, 2016).

Local Ecological Knowledge-Based Coexistence Mechanisms

Animals engaged in human-fauna negative interactions with cattle, crops, and human health were in line with those previously reported for México (Flores-Armillas et al., 2020b). Besides, like in other regions in Mesoamerica, human-human conflicts can take the form of human-fauna negative interactions because of the beliefs about people taking the form of animals (Beaucage and Taller de Tradicion Oral del CEPEC, 2012). However, the effects of grazing on vegetation or the predation on native fauna (Ojasti, 2000) were not considered by people as a cause of concern.

Techniques of crop seed protection based on LEK suggest human learning to prevent damage or tolerate small losses without killing the predator animals (Carter and Linell, 2016). To better understand its foundations and the reasons for its abandonment, we encourage mixed ethnobiological and ecological chemistry approaches. However, after seed germination, damage control by hunting of mammals and quails follows the "garden hunting model," in that the extraction of animals attracted to crops (maize, beans, fruits) allow to complement a diet based in carbohydrates (Stahl, 2014). In an analogous way, wild animals attracted to domestic animals can also provide resources, unless they have been poisoned.

Our results suggest that the magnitude of the damage caused by white-nosed coati and deer in maize crop fields decreases as the distance to mature forest vegetation increases. Such relation has been already documented for tropical dry forest in central México (Flores-Armillas et al., 2020a) and we suggest further studies in the dynamic of fauna damages, their magnitude and the human tolerance towards it, incorporating land use dynamics at a landscape scale.

Local *Canis latrans* Say populations may have adapted (Lute and Carter, 2020) to the lack of human tolerance to damage by changing their home range area to overlap less with human activities and only sporadically feeding on cattle. It is likely that after fires, the presence of this and other animals has diminished only temporarily (Cunningham et al., 2006; Blancas et al., 2014; Pausas, 2019; Stevenson et al., 2019).

Recognition of spiritual beings (Lazos and Paré, 2000; González-Jácome, 2004; Beaucage and Taller de Tradicion Oral del CEPEC, 2012; Santos-Fita et al., 2015) and hunting bans in sacred sites (López-Austin, 1999; Schaaf and Rossler, 2010) have a role as mechanisms to avoid misuse and over-extraction of natural resources. This is likely the case in our study area, where the decrease of animal populations is attributed to anthropogenic factors. Therefore, spatial restrictions to fauna extraction also operate at the meta-community level and is related to group property (Ostrom et al., 1999). Rights on resource access are held by all members of a community who can exclude access to members of another community. However, regulations for fauna extraction within the community seem to be associated to private property of land and resource rights held by individuals who exclude others (Ostrom et al., 1999). Although temporal bans were absent for hunting of white-tailed deer, their reproductive calendar is locally known and similar to that reported for tropical dry forest and shrubland of the Tehuacán-Cuicatlán Biosphere Reserve (López-Tello et al., 2015) and the north, western, and central México (Gallina-Tessaro et al., 2019).

Coexistence with fauna may engage in cognitive processing and cultural transmission dimensions (Albuquerque et al., 2020) that are not documented in this study case. For example, in Veracruz, México, music is dedicated to the white-nosed coati and to snakes to reduce damages to the milpa and to avoid snake bites while working (Nava-Vite, 2012). The celebration known as "*mapachi iljuitl*" (racoon party) provides a context in which elders give advice to youths about how to reduce damages by mammals in the milpa (Argüelles-Santiago, 2012). All these aspects are crucial to attending goals for biodiversity and biocultural diversity conservation.

A Local Intensity Gradient in the Human-Fauna Interactions

The management typology presented in this work is based on Melinda Zeder's frame of fauna management and domestication (Zeder, 2006). According to Zeder, a huge diversity of human-fauna management interactions is possible. In addition, on one side, each of these interactions may or not result in differential genetic and phenotypic-behavioural changes in fauna populations compared to those unmanaged populations. On the other side, these interactions can also result in the differential human investment (i.e., time, effort, social organisation, property rights, regulatory mechanisms) in labours directed to maintain animals, such as protecting animal populations or their habitats, taming individuals, feeding-grazing choices, or performing selective extraction or husbandry, and in the differential incorporation of managed animal populations to a socio-economic system. More precisely, with this work, we have provided an example of how even within a small spatial scale (<10 km), a diverse typology of management practices can arise, related to the knowledge of biodiversity and natural history and to the perceptions of benefit an animal can provide, the damage an animal can cause, and to cultural local criteria.

On one end of this gradient, we distinguished the extractive practices aimed to use or mitigate negative interactions with wild fauna, which show variations related to local regulatory mechanisms, to actions on elements engaged in ecological community processes (i.e., plant-host interactions in the case of edible Lepidoptera, successional dynamics in the case of Coleoptera plague prevention, local technology to prevent seed predation by mammals), and to the temporal captivity or relocation of individuals without its reproduction or taming. In the middle of the gradient, we would have located wild fauna husbandry. However, this was not the case in the studied localities. On the opposite end, we distinguished the husbandry practices towards domesticated animals, associated to health, reproduction and feeding choices. People may apply, or not, post-domestication artificial selection criteria, guided by cultural mechanisms and possibly favouring the proportion of some genetic or phenotypic traits. However, a question that was not directly addressed in this work is to what extent and in which direction the local biodiversity management practices act as selective pressures on wild and domestic fauna populations (Zeder, 2015).

Around the Global Value of Local Ecological Knowledge

The multiple forms of LEK around the world have been fundamental for human societies' subsistence. Each of them is a way of knowing the world beyond a utilitarian value (Nóbrega-Alves and Albuquerque, 2018). However, based on LEK, human societies have solved provisioning needs and coexistence with fauna.

Western science has increased its corpus of knowledge through LEK, a process that has been often dismissed. One example is the contribution of knowledge and specimens to the European natural history collections from worldwide expeditions (Alves and Silva, 2015). In a similar way, scientific literature in the last 10 years has evaluated and discussed the advantages of including LEK as a source of information to increase scientific knowledge. For example, in the case of fauna monitoring and conservation. Our work was not devoted to systematically researching about the people's perspective about Western science or their thoughts about how to articulate ecological knowledge (i.e., coming from different ontologies and epistemologies) (Reid et al., 2020). Rather, we adopted a perspective in which the "management" of biodiversity for conservation (including regulatory mechanisms and local technology) is already happening locally. It is LEK-based (Romero-Bautista et al., 2020; Solís and Casas, 2020; Rocha et al., 2021) and the "expert managers" are the *Mexicatl* inhabitants of the local communities.

As part of a scholar community of a public university, in a multicultural country, where at least 68 main languages and 364 linguistic variants are spoken (INALI, 2008), the authors hope to contribute to make visible the multiple bio-cultural approaches to fauna management. In such perspective, this work constitutes a modest approach to the ecological knowledge processes related to the local fauna management practices. These, in turn, have emerged as a set of diverse practices similar to what previous research has documented along three axes: a rich typology of adaptive LEK-based management practices (Berkes et al., 2000), the frame of human-fauna coexistence mechanisms (Madden, 2004; Carter and Linell, 2016), and a perspective of a gradient management-domestication typology (Zeder, 2006, 2015).

CONCLUSION

People are engaged in complex relations with wild and domestic fauna and perform local management practices within categories that can be framed in the management and domestication theory. Supply practices in the case of wild animals were extractive, and there was no evidence of reproduction in captivity. Management practices aimed to assure the availability of domestic animals, insects, and some wild vertebrates included agreements with land

and animal human right holders. However, extraction is also likely regulated by the recognition of rules and agreements with divine non-human owners. Better understanding of the strengths these rules and agreements have to prevent fauna extirpation would be needed.

We found evidence of the lack of tolerance to cattle losses attributed to *C. latrans*. However, the use of local technology based on LEK could be an example of co-adaptation for the coexistence with medium sized mammals. Negative human-fauna interactions involving domestic animals were mainly categorised as crop losses, attacks to cattle from feral dogs, and human-human disagreements.

Fauna management is expressed in a broad spectrum of practices and techniques, which all respond not only utilitarian or conflictive situations, but also to levels of interest of people on animals and their relevance in all dimensions of peoples' life. Presence, distribution, abundance, interactions with other organisms, plants, and animals are all relevant aspects that modulate interactions between people and fauna. Some general similarities are shared and more widely analysed with interactions and motivations related to plant management and domestication. An integrated theoretical synthesis about management and domestication of biodiversity is possible, and all these elements found and discussed here will be important for such a purpose.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Reserva de la Biosfera Tehuacán-Cuicatlán. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. The animal study was reviewed and approved by Dirección de la Reserva de la Biosfera Tehuacán-Cuicatlán. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

MZ-C and MC-G facilitated student workshops and systematised its results. MZ-C performed adult interviews, analysed fieldwork results, and prepared the first draft of the manuscript. AC was the main coordinator-supervisor of the research project and also contributed to all steps of the research and reviewed several drafts of the manuscript. MZ-C, MC-G, JP-M, and AC reviewed the manuscript and contributed conceptually to achieve its final version. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.760805/full#supplementary-material

Supplementary Additional File 1 | Relation of workshops and interviews, interview checklist, and list of animal images used for visual stimulus instrument (docx).

Supplementary Additional File 2 | Complete outputs of salience analysis (xlsx).

Supplementary Additional File 3 | Uses, management, human-fauna negative interactions, and animal diet as reported in student and adult interviews (xlsx).

Supplementary Additional File 4 | Singing to feed juvenile *M. gallopavo.* (a) woman in Sierra and (b) girl in Tierra Caliente (TC). (c) *Potos flavus* call mimicked by a boy in TC; (mp3).

Supplementary Additional File 5 | Simplified general management scheme. Use of fauna can become in human- fauna negative interactions if native animal populations are stressed or pushed towards local extirpation by human demand for wild fauna or domestic cattle (as perceived by interviewed people). Negative human-fauna interactions can become in human-human conflict. These three interactions are related to five local management categories intended to supply animal resources and mitigate the damages caused by fauna or human conflicts, but also to regulate fauna extraction. Figure elaborated with Cmap tools (https://cmap.ihmc.us/) (jpg).

Supplementary Additional File 6 | Environmental units in which presence of fauna was reported. Three categories of environmental units in which animals were reported to be present. Figure elaborated with Cmap tools (https://cmap.ihmc.us/) (jpg).

REFERENCES

Agatha, A. (2016). Traditional wisdom in land use and resource management among the Lugbara of Uganda: a historical perspective. *SAGE Open* 6, 1–13. doi: 10.1177/2158244016664562

Albuquerque, U. P., Ludwig, D., Feitosa, I. S., Brito de Moura, J. M., Medeiros, P., de Medeiros, P. M., et al. (2020). Addressing social-ecological systems across temporal and spatial scales: a conceptual synthesis for ethnobiology. *Hum. Ecol.* 48, 557–571. doi: 10.1007/s10745-020-00189-7

Aldasoro-Maya, M., and Gómez, B. (2016). Insects and other invertebrates in the Pjiekakjoo (Tlahuica) culture in Mexico State, Mexico. *J. Insects Food Feed.* 2, 43–52. doi: 10.3920/JIFF2015.0090

Alonso-Castro, A. J. (2014). Use of medicinal fauna in Mexican traditional medicine. *J. Ethnopharmacol.* 152, 53–70. doi: 10.1016/j.jep.2014.01.005

Alves, R., and Silva, W. M. (2015). Ethnozoology: a brief introduction. *Ethnobiol. Conserv.* 4, 1–13. doi: 10.15451/ec2015-1-4.1-1-13

Argüelles-Santiago, J. N. (2012). "El maíz en la construcción y transmisión de una identidad cultural de la Huasteca Veracruzana," in *Estudios de Lengua y Cultura Náhuatl de la Huasteca*, eds A. van't Hooft and J. A. Flores-Farfán (Mexico: Linguapax, CCSYH-UASLP, CIGA-UNAM), 11–29.

Argueta, A., Corona, E., Alcántara-Salinas, G., Santos-Fita, D., Aldasoro, E., Serrano, R., et al. (2012). Historia, situación actual y perspectivas de la etnozoología en México. *Etnobiologia* 10, 18–40.

ATLAS.ti 8 (2021). *NEW! ATLAS.ti 22 Analyze Anything, Faster*. Available online at: https://atlasti.com/ (accesed March 29, 2022).

Ávila-Blomberg, A., and Moreno-Díaz, N. G. (2008). *Distribución de las Lenguas Indígenas de México. Catálogo de Metadatos Geográficos*. Mexico City: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Beaucage, P., and Taller de Tradicion Oral del CEPEC (2012). *Cuerpo, Cosmos y Medio Ambiente Entre los Nahuas de la Sierra Norte de Puebla. Una Aventura en Antropologia*. Ciudad de México: UNAM. Instituto de Investigaciones Antropológicas.

Berkes, F. (2008). *Sacred Ecology*, 2nd Edn. New York, NY: Routledge, Taylor and Francis.

Berkes, F., Colding, J., and Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecol. Appl.* 10, 1251–1262.

Blancas, J., Casas, A., and Pérez-Salicrup, D. (2014). Evaluando la incertidumbre en la disponibilidad de recursos vegetales. *Gaia Sci.* 8, 137–160. doi: 10.21707/gs.v8i2.22419

Blancas, J., Casas, A., Pérez-Salicrup, D., Caballero, J., and Vega, E. (2013). Ecological and socio-cultural factors influencing plant management in Náhuatl communities of the Tehuacán Valley, Mexico. *J. Ethnobiol. Ethnomed.* 9:39. doi: 10.1186/1746-4269-9-39

Canseco, L., and Gutiérrez, M. (2010). *Anfibios y Reptiles del Valle de Tehuacán-Cuicatlán*. Ciudad de México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Carter, N. H., and Linell, J. D. C. (2016). Co-adaptation is key to coexisting with large carnivores. *Trends Ecol. Evol.* 31:8. doi: 10.1016/j.tree.2016.05.006

Casas, A., Lira, R., Torres, I., Delgado, A., Moreno-Calles, A. I., Rangel-Landa, S., et al. (2016). "Ethnobotany for sustainable ecosystem management: a regional perspective in the TehuacánValley," in *Ethnobotany of Mexico: Interactions of People and Plants in Mesoamerica*, eds A. Casas, R. Lira, and J. Blancas (Cham: Springer), 179–206.

Castillo, A., Bullen, A. A., Peña-Mondragón, J. L., and Gutiérrez-Serrano, N. D. (2020). The social component of social-ecological research: moving from the periphery to the center. *Ecol. Soc.* 25:6. doi: 10.5751/ES-11345-250106

Ceausu, S., Graves, R., Killion, A., Svenning, J. C., and Carter, N. (2018). Governing trade-offs in ecosystem services and disservices to achieve human-wildlife coexistence. *Conserv. Biol.* 33, 543–553. doi: 10.1111/cobi.13241

CONABIO (1998). *Curvas de Nivel Para la República Mexicana. Catálogo de Metadatos Geográficos*. Ciudad de México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Cunningham, S., Kinkerdall, L., and Ballard, W. (2006). Gray fox and coyote abundance and diet responses after a wildfire in central Arizona. *West N. Am. Nat.* 66, 169–180. doi: 10.3398/1527-0904(2006)66[169:GFACAA]2.0.CO;2

da Silva, L., Borba do Nascimento, A. L., and Albuquerque, U. P. (2019). What matters in free listing? A probabilistic interpretation of the Salience Index. *Acta Bot. Bras.* 33, 360–369. doi: 10.1590/0102-33062018abb0330

de Paula, M. J., Xerente, V. S., Feraz-Silva, A. A., Godoy, B. S., and Brito-Pezzuti, J. P. (2018). Collaborative research and the hunting in the Brazilian Cerrado: the case of Xerente Indigenous Land. *Biota Neotrop.* 18:e20180556. doi: 10.1590/1676-0611-BN-2018-0556

Drury, R., Homewood, K., and Randall, S. (2011). Less is more: the potential of qualitative approaches in conservation research. *Anim. Conserv.* 14, 18–24. doi: 10.1111/j.1469-1795.2010.00375.x

Escamilla-Prado, E., Escamilla-Femat, S., Gómez-Utrilla, J. M., Tuxtla-Andrade, M., Ramos-Elorduy, J., and Pino-Moreno, J. M. (2012). Uso tradicional de tres especies de insectos comestibles en agroecosistemas cafetaleros del estado de Veracruz. *Trop. Subtrop. Agroecosyst.* 15, S101–S109.

Fernández-Llamazares, A., and Reyes-García, V. (2016). "An ethnobiology of change," in *Introduction to Ethnobiology*, eds U. Albuquerque and R. Nóbrega-Alves (Cham: Springer), 69–74. doi: 10.1007/978-3-319-28155-1_11

Flores-Armillas, V. H., López-Medellín, X., García-Barrios, R., MacGregor-Fors, I., and Valenzuela-Galván, D. (2020a). Landscape features associated with damage to maize (*Zea mays*) fields in Central México: a comparison of wind and wildlife damage. *Agriculture* 10:460. doi: 10.3390/agriculture10100460

Flores-Armillas, V. H., Valenzuela-Galván, D., Peña-Mondragón, J. L., and López-Medellín, X. L. (2020b). Human wildlife conflicts studies in Mexico. *Ecosist. Recur. Agropec.* 7:e2274. doi: 10.19136/era.a7n1.2274

Gallina, S., Pérez-Torres, J., and Guzmán-Aguirre, C. G. (2012). Use of the paca, *Cuniculus paca* (Rodentia: Agoutidae) in the Sierra de Tabasco State Park, Mexico. *Rev. Biol. Trop.* 60, 1345–1355. doi: 10.15517/rbt.v60i3.1812

Gallina-Tessaro, S., López-Tello, E., and Mandujano, S. (2019). "Recent studies of white-tailed deer in the Neotropics," in *Ecology and Conservation of Tropical Ungulates in Latin América*, ed. S. Gallina-Tessaro (Cham: Springer), 371–394. doi: 10.1007/978-3-030-28868-6_15

Garnier, S., Ross, N., Rudis, B., Sciaini, M., Camargo, A. P., and Scherer, C. (2021). *Viridis*. Available at: https://cran.r-project.org/web/packages/viridis/index.html (accessed March 29, 2022).

Giovannini, P., Reyes-García, V., Waldstein, A., and Heinrich, M. (2011). Do pharmaceuticals displace local knowledge and use of medicinal plants? Estimates from a cross-sectional study in a rural indigenous community, Mexico. *Soc. Sci. Med.* 72, 928–936. doi: 10.1016/j.socscimed.2011.01.007

Gómez, B., Junghans, C., Aldasoro, E. M., and Grehan, J. R. (2015). The ghost moth (Lepidoptera: Hepialidae) as food of indigenous people in Mexico. *J. Insects Food Feed.* 2, 53–59. doi: 10.3920/JIFF2015.0092

González-Jácome, A. (2004). Ambiente y cultura en la agricultura tradicional de México: Casos y perspectivas. *CIENCIA Ergo Sum* 11, 153–163.

Hernández-Atlahua, F. L. (2015). *Propagación de dos Especies Arbóreas del Bosque Mesófilo de Montaña, Hospederas de las Polillas Comestibles del Género Phassus spp. en Zongolica, Veracruz. Tesis de Ingenieria Forestal*. Veracruz: Instituto Tecnológico Superior de Zongolica.

INALI (2008). *Catálogo de las Lenguas Indígenas Nacionales*. Available online at: https://www.inali.gob.mx/pdf/CLIN_completo.pdf (accesed December 2021).

Instituto Nacional de Estadística, Geografía e Informática [INEGI] (2020). *Censo de Población y Vivienda. Datos Abiertos. Principales Resultados por Localidad*. Saint-Paul-lez-Durance: ITER.

Instituto Nacional de Estadística, Geografía e Informática [INEGI] (2018). *División Política Municipal. Catálogo de Metadatos Geográficos*. Ciudad de México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Knox, J., Ruppert, K., Frank, B., Sponarski, C., and Glikmanet, A. J. (2020). Usage, definition, and measurement of coexistence, tolerance and acceptance in wildlife conservation research in Africa. *Ambio* 50, 301–313. doi: 10.1007/s13280-020-01352

Lazos, E., and Paré, L. (2000). *Miradas Indígenas sobre Una Naturaleza Entristecida*. México: Instituto de Investigaciones Sociales.

Linares-Rosas, M., Gómez, B., Aldasoro-Maya, M., and Casas, A. (2021). Nahua biocultural richness: an ethnoherpetological perspective. *J. Ethnobiol. Ethnomed.* 17:33. doi: 10.1186/s13002-021-00460-1

López-Austin, A. (1999). *Tamoanchan y Tlalocan*. Brasília: Fondo de Cultura Económica.

López-Tello, E., Gallina, S., and Mandujano, S. (2015). Activity patterns of white-tailed deer in the Tehuacán-Cuicatlán Biosphere Reserve, Puebla-Oaxaca, Mexico. *Deer Spec. Group IUCN Newslett.* 27, 32–43.

Lute, M. L., and Carter, N. H. (2020). Are we coexisting with carnivores in the American west? *Front. Ecol. Evol.* 8:48. doi: 10.3389/fevo.2020.00048

Madden, F. (2004). Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Hum. Dimens. Wildlife* 9, 247–257. doi: 10.1080/10871200490505675

Marchini, S. (2014). "Who's in conflict with whom? Human dimensions of the conflicts involving wildlife," in *Applied Ecology and Human Dimensions in Biological Conservation*, eds L. M. Verdade, M. C. Lyra-Jorge, and C. I. Piña (New York, NY: Springer Press), 189–209. doi: 10.1007/978-3-642-54751-5_13

Maxwell, J. A. (2013). *Qualitative Research Design. An Interactive Approach*, 3rd Edn. Thousand Oaks, CA: SAGE.

Meireles, M. P. A., de Albuquerque, U. P., and de Medeiros, P. M. (2021). What interferes with conducting free lists? A comparative ethnobotanical experiment. *J. Ethnobiol. Ethnomed.* 17:4. doi: 10.1186/s13002-021-00432-5

Molina-Nery, M. C., Ruiz-Montoya, L., Castro-Ramírez, A. E., González-Díaz, A. A., and Caballero-Roque, A. (2017). The effect of agricultural management on the distribution and abundance of *Arsenura armida* (Lepidoptera: Saturniidae) in Chiapas, Mexico. *J. Lepid. Soc.* 71, 236–248. doi: 10.18473/lepi.71i4.a6

Nava-Vite, R. (2012). "El Costumbre: ofrendas y música a Chikomexochitl en Ixhuatlán de Madero, Veracruz," in *Estudios de Lengua y Cultura Náhuatl de la Huasteca*, eds A. van't Hooft and J. A. Flores-Farfán (Mexico: Linguapax, CCSYH-UASLP, CIGA-UNAM), 30–66.

Newing, H., Eagle, C. M., Puri, R. K., and Watson, C. W. (2011). *Conducting Research in Conservation. Social Science Methods and Practice*. New York, NY: Routledge, Taylor and Francis. doi: 10.4324/9780203846452

Nóbrega-Alves, R. (2012). Relationships between fauna and people and the role of ethnozoology in animal conservation. *Ethnobiol. Conserv.* 1, 1–69. doi: 10.15451/ec2012-8-1.2-1-69

Nóbrega-Alves, R., and Albuquerque, U. (eds) (2018). *Ethnozoology: Animals in Our Lives*. Gewerbestrasse: Elsevier. doi: 10.1016/B978-0-12-809913-1.00002-8

Nóbrega-Alves, R., and Duarte-Barboza, R. (2018). "Animals as Ethnozooindicators of Weather and Climate," in *Ethnozoology: Animals in our lives*, eds R. Nóbrega-Alves and P. Albuquerque (London: Academic Press), 383–420. doi: 10.1016/B978-0-12-809913-1.00021-1

Ojasti, J. (2000). *Manejo de Fauna Silvestre Neotropical*. Washington, DC: Smithsonian Institution.

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2020). *Vegan*. Available online at: https://cran.r-project.org/web/packages/vegan/vegan.pdf (accessed March 29, 2022).

Oltehua-Tzitzihua, J. L. (2016). *Estudio Poblacional de las Polillas Comestibles Popotocas (Phassus spp. Hepialidae) en dos Localidades de la Sierra de Zongolica, Veracruz. Tesis de Ingeniería Forestal*. Veracruz: Instituto Tecnológico Superior de Zongolica.

Olubukola, T., Abdalla, M. A., and McGaw, L. J. (2020). "Ethnoveterinary plants and practices for the control of ticks and tick-borne diseases in South Africa," in *Ethnoveterinary Medicine: Present and Future Concepts*, eds L. McGaw and M. A. Abdalla (Cham: Springer), 251–267. doi: 10.1007/978-3-030-32270-0_11

Open Source Geospatial foundation [OsGeo] (2020). *Qgis 3.8. Creative Commons Attribution-ShareAlike 3.0 License*. Available online at: https://www.qgis.org/en/site/about/index.html (accessed January 3, 2020).

Ostrom, E., Burguer, J., Field, C., Norgaard, R., and Policansky, D. (1999). Revisiting the commons: local lessons, global challenges. *Science* 284, 278–282. doi: 10.1126/science.284.5412.278

Pausas, J. G. (2019). Generalized fire response strategies in plants and animals. *Oikos* 128, 147–153. doi: 10.1111/oik.05907

Pérez-Solano, L., Mandujano, S., Contreras-Moreno, F., and Salazar, J. M. (2012). Primeros registros del temazate rojo *Mazama temama* en áreas aledañas a la reserva de la biosfera de Tehuacán-Cuicatlan Mexico. *Rev. Mex. de Biodivers.* 83, 875–878. doi: 10.7550/rmb.27007

Pinto, M., Pereira, T., Alves, L., and Nóbrega-Alves, R. (2018). "People and fishery resources: a multidimensional approach," in *Ethnozoology: Animals in Our Lives*, eds R. Nóbrega-Alves and P. Albuquerque (London: Academic Press), 119–149. doi: 10.1016/B978-0-12-809913-1.00008-9

Quinland, M. (2005). Considerations for collecting freelists in the field: examples from ethnobotany. *Field Methods* 17, 219–234. doi: 10.1177/1525822X05277460

R software (2020). *R-3.6.3 for Windows (32/64 bit)*. Avilable online at: https://cran.r-project.org/bin/windows/base/old/3.6.3/ (accessed July 30, 2021).

R studio (2021). *RStudio Academy*. Available online at: https://rstudio.com (accessed July 30, 2021).

Ramos-Elorduy, J., Landero-Torres, I., Murguía-González, J., and Pino, J. M. (2008). Biodiversidad antropoentomofágica de la región de Zongolica, Veracruz, México. *Rev. Biol. Trop.* 56, 303–316. doi: 10.15517/rbt.v56i1.5526

Rangel-Landa, S., Casas, A., Rivera-Lozoya, E., Torres-García, I., and Vallejo-Ramos, M. (2016). Ixcatec ethnoecology: plant management and biocultural heritage in Oaxaca, Mexico. *J. Ethnobiol. Ethnomed.* 12, 30. doi: 10.1186/s13002-016-0101-3

Reid, A. J., Eckert, L. E., Lane, J., Young, N., Hinch, S., Darimont, C., et al. (2020). Two-eyed Seeing": an indigenous framework to transform fisheries research and management. *Fish Fish.* 22, 243–261. doi: 10.1111/faf.12516

Rivero-Romero, A. D., Moreno-Calles, A. I., Casas, A., Castillo, A., and Camou-Guerrero, A. (2016). Traditional climate knowledge: a case study in a peasant community of Tlaxcala, Mexico. *J. Ethnobiol. Ethnomed.* 12:33. doi: 10.1186/s13002-016-0105-z

Rocha, R., López-Baucells, A., and Fernández-Llamazares, A. (2021). Ethnobiology of bats: exploring human-bat inter-relationships in a rapidly changing world. *J. Ethnobiol.* 41, 3–17. doi: 10.2993/0278-0771-41.1.3

Romero-Bautista, Y. A., Moreno-Calles, A. I., Alvarado-Ramos, F., Reyes-Castillo, M., and Casas, A. (2020). Environmental interactions between people and birds in semiarid lands of the Zapotitlán Valley, Central Mexico. *J. Ethnobiol. Ethnomed.* 16:32. doi: 10.1186/s13002-020-00385-1

Rudis, B., Kennedy, P., Reiner, P., Wilson, D., Adam, X., Barnett, J., et al. (2020). *hrbrthemes*. Available online at: https://cran.r-project.org/web/packages/hrbrthemes/index.html (accessed March 29, 2022).

Sánchez, O. (1999). "Biodiversidad, conservación y Manejo," in *Diplomado en Manejo de Vida Silvestre. Conservación y Manejo de Vertebrados del Norte Árido y Semi-Árido de México*, eds O. Sánchez and E. Vázquez-Domínguez (México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad), 13–23.

Secretaría de Medio Ambiente y Recursos Naturales-Comisión Nacional de ÁĄreas Naturales Protegidas [SEMARNAT- CONANP] (2013). Programa de Manejo de la Reserva de la Biosfera de Tehuacán-Cuicatlán. *Ciudad de México: SEMARNAT-CONANP*

Santos-Fita, D., Naranjo, E., and Rangel-Salazar, J. L. (2012). Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, Mexico. *J. Ethnobiol. Ethnomed.* 8:38. doi: 10.1186/1746-4269-8-38

Santos-Fita, D., Naranjo, E., Estrada, E., Mariaca, R., and Bello, E. (2015). Symbolism and ritual practices related to hunting in Maya communities from central Quintana Roo, Mexico. *J. Ethnobiol. Ethnomed.* 11:71. doi: 10.1186/s13002-015-0055-x

Schaaf, T., and Rossler, M. (2010). "Sacred natural sites, cultural landscapes and UNESCO's action," in *Sacred Natural Sites, Conserving Nature and Cultures*, eds B. Verschuuren, R. Wild, J. McNeely, and G. Oviedo (London: Earthscan), 161–169.

Sinclair, A., Fryxell, J. M., and Caughley, G. (2006). *Wildlife Ecology, Conservation and Management*, 2nd Edn. Malden, MA: Blackwell Publishing.

Smith, J. J., and Borgatti, S. P. (1997). Salience counts and so does accuracy: correcting and updating a measure for free-list-item salience. *J. Linguist. Anthropol.* 7, 208–209.

Solís, L., and Casas, A. (2020). Cuicatec ethnozoology: traditional knowledge, use, and management of fauna by people of San Lorenzo Pápalo, Oaxaca, México. *J. Ethnobiol. Ethnomed.* 15:58. doi: 10.1186/s13002-019-0340-1

Stahl, P. W. (2014). "Garden hunting," in *Encyclopedia of Global Archaeology*, ed. C. Smith (New York, NY: Springer), doi: 10.1007/978-1-4419-0465-2_2132

Stevenson, E. R., Lashley, M. A., Chitwood, M. C., Garabedian, J. E., Swingen, M. B., DePerno, C. S., et al. (2019). Resource selection by coyotes (*Canis latrans*) in a longleaf pine (*Pinus palustris*) ecosystem: effects of anthropogenic fires and landscape features. *Can. J. Zool.* 97, 165–171. doi: 10.1139/cjz-2018-0150

Strauss, A., and Corbin, J. M. (1998). *Basics of Qualitative Research: Techniques and Procedures for Developing Grounded Theory*, 2nd Edn. Thousand Oaks, CA: SAGE.

Valsecchi, J., El-Bizri, H. R., and Figueira, J. E. C. (2014). Subsistence hunting of *Cuniculus paca* in the middle of the Solimões River, Amazonas, Brazil. *Braz. J. Biol.* 74, 560–568. doi: 10.1590/bjb.2014.0098

van't Hooft, A., and Flores-Farfán, J. A. (eds). (2012). *Estudios de Lengua y Cultura Náhuatl de la Huasteca*. México: Linguapax, CCSYH-UASLP, CIGA-UNAM.

Wickham, H., Chang, W., Henry, L., Lin, T., Takahashi, K., Wilke, C., et al. (2021). *ggplot2*. Available online at: https://cloud.r-project.org/web/packages/ggplot2/index.html (accesed March 29, 2022).

Willerslev, R., and Vitebsky, P. (2014). Sacrifice as the ideal hunt: a cosmological explanation for the origin of reindeer domestication. *J. R. Anthropol. Inst.* 21, 1–23. doi: 10.1111/1467-9655.12142

Zarazúa, M. (2016). "Del guajolote a las chicatanas. Uso, manejo y domesticación de recursos genéticos animales en Mesoamérica," in *Domesticación en el Continente Americano*, Vol. 1, eds A. Casas, J. Torres-Guevara, and F. Parra (Lima: Universidad Nacional Autónoma de México, Universidad Nacional Agraria La Molina), 283–316.

Zarazúa-Carbajal, M., Chávez-Gutiérrez, M., Romero-Bautista, Y., Rangel-Landa, S., Moreno-Calles, A. I., Ramos, L. F. A., et al. (2020). Use and management of wild fauna by people of the Tehuacán-Cuicatlán Valley and surrounding areas, Mexico. *J. Ethnobiol. Ethnomed.* 16:4. doi: 10.1186/s13002-020-0354-8

Zeder, M. (2006). Central questions in the domestication of plants and animals. *Evol. Anthropol.* 15, 105–117. doi: 10.1002/evan.20101

Zeder, M. (2015). Core questions in domestication research. *Proc. Natl. Acad. Sci. U.S.A.* 112, 3191–3198. doi: 10.1073/pnas.1501711112

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Ethnoichthyology and Ethnotaxonomy of the Kichwa Indigenous People of *Arawanu* (Arajuno), in the Ecuadorian Amazon

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The Amazon Basin is home to a great number of Indigenous nationalities that have coevolved with aquatic habitats and fish resulting in a precise traditional ecological knowledge. Nevertheless, this biocultural heritage is threatened by the degradation of rivers and fisheries, and cultural erosion. This research was designed and carried out in the community of *Arawanu* (Arajuno in Spanish), in the Ecuadorian Amazon, and was requested by the local Kichwa people looking for guidance to gather, systematize and disseminate their ethnoichthyological knowledge. Data collection was carried out through participatory workshops using the pile sorting technique in group dynamics, to identify, name and classify local fish and compile biocultural information about them. From the Linnaean taxonomic perspective, 86 taxa were identified, included in 26 families, and corresponded with 16 Kichwa ethnofamilies and 58 ethnospecies. Five classification levels were identified: (I) *Aycha*: unique beginner–Animalia kingdom; (II) *Yaku Aycha*: life form–Pisces superclass; (III) *Ayllukuna*: ethnofamilies–Linnaean families; (IV) Ethnogenera–Linnaean genus; and (V) Ethnospecies–Linnaean species. A one-to-one correspondence was registered between 35 Kichwa ethnospecies and Linnean species, along with one case of over-differentiation and 21 cases of subdifferentiation (Type A: 7; Type B: 14). The Kichwa ethnoichthyological classification is multidimensional and considers attributes like skin and scales, fishbones and spines, meat quality, body shape, diet, and salience. Of the 58 ethnospecies, 38 were valued for consumption, while medicinal and spiritual uses were mentioned for 40 of them. The participatory work created a forum to discuss the value and threats to ichthyofauna and freshwater systems, enabled the dissemination of their biocultural heritage, and highlighted the cultural relevance of hydro-social ecosystems in their livelihood. The collected information may be critical to adapt local education systems to the Kichwa worldview and to pass down traditional ecological knowledge to future generations, fostering a respectful, careful and conscious relationship between humans and nature. Our results offer a solid and novel information compilation and practical guidance for participatory ethnobiological surveys. Additionally, the ethnobiological and the ethnotaxonomical information establishes the basis to develop sustainable fishing strategies and promote conservation of the local ichthyofauna.

Keywords: ethnoclassification, traditional ecological knowledge, fish, Amazon Basin, Indigenous community, folk taxonomy, biocultural diversity

INTRODUCTION

The Amazon Basin is one of the global hotspots of biocultural diversity, nurtured by the Indigenous communities living in the rainforest and along the riverbanks of an intricate water system (Loh and Harmon, 2005). Rivers play a key socio-cultural role for many of these human groups. They are a source of food and medicines, are used as waterways, and have important spiritual relevance while the identity of many of the local native cultures emerges from their relationship with water and rivers (Angarita-Baéz et al., 2017).

The Amazon River system supports the greatest freshwater biodiversity on Earth, with more than 2,200 strictly freshwater species, representing around 15% of all freshwater fish worldwide (Jézéquel et al., 2020). However, many basins and large territories remain poorly studied and a great number of species are yet unknown to western science (Antonelli et al., 2018). Fishing is an important subsistence activity for many human groups in the Amazon and reflects a deep relationship between humans and water landscapes (Alves, 2012). It also indicates both a precise and diverse traditional ecological knowledge (*corpus*); is the source and inspiration for a wide variety of tools, techniques and practices (*praxis*); and is crucial to understand the worldview and spiritual links (*kosmos*) of numerous Indigenous people related to fish and rivers (Alves and Souto, 2011; Jácome-Negrete, 2012; Toledo and Alarcón-Cháires, 2012).

Fishing is transcendental in the Amazon, since fish represent the main protein source for the local inhabitants and guarantee the food sovereignty of many human cultures (Mertens et al., 2015; Val et al., 2017). Specifically, the Amazonian Kichwas stand out as a culture with extraordinary fishing skills and detailed knowledge about fish and other aquatic organisms. Above other uses, fish are the key alimentary source for them. Vasco and Sirén (2019) estimated a fish consumption among the Kichwas in Pastaza of 104 g/person/day. This is the result of a historical cohabitation and coevolution between fish, rivers, and people, and points out the critical dependence on this resource (Vacacela, 2007; Jácome-Negrete, 2013).

The study of local classification systems is a practical way to address ethnobiological knowledge and understand traditional cultures and their world view (Posey, 1985; Berlin, 1992; Lepofsky, 2009; Hunn, 2014). The ethnoclassification approach has also proven to be an effective way to compile and assess ethnoichthyological information (Forth, 2017). It is a good starting point to unveil a wide variety of traditional ecological knowledge related to fish species, fishing techniques, biological and ecological information, fishing areas, social norms, beliefs and even the history of the local community and the rivers around them (Alves and Souto, 2011; Previero et al., 2013). It also allows us to approach the sociocultural mindset of the community, expressed in the naming and ordering of the natural world, the basis that determines the way humans relate and interact with their environment (Berlin, 1992; Kakudidi, 2004; Hunn, 2014). Therefore, the ethnotaxonomic approach is crucial to register, classify and value biodiversity from the local point of view, and stands out as a keystone discipline to adapt and foster biocultural conservation strategies (Mourão and Barbosa Filho, 2018; Barbosa-Filho et al., 2021). It also stands out as a crucial tool for academics to disclose the diverse and complex ichthyofauna of the Amazon and to protect and manage it (Alves, 2012).

However, Pauly et al. (2005) and Pinto et al. (2013) warn us about how the accelerated degradation of hydrosocial systems and fisheries drastically affects those communities that rely on subsistence fishing, such as the Amazonian Kichwas in Ecuador, whose livelihood and the conservation of their culture is severely threatened (Cevallos, 2020). The traditional ecological knowledge they retain is also suffering from the arrival of new external actors and accelerated globalization processes related to this connection to the "outside world" that triggers rapid socio-cultural changes. The imposition of a generic nationwide education system, not adapted to the local cultural and environmental context (even been bilingual), is also hampering intergenerational transmission of local knowledge and homogenizing their culture (Weckmüller et al., 2019).

To face the challenge of fighting against this environmental degradation and acculturation, while conserving the biocultural heritage related to fish and rivers, the Kichwa leaders of the *Puka Rumi* Community Center, part of the Community Organization of the Kichwa of Arajuno (*Arawanu Kichwa Ayllu Tantanakuy*) in the Pastaza Province of the Ecuadorian Amazon, asked the authors for guidance and help. Specifically, they needed advice and assistance to gather and systematize their ethnoichthyological knowledge for conservation management and educational purposes. Therefore, this project was designed and carried out through participatory processes involving academics and local inhabitants, seeking solutions that could help tackle the ongoing threats to the local environment and culture.

In this collaborative context, many questions arose from the beginning: how is the relation between the Kichwas, fish and rivers? How deep and precise is the knowledge they have about fish? How do they identify and classify fish? How do they capture and use fish? How relevant are the fish ecologically, culturally and socially for the Kichwas in Arajuno? How can the ethnotaxonomy and classification help to address sustainable fishing and the conservation of biocultural diversity?

MATERIALS AND METHODS

This collaborative research process combining western science and traditional knowledge was inspired and guided by two deep-rooted Kichwa concepts, *mink'a* and *randi-randi*. The workshops were presented to the Kichwa participants as a *mink'a*, a gathering of the community working together for the common good, without any economic benefit. They shared their time and information to help us collect all the common knowledge around fish and make it available for everyone afterward. The relation between the scientists and the Kichwa participants was guided by the *randi-randi*, giving and giving, a reciprocal relational principle that encourages people to share. The authors offered help to organize workshops and prepare popular science materials for the community, while the Kichwa offered their time and knowledge and their permission to use the information for scientific purposes, like this manuscript. As one of the Kichwa leaders said when presenting us to the community, "These scientists have come to work with us like many others before them, but this time they won't leave without previously returning to us all the results of the research." The project began in October 2018, and the presentation of the results along with the environmental education materials were handed out to the community on November 29, 2019, thus fulfilling our promises.

To facilitate the intercultural relations and guide the research, our team included three experienced ethnoichthyologists who have been working with the Ecuadorian Kichwas in the Amazon for years (Iván Jacóme-Negrete and Lida Guarderas-Flores since 2001, and Carolina Carrillo-Moreno since 2012) and have published many scientific and technical documents (Jácome-Negrete, 2012, 2013, 2021; Valdiviezo-Rivera et al., 2012; Jácome-Negrete and Guarderas-Flores, 2015; Carrillo-Moreno, 2017). Their knowledge about the Kichwa culture and their relationship with fish was crucial to facilitate data collection and interpretation.

Study Area

The study was carried out in the Arajuno Canton (*Arawanu*, in Kichwa), in the Ecuadorian province of Pastaza, in the territory of the *Puka Rumi* Community Center (1°14′0.89″S; 77°42′6.63″W) (**Figure 1**). *Puka Rumi* covers an area of more than 600 ha within the upper basin of the Arajuno River, a tributary of the Napo River, inside the Amazon River system. The territory is not yet legally recognized as property of the community and the boundaries are in the process of being officially established.

According to zoogeographic criteria, this area is part of the Eastern Tropical Floor (Albuja, 2011). It comprises ecosystems of evergreen forest of the peneplain in the Napo-Curaray area, floodplain forests of the alluvial plain rivers in the Andean and Amazonian Mountain ranges, and flooded palm forests in the Amazonian floodplains (MAE, 2012). The studied ecosystems were the Arajuno River and its tributaries. The sampled rivers flow along the Andean-Amazonian foothills, in an altitude range between 460 and 491 m.a.s.l. and belong to the Alto Napo ichthyohydrographic zone (Barriga, 2012). The sampled rivers were the Arajuno River (*Arawanu Mayu* in Kichwa), Huapuno River (*Wapunu Mayu*), and Inayaku River (*Inayaku Mayu*) (**Figure 1**).

Study Population

Our research was carried out with the collaboration of the Community Organization of the Kichwa of Arajuno, comprising 26 communities inside the Arajuno Canton, totaling 2648

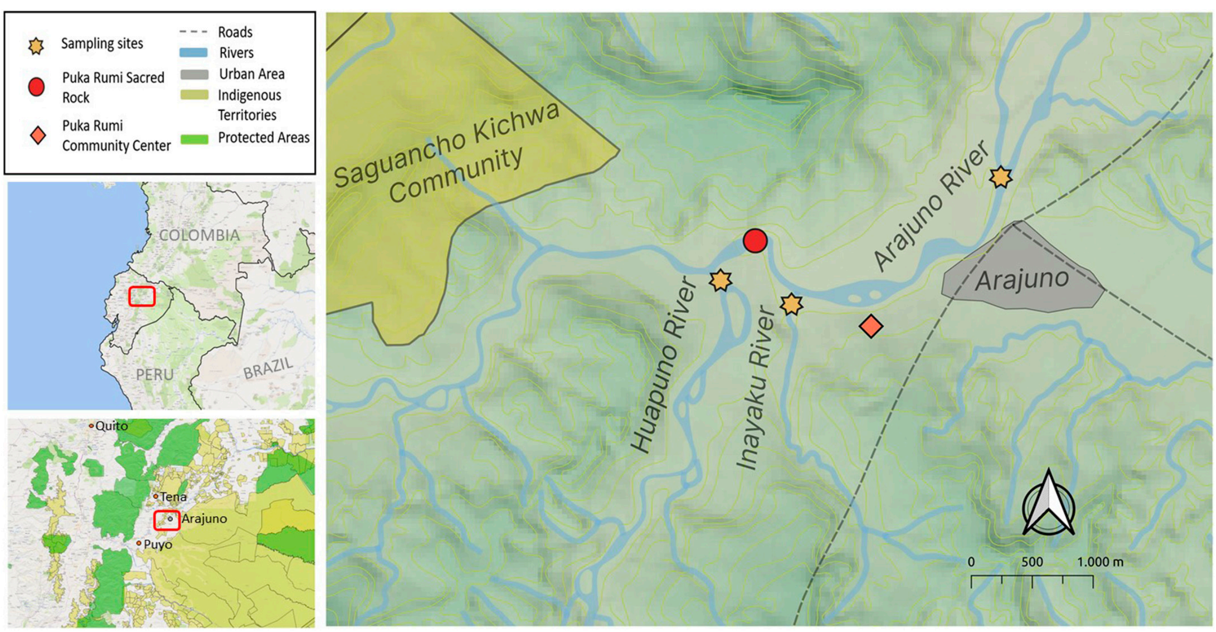

FIGURE 1 | Map of the study area and study sites in Arajuno, in the Ecuadorian Amazon (IGM, 2020; Ministerio del Ambiente, Agua y Transición Ecológica, 2021; Raisg, 2021).

inhabitants (GADMCA, 2014). Many of the participants were part of the *Puka Rumi* Community Center, formed by 24 families (whose leaders were the promoters of the project), and from other communities close to the Arajuno village. All the collaborators were of Kichwa origin: their mother tongue is Kichwa, while Spanish is their second language and they use it fluently. Their main activities are principally for subsistence, which include: fishing, hunting, agriculture and the gathering of wild fruits, and materials (GADMCA, 2014). The Kichwa of *Puka Rumi* settled in the area in 1907 migrating from the surrounding areas of Tena, an Amazonian city north of Arajuno (**Figure 1**). They established their village around the *Puka Rumi* (red rock), a big boulder in the Arajuno River, which the Kichwa considered sacred, and represents the spiritual core of the community (**Figure 1**). The Community Center was created to centralize and guide governance efforts in the territory. It describes itself as: "A life project that aims to contribute and guide the joint action for the conservation, recovery and sustainable use and management of natural resources, strengthening the Kichwa cultural identity through the transference of local knowledge."

Data Collection

The project was designed following the previous successful experiences of the authors work with other Kichwa communities in the Amazon. The leaders of *Puka Rumi* knew about these other projects and they also knew two of the authors personally thanks to those previous works, and they wanted to replicate them in Arajuno. This predisposition made it easy to come to the terms of collaboration and sign an agreement between the community representatives and the research team.

Besides the general agreement with community authorities, before every workshop we also explained the objectives and activities to be carried out in that session as well as the products to be generated, which were later checked and approved by the attendees. At each session, the participants signed a letter where they authorized us to compile and use the information gathered for environmental education materials and scientific publications. The entire research process, the data collection, the analysis of the results and the publication of this manuscript followed the guidelines of the Code of Ethics for Ethnobiological Research in Latin America (Argueta et al., 2018).

Participatory Community Fishing

Participatory fishing was carried out with local community members during five sampling days in October and November 2018 (**Figure 2**). Two adult women and four adult men helped us throughout the surveys. We combined artisanal fishing techniques like hooks, throw nets and harpoons, with electrofishing, trawl and trammel nets, including some night samplings too. Captured fish were kept alive in an aquarium with an oxygen pump, identified using both Kichwa and Linnaean taxonomy, photographed and released back to the river at

FIGURE 2 | Participatory fishing surveys: **(A)** Throw net; **(B)** Free diving; **(C)** Trawl net; **(D)** Electrofishing.

the end of the sampling (**Figure 2**). Those fish specimens difficult to be correctly identified in the field were anesthetized (2% lidocaine hydrochloride) and fixed (10% formol) for their subsequent analysis in the Museum of Zoology of the Universidad Tecnológica Indoamérica, located in Quito. The laboratory identification was carried out using the following publications: Gèry (1977), Kullander (1986), Chernoff and Machado-Allison (1990), Vari and Harold (2001), Armbruster (2005), de Melo and Buckup (2006), Jácome-Negrete and Guarderas-Flores (2015), Lujan et al. (2015), van der Sleen and Albert (2017), and Provenzano and Barriga-Salazar (2018).

Ethnobiological Workshops

After the fishing campaign, three participatory workshops were organized in the community to identify and classify local fish, and to gather ethnobiological, ethnoecological and ethnotaxonomical information. The first one was carried out on October 27, 2018, in the Community Organization of the Kichwa of Arajuno facilities (**Figure 3**). For the identification of the ichthyofauna, photographs were used as visual stimuli (Ellen, 1986; Albuquerque et al., 2014) following the pile sorting technique (Gollin et al., 2004). Twenty-three Kichwa people attended this workshop, twelve women and eleven men, ranging from 7 to 71 years old. All of them practiced subsistence fishing, and four of them had helped us during the previous sampling campaign. Six researchers participated in the process: two of them guided the group dynamics, two took notes of the important information during the group discussion and the remaining two recorded the workshop on video and took pictures. A total of 60 color photographs of fish were used, including the photographs taken during the fishing campaigns (24) and additional photographs of other species potentially inhabiting the rivers and tributaries in the area (**Figure 3**). One of the photographs was a species from another biome, *Oncorhynchus mykiss* (Walbaum, 1792), which was included to confirm that the attendees could recognize fish that were not found in the community. Additionally, some books and posters containing a wider set of pictures were used to complement the photographs. In some cases, some additional information about the size of the fish was given by the researchers to facilitate the identification without interfering too much in the process.

During the pile-sorting dynamic (**Figure 3**), all the participants worked as a group selecting the pictures of the fish they could recognize as local. The researchers interceded when trying to give voice to everybody and encouraged the participation and the debate of all the attendees. For each one of the fish, participants would discuss and agree on the local name, the recognizable attributes, the common uses and other relevant biological and practical information (habitat use, reproduction, migration, trophic niche, and fishing techniques). The Kichwa names of the species were written on the front of each picture and the rest of the information was written on the back. While

FIGURE 3 | Ethnobiological workshops: **(A)** First workshop: pile sorting; **(B)** First workshop: local fish identification and discussion about their names and information; **(C)** First workshop: grouping fish within their families, including the description of classification criteria and additional information; **(D)** Second workshop: revision and correction of the data collected during the first workshop; **(E)** Third workshop: final revision and validation of the ethobiological and ethnotaxonomical information; **(F)** Public presentation of the results and the poster.

identifying and naming, the first steps of the classification were made simultaneously because the Kichwa would immediately group the fish usually repeating "this fish is from the same family as this one here." Once all the local fish were placed on a wall, a large paper was stuck next to the pictures to be used like a blackboard, where participants grouped the fish, one by one, into each of their families (**Figure 3**). Once all the fish were classified, the common characteristics of each family were discussed and written on the "blackboard." The entire process was easy to follow as all the information was visible, so all participants could check and verify details throughout the process. Finally, the attendees were asked about the importance of fish and rivers in their culture, including spirituality and the human actions that may affect river ecosystems, helping us to better understand their cultural bonds with fish. It also created a forum where all the Kichwas could share and debate their individual perspective and build a collective agreement.

The second workshop was organized on November 17, 2018 (**Figure 3**). The aim of this workshop was to corroborate and validate the information collected and systematized during the first meeting. Six Kichwa participants assisted in this workshop (three men and three women, four of them were present in the first workshop) ranging from 33 to 71 years old. Here, all the names, classification, characteristics, and additional information of every fish were verified using the photograph collage created during the first session, supported by books and a laptop with additional pictures. The attendees worked together and were guided by three researchers that registered the comments and corrections. A fourth researcher video recorded the session.

The third workshop was held April 13, 2019, to present all the available data and allow community members to give their final validation of the information. Eleven Kichwa people assisted this last workshop (one child, one teenager, and nine adults, ranging from 7 to 71 years old, seven men and four women). All of them had participated on the first workshop, while the six participants from the second workshop were also present. Apart from the final review of all the ethnotaxonomic and ethnobiologic information, a poster created for environmental education purposes and to foster public outreach of the research was presented and discussed (**Figure 4**). Once the materials were validated and accepted, the informative posters were printed in Kichwa and Spanish and handed over to the community in a public presentation on November 29, 2019 (**Figure 3**).

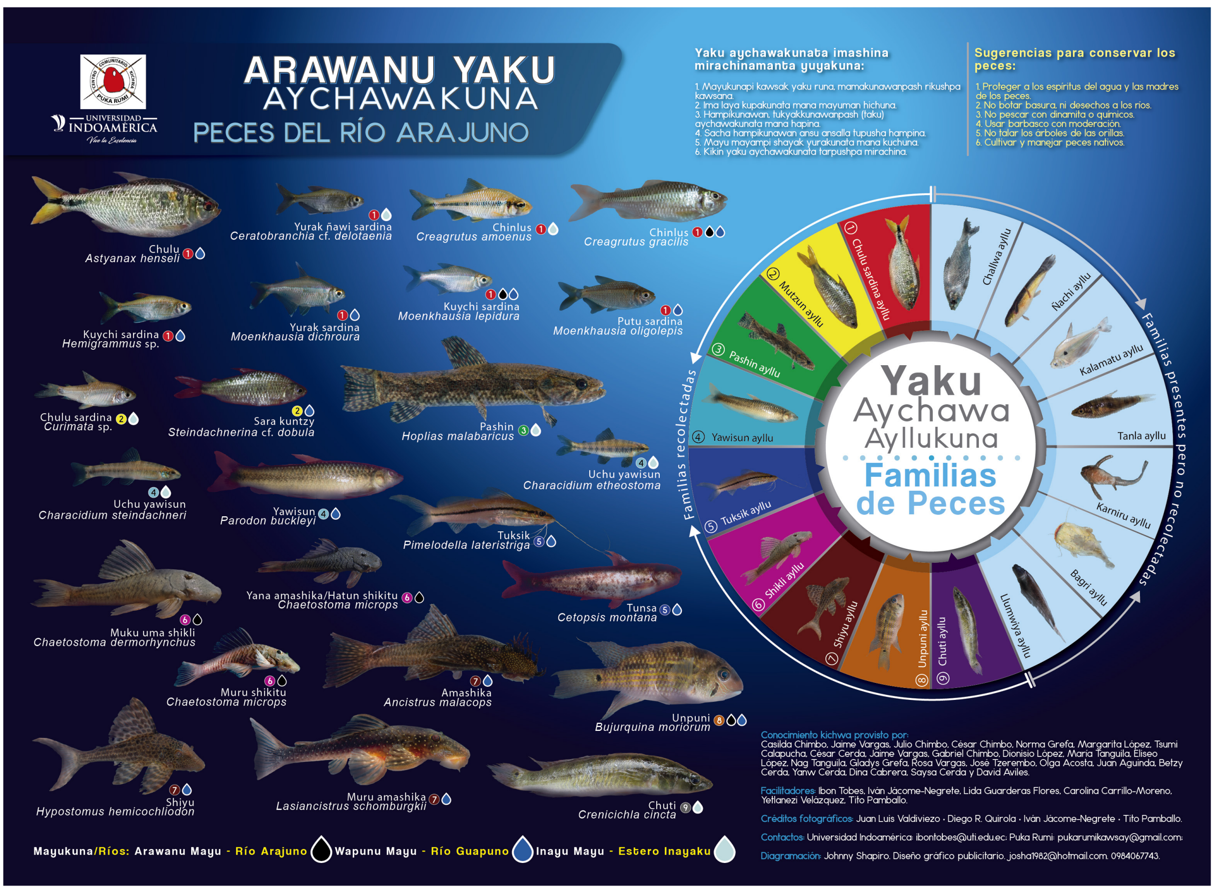

FIGURE 4 | Bilingual poster designed with the Kichwa participants. Includes a schematic diagram with the sixteen ethnofamilies, pictures of the 24 fish taxa captured during the field sampling and the recommendations of the Kichwa collaborators for conserving fish and rivers. The poster can be found and downloaded in high resolution from this link: https://figshare.com/articles/figure/Poster_Peces_Arajuno_png/19364306.

RESULTS

Participatory Fishing

The Kichwas of Arajuno showed outstanding fishing abilities. They were able to swim and walk in the river even against very strong water currents, they knew the best places for fishing and where they could find each species, and they were very skillful using all the fishing techniques. They were able to free dive for long periods of time, find fish underwater with low visibility and catch them using their bare hands, a machete or the harpoon, and also used hooks and throw nets with expertise. The combination of traditional fishing techniques with electric fishing, the trawl and trammel net, resulted in the collection of 24 Linnaean species, belonging to 19 genera (**Table 1**).

Ethnoclassification

The participatory fishing and the use of photographs allowed us to record 58 Kichwa species recognized by the participants: 52 of them had Kichwa names, five species had mixed Kichwa-Spanish names (five adding *sardina* and one adding *lisa* to the Kichwa name), and one species was only named in Spanish, *Anguila*, *Electrophorus electricus* (Linnaeus, 1766). All the species were grouped in 16 families, called *ayllu* in Kichwa (*ayllukuna* in plural). From the perspective of the Linnaean taxonomy, 86 taxa were identified and included in 26 families. From those, 17 were identified at the genus level, one was identified as *affinis* and two as *confer* (**Table 1**). This under identification is related to the inability to precisely determine some of the captured fish and with the identification of some taxa during the workshops that were not included in the pile of photographs but could be somehow tracked using the additional books and materials. Considering all the recorded Kichwa names, 57% (33) had monomial names, while the remaining 43% (25) had polynomial names (23 binomial and two trinomial). No participant recognized the "trap species" as local.

To establish the relationship between the Kichwa and Linnaean classification systems we considered the types of correspondence proposed by Berlin (1973) (**Table 1**):

(a) One-to-one correspondence: 35 Kichwa species are related to 35 Linnaean species.
(b) Over-differentiation: three local species were related to one Linnaean species. The Kichwa nomenclature differentiates *Hatun shikitu, Yana shikitu*, and *Muru shikitu* from the Linnaean species complex *Chaetostoma microps* (Günther, 1864).
(c) Type A subdifferentiation: seven Kichwa species correspond to two or more Linnaean species of the same genus, such as *Chuti*, which includes *Crenicichla johanna* (Heckel, 1840), *Crenicichla saxatilis* (Linnaeus, 1758), and *Crenicichla cincta* (Regan, 1905).
(d) Type B subdifferentiation: 14 Kichwa taxa were identified that correspond to two or more Linnaean species of different genus, p. ex. *Uchu yawisun* and its relationship with *Characidium etheostoma* (Cope, 1872), *Characidium steindachneri* (Cope, 1878), and *Nannostomus eques* (Steindachner, 1876).

The sixteen families, or *ayllukuna*, mentioned by the Kichwa were also compared with the families of the Linnaean taxonomy: seven of them had 1:1 equivalence; four ethnofamilies grouped fish from two Linnaean families each with 1:2 equivalence; three Kichwa families had 1:3 equivalence; and two of them had 1:4 equivalence (**Table 2**).

The Kichwa ethnoichthyological classification is multidimensional. The most common classification criteria are morphological attributes, but other biological, ecological and gastronomical characteristics are also considered (**Table 3**). These include: (1) skin and scales (scutes, irregular scales, small scales, medium-sized scales, big scales, bare skin/no scales); (2) fishbones and spines (abundant fishbones, medium presence of fishbones, few fishbones/meaty, spiny); (3) meat quality (greasy and valued, lean and valued, not valued); (4) body shape (oval, elongated, "machete"-like, flat-belly); (5) diet (detritus, fruits, fish, blood, omnivore); (6) salience (upper lip tick, big eyes, strong teeth, parental care).

Morphological features are the most common ways the Kichwa name the local ichthyofauna. This includes: (1) size: *Hatun tiksa* (big *tiksa*), *Hatun shikitu* (big *shikitu*), *Hatun yayu* (big *yayu*); (2) color: *Yana shikitu* (black *shikitu*), *Puka kalamatu* (red *kalamatu*), *Muru amashika* (dotted *amashika*), *Muru shikitu* (dotted *shikitu*), *Kuychi sardina* (rainbow *sardina*), *Yurak ñawi sardina* (white eye *sardina*); (3) related to animals: *Ukucha bagri* (mouse *bagri*), *Manku tanla* (oriole *tanla*); (4) related to plants: *Uchu yawisun* (chili pepper *yawisun*), *Sara kuntzy* (corn *kuntzy*), *Putu sardina* (kapok tree *sardina*); (5) habitat: *Kucha lisa* (lake *lisa*), *Turu yayu* (swamp *yayu*), *Tiur anku* (sand liana); (6) related to tools: *Muku uma shikli* (*muku* head *shikli*; *muku* is the cudgel-like tool used to smash yuca and prepare *aswa*, chicha, a traditional drink).

In addition, this ichthyological classification recognizes the kinship between some *ayllukuna* (families). For example, fish from the *Bagri ayllu* are the parents of the *Tuksik* species, while fish from the *Challwa ayllu* are recognized as the parents of the species of the *Chulu sardina ayllu* and *Mutzun ayllu*. Furthermore, the anaconda, *Eunectes murinus* (Linnaeus, 1758), is the mother of all fish, and the common lancehead (*Bothrops atrox* Linnaeus, 1758), a terrestrial viper, is recognized as the mother of the *Pashin ayllu*.

Cultural Relevance of Fish

To avoid any interference by the authors in trying to interpret the information related to the cultural relevance of fish for the Kichwa including the uses, prescriptions and advice, the comments recorded during the workshops were literally transcribed and translated and are cited in quotation marks bellow.

From the 58 Kichwa taxa, 38 are valued for consumption while the two species of the *Karniru* family, the *Amarun chuchu* (nipple snake), *Bunocephalus coracoideus* (Cope, 1874), and *Karniru, Vandellia* spp., are not accepted as food. No use was registered for the remaining 18 taxa. Three of the fish "are only eaten when there is nothing else": the *Pashin, Hoplias malabaricus* (Bloch, 1794), because "it's meat is sweet and with abundant fishbones," while the *Ñachi*, *Erythrinus erythrinus* (Bloch and Schneider, 1801) and the *Willi*, *Hoplerythrinus unitaeniatus* (Spix

TABLE 1 | Names and classification of Kichwa ethnofamilies, ethnogenera, and ethnospecies, compared to Linnaean families and species.

Ethnofamily	Ethnogenus	Ethnospecies	Linnaean species	Linnaean family
Bagri ayllu	Bagri	Kumal Bagri	*Brachyplatystoma juruense*	Pimelodidae
			Zungaro zungaro	
		Ukucha Bagri	*Brachyplatystoma tigrinum*	
	Pintarillu	Pintarillu*	*Pseudoplatystoma punctifer*	
			Pseudoplatystoma tigrinum	
Tuksik ayllu		Kumparama	*Pimelodus blochii*	
		Muta	*Calophysus macropterus*	
		Tumsa	*Cetopsis oliveirai*	Cetopsidae
			Cetopsis montana	
		Lunkutsu	*Rhamdia quelen*	Heptapteridae
		Tuksik	***Pimelodella lateristriga***	
Challwa ayllu		Hantya	*Brycon spp.*	Bryconidae
		Shankatima	*Brycon melanopterus*	
			Brycon amazonicus	
		Wal	*Salminus brasiliensis*	
	Challwa	Pita Challwa	*Rhaphiodon vulpinus*	Cynodontidae
		Challwa	*Prochilodus nigricans*	Prochilodontidae
Mutzun ayllu		Mutzun	***Curimata spp.***	Curimatidae
			Cyphocharax spiluropsis	
			Steindachnerina argentea	
			Curimatella alburna	
	Kuntzy	Sara Kuntzy	***Steindachnerina* cf. *dobula***	
			Steindachnerina bimaculata	
Chulu sardina ayllu	Sardina	Kuychi sardina	*Triportheus spp.*	Triportheidae
			Hemigrammus spp.	Characidae
			Moenkhausia lepidura	
			Paragoniates alburnus	
		Putu sardina	***Moenkhausia oligolepis***	
			Astyanax bimaculatus	
		Yurak sardina	***Moenkhausia dichroura***	
		Yurak ñawi sardina	***Ceratobranchia* cf. *delotaenia***	
	Chinlus	Chinlus*	***Creagrutus amoenus***	
			Creagrutus gracilis	
	Chulu	Chulu*	***Astyanax henseli***	
		Sichi	*Hyphessobrycon spp.*	
			Bryconamericus spp.	
		Tawaki	*Astyanax spp.*	
Kalamatu ayllu	Tiksa	Hatun tiksa	*Charax gibbosus*	
		Tiksa	*Roeboides myersii*	
	Kalamatu	Puka kalamatu	*Charax caudimaculatus*	
		Kalamatu	*Ctenobrycon hauxwellianus*	
	Pirruru	Pirruru*	*Tetragonopterus argenteus*	
			Thoracocharax spp.	Gasteropelecidae
			Gasteropelecus spp.	
		Sinkuana	*Acestrorhynchus lacustris*	Acestrorhynchidae
		Tsakama	*Plagioscion squamosissimus*	Sciaenidae
Chuti ayllu	Chuti	Chuti*	***Crenicichla cincta***	Cichlidae
			Crenicichla johanna	
			Crenicichla saxatilis	
Unpuni ayllu	Unpuni	Unpuni*	*Bujurquina moriorum*	
			Oreochromis mossambicus	
			Apistogramma spp. 1	
	Uputasa	Uputasa*	*Apistogramma spp. 2*	
			Cichlasoma spp.	
			Aequidens tetramerus	

(Continued)

TABLE 1 | (Continued)

Ethnofamily	Ethnogenus	Ethnospecies	Linnaean species	Linnaean family
Karniru ayllu		Amarun chuchu	*Bunocephalus coracoideus*	Aspredinidae
	Karniru	Karniru	*Vandellia spp.*	Trichomycteridae
Llumwiya ayllu	Llumwiya	Llumwiya*	*Sternarchorhynchus curvirostris*	Apteronotidae
			Apteronotus albifrons	
		Anguila	*Electrophorus electricus*	Gymnotidae
	Yayu	Turu yayu	*Gymnotus carapo*	
		Hatun yayu	*Eigenmannia virescens*	Sternopygidae
		Tiur anku	*Synbranchus marmoratus*	Synbranchidae
Yawisun ayllu	Yawisun	Yawisun	***Parodon buckleyi***	Parodontidae
			Parodon pongoensis	
		Uchu yawisun	***Characidium steindachneri***	Crenuchidae
			Characidium etheostoma	
			Nannostomus eques	Lebiasinidae
Ñachi ayllu		Ñachi	*Lebiasina erythrinoides*	
			Erythrinus erythrinus	Erythrinidae
		Willi	*Hoplerythrinus unitaeniatus*	
Pashin ayllu	Pashin	Pashin	***Hoplias malabaricus***	
		Rayu Pashin	*Rivulus spp.*	Rivulidae
Shikli ayllu	Shikli	Muku uma shikli	***Chaetostoma dermorhynchus***	Loricariidae
	Shikitu	Muru shikitu	***Lipopterichthys carrioni***	
			Chaetostoma microps	
		Yana shikitu		
		Hatun shikitu		
Shiyu ayllu	Amashika	Amashika	***Ancistrus malacops***	
			Panaque spp.	
		Muru amashika	***Lasiancistrus schomburgkii***	
	Shiyu	Makana shiyu	*Loricaria spp.*	
		Pinduk shiyu	*Farlowella platorynchus*	
			Rineloricaria spp.	
		Shiyu	***Hypostomus hemicochliodon***	
Tanla ayllu	Lisa	Kucha lisa	*Schizodon fasciatus*	Anostomidae
	Tanla	Manku tanla	*Leporinus* aff. *fasciatus*	
		Tanla	*Leporinus friderici*	

Names in bold indicate the species captured during the sampling campaign.
The asterisk indicates the ethnogenera whose ethnospecies couldn't be identified.

and Agassiz, 1829), "are not recommended for children or people with delicate skin, because their consumption can produce irritation and rash." On the other hand, *Yawisun*, *Parodon buckleyi* (Boulenger, 1887) and *Parodon pongoensis* (Allen, 1942), are their favorite fish to eat, prepared as a traditional dish, the *maytu*, cooked wrapped with *bijao* leaves (*Calathea lutea*). Two other species need a special preparation before being eaten: the *Yana shikitu*, *Chaetostoma microps*, "has to be cooked wrapped in banana leaves to make the meat soft and edible," and the *Pita challwa*, *Rhaphiodon vulpinus* (Spix and Agassiz, 1829), "although its meat is the most appetizing, eating it during childhood can cause the hair to go gray, and to avoid that, one of the bones has to be braided in the hair of the person after eating it." Other fish have some prescriptions, like the *Tumsa*, fish from the *Cetopsis* genus, considered "blind fishes" due to their reduced eyes. Although they are valued and commonly eaten by adults, "they are not used to feed children because, as the fish have small eyes, they can cause blindness." Other prescriptions indicate that "women shouldn't eat fish while menstruating because it can cause cramping and increased bleeding, and neither should they after giving birth." It is also believed that "children and young people shouldn't be fed fish eggs, as their consumption can make them grow weaker." The participants mentioned that "this last rule is no longer respected, and it is causing more vulnerability among the youth."

Fish and Health

The Kichwa consider some fish potentially dangerous for people. We identified two species that can be harmful: the *Tuksik*, *Pimelodella lateristriga* (Lichtenstein, 1823), "whose spines can cause serious poisoning," and the *Karniru*, *Vandellia* spp., believed to be "a human parasite that can enter the organism through corporal orifices (anus, penis, and vagina)." We also recorded some medicinal uses of fish like ingesting the intestine contents of the *Yana shikitu, Chaetostoma microps,* to treat

TABLE 2 | Correspondence between Kichwa ethnofamilies and Linnaean families, including the number of Linnaean species considered.

Ayllu	Linnaean family	N° Linnaean species	Correspondence
Tanla	Anostomidae	3	1:1
Chuti	Cichlidae	3	
Unpuni	Cichlidae	6	
Mutzun	Curimatidae	6	
Shikli	Loricariidae	3	
Shiyu	Loricariidae	7	
Bagri	Pimelodidae	5	
Karniru	Trichomycteridae	1	1:2
	Aspredinidae	1	
Chulu sardina	Characidae	13	
	Triportheidae	1	
Ñachi	Erythrinidae	2	
	Lebiasinidae	1	
Pashin	Erythrinidae	1	
	Rivulidae	1	
Challwa	Bryconidae	4	1:3
	Cynodontidae	1	
	Prochilodontidae	1	
Tuksik	Cetopsidae	2	
	Heptapteridae	2	
	Pimelodidae	2	
Yawisun	Crenuchidae	2	
	Lebiasinidae	1	
	Parodontidae	2	
Kalamatu	Acestrorhynchidae	1	1:4
	Characidae	5	
	Gasteropelecidae	2	
	Sciaenidae	1	
Llumwiya	Apteronotidae	2	
	Gymnotidae	2	
	Sternopygidae	1	
	Synbranchidae	1	
16	**32**	**86**	**Total**

diabetes. The *Tiur anku*, *Synbranchus marmoratus* (Bloch, 1795), is a "fish that has a slippery skin, and that characteristic, after been eaten, helps pregnant women to lubricate and facilitate labor." This species also has a medicinal-ritual use by men and "as it is a slippery fish, it is consumed before fighting to become more elusive." Fish of the *Unpuni* family (Cichlidae) like the *Unpuni*, *Aequidens tetramerus* (Heckel, 1840), *Chuti*, *Crenicichla saxatilis* and *Chinlus, Creagrutus gracilis* (Vari and Harold, 2001) "are used for *sasi* (a ritual and healthcare diet) due to their low-fat content."

Spirituality

Fish and rivers have an important spiritual relevance for the Kichwa in Arajuno. In their worldview, "the rivers are inhabited and guarded by *Tzumi* (men of the water) and they are the fathers of the water." "Fish are protected and guided by *Amarun*, the anaconda, mother of all fish." The *Atakapi*, a giant stingray, is also believed to inhabit the rivers of Arajuno and "if cut by half or on the side, it releases human souls." Waterfalls, *pakcha*, and salt licks, *kachikuna*, are considered sacred places. Shamans are recognized as *Yachak*, wise persons with material, ancestral and spiritual knowledge: "they have the power to heal or to harm, and they can cast a barrier, a *nina amarun* (fire snake), to block fish migration upstream."

Every year fish migrate upstream through *Puka Rumi* to the headwaters of the Arajuno River. This migration, the *mijanada* or *mijanu*, is believed to be led by *Amarun*: "when the snake goes up the river carrying all the fish it is dangerous to enter the water." "The snake guides fish grouped in order: the small ones go first, followed by the medium ones and the largest ones last. *Amarun* leaves them spread along the lagoons connected to the main river, so they can lay their eggs in a safe environment."

Ritual uses of fish were registered for the *Karniru* (*Vandellia* spp.), "used by shamans to threaten or harm people." The *Anguila* (*Electrophorus electricus*), electric eel, "can be used to increase the strength of a fighter by sticking a needle in its lateral line." It can also be used for pest control "burying the skin of its head around palm trees to shoo away the animals that eat their fruits." Morevover, "to fish and cook the *Anguila* the Kichwa must previously undergo a fasting."

Threats to Fish Conservation

The participants mentioned that during the last 30 years the fish population has significantly decreased and many of the species are gone, like the *Turu yayu, Gymnotus carapo* (Linnaeus, 1758) or *Hatun yayu*, *Eigenmannia virescens* (Valenciennes, 1836). Other fish were mentioned as locally extinct such as the *Tururu*, *Kinti yayu*, *Sara challwa*, and *Hantya*, but they couldn't be identified properly because they were not among the pile of photographs. These observations about the loss of fish species came spontaneously, while identifying the fish, illustrating that the participants are worried about the degradation of rivers and disappearance of certain fish species. The Kichwa believe "the spirits have taken these species elsewhere because the rivers and fish have been abused, fishing rules from the ancestors are no longer respected and many harmful and unruly activities are carried out, like overfishing, or the use of aggressive techniques (dynamite, chemical products, gillnets, diver goggles)." Over cultivation of tilapia was also mentioned as an increasing threat to local fish. The Kichwa feel somehow overwhelmed with the intensity of these new environmental issues related to the accelerated arrival of foreign people, but they lack any technical assistance from the local or national government to properly face them.

Dissemination of the Results

To present the results of this research within the community and to promote biocultural conservation and environmental education, a bilingual poster (Kichwa-Spanish) was created and delivered to the people in Arajuno (**Figure 4**). It includes the sixteen *ayllukuna* and the 24 fish we could capture and photograph with their Kichwa and Linnean names. The local inhabitants also asked to include some basic norms to foster fish conservation. These are: (1) protect water spirits and the mothers of the fish, (2) don't pollute or throw garbage in the rivers, (3)

TABLE 3 | Classification criteria for the sixteen ethnofamilies.

Ayllu	(1) Skin and scales	(2) Fishbones and spines	(3) Meat quality	(4) Body shape	(5) Diet	(6) Salience
Chulu sardina	Small and thin scales	Abundant and soft fishbones that can be eaten without problems	Greasy and very tasty meat. Cooked in "maytu"	Small size and diverse body shapes	Feed on any kind of food	-
Challwa	Medium-sized scales, soft to be taken out	Less fishbones than Chulu sardina ayllu. Adults have less spines	Very greasy meat, very tasty. Highly valued food	Diverse body shapes. Big and medium-sized fish	Feed on mud, algae and some of them on fruits and flowers	Fathers of Chulu sardina ayllu and Mutzun ayllu
Mutzun	Small and thin scales. Soft and easy to be taken out, forming bulks	Spinny	Valued and lean meat	Elongated body shape and diverse size, from small to medium	Feed on mud and lick rocks and clay walls	Can't be fished with hooks. Children of Challwa ayllu
Kalamatu	Small and delicate scales, generally silver colored. Hard fins. Kind of slimy.	Few fishbones	-	Oval-puffy shape. Some species are transparent	-	Strong and sharp teeth. Bad and slow swimmers
Tanla	Thick, big and hard scales	Spiny	Good and greasy meat	Elongated body shape	Feed on fruits	Upper lip thick with a greasy layer
Ñachi	Medium-sized scales	Spiny	Not valued meat. It can be harmful to people with delicate skin	Small sized	Gluttonous. Feed on any kind of food	Watery consistency
Pashin	-	Abundant fishbones	Sweet meat, not valued, only eaten when there is no other fish	Elongated body shape	-	Strong teeth
Yawisun	Hard scales	Abundant fishbones	-	Elongated body shape. Small size	Feed on mud	Fast swimmers. Only found in high current water
Tuksik	No scales. Slimy skin	Medium presence of fishbones, with strong, hard and dangerous spines in dorsal and pectoral fins	Valued and tasty meat	Small size	-	They can prick and cause hospitalization. They are children of Bagri ayllu
Bagri	No scales or small scales. Slimy skin	Few fishbones	Highly valued meat	Big size	-	Fathers of Tuksi ayllu
Llumwiya	Very thin and small scales	Abundant fishbones	Greasy and good for preparing "maytu"	Elongated with machete shape	-	-
Karniru	-	-	Not consumed	Elongated and thin like a spear. Hook-like fins with spines	Feed sucking blood	Parasites. They can enter corporal orifices in humans
Shikli	Scutes all along the body	Meaty. They have more meat than Shiyu ayllu	-	Small and thick	Feed on mud	-
Shiyu	Thicker scutes covering all the body	Less meat than Shikli ayllu	-	Elongated. Bigger than Shikli ayllu	Feed on mud	They live in wall holes, rocks and submerged trunks
Unpuni	Irregular scales	Abundant fishbones	Valued and lean meat, useful for "sasi" (diet)	Small and medium size	-	They have big eyes
Chuti	-	Less fishbones than Upunti ayllu	Very valued meat, especially for "sasi" (diet)	Elongated. Big and medium size	-	-

don't fish with dynamite or chemicals, (4) use *barbasco* (*cubé* resin) moderately, (5) use native fish for aquaculture.

DISCUSSION

Strengths and Limitations of the Methods

The greatest strength of our research comes from the origin of the proposal: we were directly asked for help and were invited to work with the community. This starting point facilitated many of the previous steps that ethnobiological research needs to solve, like: making personal connections before entering the community, gaining the trust of the local inhabitants, agreeing to terms of the collaboration with the community and obtaining previous informed consent (Argueta et al., 2018; Medinaceli, 2018). The long and successful experience of some of the authors working in the Amazon with other Kichwa people (Jácome-Negrete, 2012, 2013, 2021; Valdiviezo-Rivera et al., 2012; Jácome-Negrete and Guarderas-Flores, 2015; Carrillo-Moreno, 2017) was the best way to gain the confidence of the community and facilitate the research process, thanks to the familiarity with the Kichwa culture. Investing time and effort to design the research in a collaborative way and listening to the advice and requirements of the participants, reinforced the trust and the involvement of the Kichwa community. Furthermore, the group dynamics created a forum that allowed the participants to share experiences and knowledge with people of different gender and ages, learn from each other, reinforce community bonds, discuss and identify their community needs and think about the best ways to meet them (Sieber et al., 2014).

Nevertheless, considering the number of participants (23 people in the first and most relevant workshop) and that most of them were from the *Puka Rumi* community, our sampling population was limited. Furthermore, although our results are solid thanks to the repeated review and correction process carried out with the participants, they should be expanded and complemented through replication of the research among other groups from the Community Organization of the Kichwa of Arajuno.

On the other hand, this participatory approach was also useful and enriching during the fish sampling (Previero et al., 2013). Working with fishermen and women, and the combination of scientific and artisanal techniques was essential to inventory ichthyological species in the area (Tobes et al., 2021). Particularly the free diving in rivers with high flow or deep pools was very useful as these conditions made those habitats poorly accessible with electric fishing, the trawl and trammel. This technique was especially effective to catch fish from the *Loricariidae* family, usually found attached to submerged wood, rocks or hidden in holes (Lujan et al., 2011). In addition, the Kichwa knowledge of the fish diet and ecology allows them to choose the best bait (usually other smaller fish or eggs) and choosing the best fishing grounds (Rebelo et al., 2010). Such is the case with members of the *Shikli* family (*Chaetostoma* genus), whose eggs are used for fishing of Characids. The detailed knowledge that fishermen have about the feeding habits and habitats was crucial to optimize sampling time, effort and costs while doing field sampling (Ramires et al., 2015). However, if we consider that we only collected 24 Linnaean species from the 86 fish identified using photographs, in an area were ichthyofauna is highly diverse and poorly known (Tobes et al., 2016, 2021), we believe that more fishing surveys are necessary to disclose the complete fish community.

Despite of the good results we obtained with the pile sorting workshops, we consider that the use of photographs for fish identification may be a good cost-effective alternative, but it is not as precise as having the fish alive and available for the participants to observe, name and classify (Lahe-Deklin and Si, 2014). Accordingly, we recommend the use of this *ex situ* methodology for making a first approach to the ethnoclassification and ethnobiological knowledge, especially in very biodiverse areas, where capturing all the local species requires huge sampling efforts (Mourão and Nordi, 2002; Jácome-Negrete, 2013). As no western ichthyologist would guarantee the correct identification of many fish species only using a single photograph without a detailed analysis of a voucher specimen, neither do the Kichwas. If we consider the multidimensional classification system they have, involving sight, taste, and touch, it is essential to offer them the complete sensorial experience and the possibility for a detailed observation of the distinctive characters that support their identification and classification system (Jácome-Negrete, 2021).

A Proposal of Taxonomic Categories

Berlin (1973) helped us to understand how humans perceive and classify nature through the discovery that some patterns are shared by many cultures worldwide. Those folk classification systems were the starting point and inspiration for the Linnaean system, and therefore, the concordances between both are common (Jácome-Negrete and Guarderas-Flores, 2015). Following that tendency, we found high levels of correspondence between the classification system of the Kichwa in Arajuno and the Linnaean classification. In general, the hierarchical levels of classification resemble those mentioned by other ethnoichthyological studies for other fishing cultures (Mourão and Nordi, 2002; Pinto et al., 2013, 2018; Mourão and Barbosa Filho, 2018) and specifically other classification systems reported for Kichwa communities in the Ecuadorian Amazon (Jácome-Negrete, 2012, 2013; Jácome-Negrete and Guarderas-Flores, 2015). Although the main goal of our research was to record the Kichwa classification system from their point of view, without interpretation or inference, returning it to them without any cultural meddling, we'll analyze and conceptualize it here from the perspective of western science in light of the theories and proposals of other academics.

Considering the information collected during the workshops and following the Berlinian hierarchy (Berlin, 2014), we identified five taxonomic categories (**Figure 5**). The superior category, the (I) Unique beginner, was *Aycha*, corresponding to the Animalia kingdom. *Aycha,* is subdivided into three subordinate groups of (II) life forms: *Yaku aycha* (water animals) = Pisces superclass; *Rigrayuc aycha* (wing animals) = Aves class; *Wilmayuc aycha* (hair animals) = Mammalia class (Jácome-Negrete, 2021). The Kichwa consider the entire fish superclass in the same life-form category, unlike other fishing communities that also consider turtles, crustaceans, mollusks, dolphins, whales, and anacondas as fish and group them together (Marques, 1991; Clément, 1995; Paz and Begossi, 1996; Costa-Neto and Marques, 2000; Pinto et al., 2013; Mourão and Barbosa Filho, 2018). This separation of fish and other aquatic animals has been recorded for other Amazonian cultures like the Aguaruna and Huambisa people (in Peru), who don't consider dolphins fish (Berlin and Berlin, 1983) and neither do other Kichwa communities in the Ecuadorian Amazon (Jácome-Negrete, 2012, 2013; Jácome-Negrete and Guarderas-Flores, 2015). We hypothesize that this could be related to the preeminence of the morphology in Kichwa classification, as having fish-shape and fins are essential criteria which exclude invertebrates and reptiles, combined with the presence of gills and the ability to breathe underwater, dismissing aquatic mammals. Nonetheless, we don't have enough evidence to prove this perception and further research should be done to understand the basis of this classification system.

Within (II) *Yaku aycha*, we identified a third taxonomic level composed of 16 subordinate groups (**Figure 5**). Given that all of them comprise numerous sub-taxa, following the

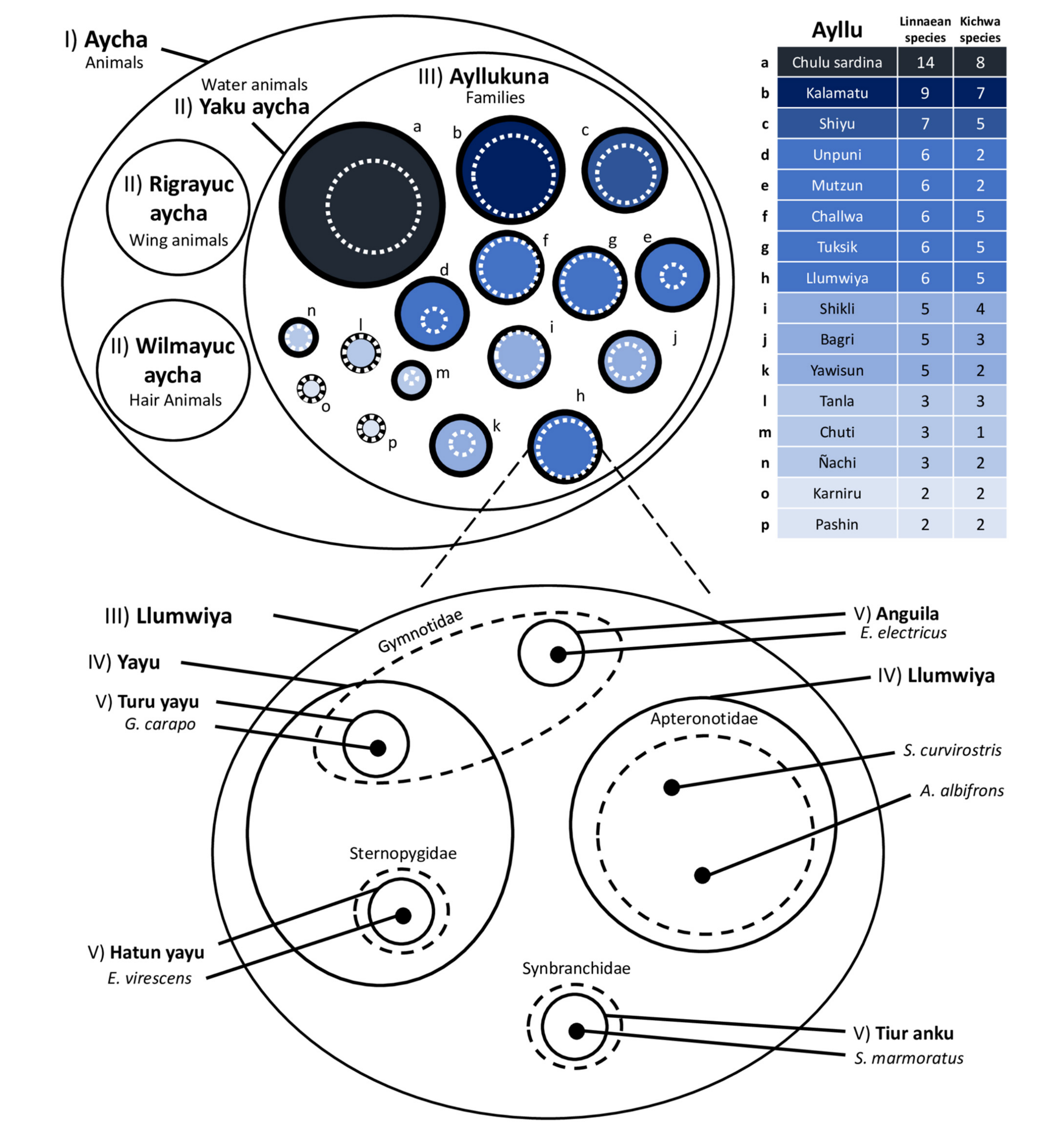

FIGURE 5 | Schematic representation of the proposed hierarchical categories, detailed for the Llumwiya ethnofamily. On the upper area of the diagram white-dotted circles are proportional to number of ethnofamilies, and the continuous black line to Linnaean families. On the bottom, for the Llumwiya ayllu, circles with dotted lines encompass Linnaean families, while continuous lines are used for the Kichwa categories.

basis of the Berlinian classification system, other research carried out with the Ecuadorian Kichwa considered this level as an intermediate (Jácome-Negrete and Guarderas-Flores, 2015). However, in light of the diversity and the high subordinate complexity of this third level, following the ideas of Jensen (1985) and Jácome-Negrete (2012), due to the high correspondence with the Linnaean families (**Table 2**), and considering that the Kichwa name for this category is *ayllu*, family, we reconsider the groups on this level as (III) Ethnofamilies (**Table 1**). The ethnofamily level has also been proposed by other authors

(Costa-Neto and Marques, 2000; Montenegro, 2001; Ferreira et al., 2009) and our results support this equivalence between Kichwa ethnofamilies and Linnaean families (**Table 2**). All the ethnofamilies except one (*Chulu sardina*) have primary and simple names. The fish among each *ayllu* are separated from the species in other groups and share morphological, ecological, and cultural criteria. The ethnofamilies are appointed after the most outstanding fish of the group, usually the biggest or the most conspicuous, and are named adding the word *ayllu* to the name of the prototypical species. This name composition helps to avoid the polysemy between the ethnofamily and ethnogenus (Mourão and Barbosa Filho, 2018).

Comprising the ethnofamilies, we found 58 names related to 86 Linnaean species. Considering that many of those names were polynomial (25%) and that some of those compound names shared lexemes, these facts point out underlying categories (Mourão and Nordi, 2002). Therefore, we propose a fourth hierarchical level to be the (IV) Ethnogenus, following the ideas of Jensen (1985). We easily identified the ethnogenus among the polytypic groups like in the case of *Yayu* (**Figure 5**), subdivided in two inferior productive taxa: *Turu yayu and Hatun yayu* (Mourão and Barbosa Filho, 2018). Considering this subdifferentiation of the *Yayu* ethnogenus in two subordinate taxa, a fifth rank of classification comes to light, the (V) Ethnospecies. This category is easily identified looking at the twelve polytypic ethnogenera (*Bagri, Sardina, Challwa, Tiksa, Kalamatu, Yayu, Yawisun, Pashin, Shikitu, Amashika, Shiyu*, and *Tanla*) (**Table 2**). On the other hand, we found that some simple primary names were used for some ethnospecies and that they had no ethnogenus. We hypothesize that this may be the case of those fish species with salience due to some biological or cultural characteristics such as *Sinkuana, Tsakama, Anguila, Ñachi*, or *Willi*, or related with genera with few different species (Mourão and Nordi, 2002).

However, to shed some light to the complex ethnogeneric and ethnospecific categories we recalled previous research carried out by the authors with other Kichwa people on lowland Amazon, close to the Peruvian border, in isolated communities with more pristine and deep knowledge (Jácome-Negrete, 2012; Jácome-Negrete and Guarderas-Flores, 2015). This familiarity with the Kichwa ethnoclassification helped us identify some extra ethnogenera during the workshops. This is the case of *Pintarillu, Chinlus, Chulu, Pirruru, Chuti, Unpuni, Uputasa*, and *Llumwiya* (**Table 1**). Although they could be easily considered as monotypic groups and classified as ethnospecies (like the examples mentioned before), we realized that the participants didn't mention any specific name among these groups because they couldn't identify any of them with the pictures on hand, or because they may have lost the knowledge to subdivide fish ethnogenuses and precisely identify some of the underlying species.

Summing up, among the Kichwa ethnogenera, 50% (12) of them were monotypic while the other 50% (12) were polytypic. Nevertheless, as said before, eight of these monotypic ethnogenera were highlighted (marked with asterisc in **Table 1**) because they have more species besides the prototypical, the only ones we could record. This result contrasts with the statements of Berlin (1992), that expected more monotypic generics than polytypic, 80 and 20%, respectively, and also disagrees with the reports of other numerous ethnoichthyological research compiled by Mourão and Barbosa Filho (2018), with polytypic ethogenera ranging from 13 to 25%. The use of the ethnogeneric category has proven to be common and widely use by the Kichwa in Arajuno, which indicates a deep and intricated knowledge and taxonomic precision compared to other fishing communities.

Correspondence, Sub-Differentiation and Over-Differentiation

Contrasting the Kichwa and Linnaean systems, one-to-one correspondence between species reached up to 41%. We identified seven cases of A sub-differentiation (17% of the Linnaean taxa) and 14 cases of B subdifferentiation (40% of the Linnaean taxa), which highlights the existing differences in taxa recognition between the two classification systems, although both perspectives can create synergies when discussed and contrasted, finally enriching the ichthyological knowledge (Pereyra et al., 2021). Pinto et al. (2013) explain that this over-differentiation in local classifications generally occurs with organisms that are culturally important and highlights the awareness and sensibility that deep-rooted cultures have in recognizing subtle attributes in their environment as described later. This is the case of three of the ethnospecies of the *Shikitu* ethnogenus, *Muru shikitu*, *Hatun shikitu*, and *Yana shikitu*. They are separately identified by the Kichwa, while for the Linnaean taxonomist they comprise the *Chaetostoma microps* species complex, a group of potentially different species that are still undefined. The distinct characteristics named by the Kichwa were: "*Muru shikitu* shows the dotted pattern in the frontal area, a more meaty maxilla and tastier meat; *Hatun shikitu* is bigger and taller than the others, without the dotted pattern in the frontal area and with reddish fins; *Yana shikitu* has a darker color, the meat is harder and dryer, the maxilla is smaller, it is not as meaty, the scutes are harder and it is rarer in the surroundings of Arajuno." This information could probably shed some light onto the identification problems experienced by Linnaean scientists and help us fill the gap of the taxonomic impediment of freshwater fish in the Neotropics (Benone et al., 2020). This fact evidences the importance of considering local knowledge and the accumulated experience of Indigenous people to enrich ichthyological inventories (Ramires et al., 2015; Aigo and Ladio, 2016).

Multidimensional Classification and Idealistic and Utilitarian Approaches

The Kichwa ichthyological classification is built with multidimensional features, a concept proposed by Santos-Fita and Costa-Neto (2009). Besides morphological features (skin and scales, fishbones and spines, body shape) they also consider ecological criteria such as diet, habitat, and parental care, the quality of meat and whether fish are harmful or beneficial to health. This diversity of morphological, ecological, utilitarian, and relational characteristics recognized by the Kichwa in Arajuno coincides with what other authors have identified in other areas where fishing is an activity of great cultural importance (Begossi and Garavello, 1990; Marques, 1991; Mourão and Nordi, 2002; Jácome-Negrete, 2012; Pinto et al., 2013; Aigo and Ladio, 2016; Castro et al., 2016; Pinto et al., 2016; Castillo et al., 2018; Mourão and Barbosa Filho, 2018; Jimbo-Campoverde, 2019).

Fishermen identify and classify principally those species they eat (Jácome-Negrete, 2012, 2013; Jácome-Negrete and Guarderas-Flores, 2015). In this sense, Mourão and Barbosa Filho (2018) say that naming and classifying the species has a close relation with those organisms that have greater cultural relevance. While Mourão and Nordi (2002) reported that even though some fish were named, they were not included in the classification system. This is not the case for the Kichwa of Arajuno where 31% of the identified ethnospecies (18 out of 58) were named and classified, but they had no use reported. Furthermore, biological and ecological information was registered for 14 of those fish with no use. *Kuychi sardina*, *Yurak ñawi sardina*, *Sichi*, and *Tawaki*, part of the *Chulu sardina ayllu*, had no use but showed some cultural relevance as they were mentioned to be the "sons" of the *Challwa ayllu*. Something similar was also reported with the Aguaruna and Huambisa communities in Peru, where fish species showing similarities were considered "relatives" and called "brothers" or "members" of the same family (Berlin and Berlin, 1983). However, this kinship reported by the Kichwa was among fish of different families.

We didn't record any information beyond the names and families of four of the unused fish, which included: *Puka kalamatu*, *Charax caudimaculatus* (Lucena, 1987); *Hatun yayu, Eigenmannia virescens* (Valenciennes, 1836); *Rayu pashin*, *Rivulus* spp.; *Makana shiyu*, *Loricaria* spp. In light of these results, it seems that the Kichwa name fish for the sake of knowing and classifying them, sometimes even without a utilitarian reason, complementing their categorization using criteria from a practical point of view (benefits or danger). This may indicate a primarily idealistic approach to naming nature supported by the utilitarian perspective, while showing the coexistence of both classification systems as proposed by Boster and Johnson (1989).

Biocultural Heritage and Conservation Challenges

The cohabitation and coevolution of the Kichwa of Arajuno with fish and rivers is the source of integrated perceptions and understandings of theses hydro-social ecosystems (Jácome-Negrete, 2013; Carrillo-Moreno, 2017). Through oral narratives, knowledge about ecology and the interrelationships between people, aquatic beings, spirits, rivers, and fish, is transmitted to the younger generations. Some glimpses of the Kichwa worldview came to light during the workshops. For example, *Amarun*, the big snake mother of all fish, is related to other similar and well-known myths involving fish, snakes and rivers registered for many Indigenous groups. This is the case of the myth of LIK, a huge snake full of fish, described by many cultures in remote regions in South America, some separated by centuries, and used by Claude Levi-Strauss to reveal the correspondences between distant cultures and highlight their strong bond to rivers and all their non-human inhabitants (Levi-Strauss et al., 1963). This fact highlights the deep-rooted and ancestral origin of the Kichwa culture.

Fishing enables the transmission of biological and ecological knowledge to new generations, such as the recognition, naming and classification of species, the use of ichthyofauna, the diversity of habitats in which they are found and appropriate fishing techniques (Silvano et al., 2006; Jácome-Negrete, 2013; Santos and Alves, 2016; Castillo et al., 2018; Pinto et al., 2018). Therefore, fishing activities of the Kichwa in Arajuno were an excellent ethnobiological approach to identify the broad ecological and cultural knowledge around the ichthyofauna and the importance that these animals and rivers have for the identity of this human group. However, all the ethnoichthyological knowledge, the cultural and identity relevance of fish, and the spiritual relationship that the Kichwa of Arajuno have with them are threatened by the accelerated cultural changes experienced during the past decades. Hence the urgency of getting involved in initiatives that revitalize and revalue local knowledge of biodiversity for future biocultural conservation.

In conclusion, although Arajuno has been heavily intervened by market dynamics and a non-adapted education system that does not consider local knowledge, the Kichwa maintain their knowledge and bonds to aquatic ecosystems and fish, and are aware of the value of this knowledge, the threats that they face and want to take action to tackle them. The ethnotaxonomical knowledge of the Kichwa has proven to be acute and reliable. It may be a useful tool to help with the taxonomic impediments the Linnaean classification is facing in trying to identify and classify Amazon fish (Carvalho et al., 2018). It could also help to strengthen conservation efforts owing to the correct identification and listing of the existing species, and unveil a great number of unknown species for the academic community. Moreover, the participatory work facilitated the identification of the threats for fish and rivers, related to harmful activities. In response to this, the recommendations included in the poster represent a first step toward the development of conservation strategies.

The Food and Agriculture Organization of the United Nations has declared 2022 The International Year of Artisanal Fisheries and Aquaculture, to focus world attention on the role of small-scale artisanal fishers, fish farmers and fish workers, who play a crucial role in food security, nutrition, and poverty eradication (Ljusenius et al., 2020). Fisheries are about people as much as they are about fish, thereby the role of local communities as resource stewards may be critical in ensuring the responsible management and sustainable use of aquatic biodiversity. Our work helped identifying the more valued and consumed species, a key information to design sustainable fishing strategies considering community needs and preferences.

As custodians of their biocultural landscape, the Kichwa people could make the difference to guarantee the conservation and sustainable use of their fisheries through practical and ethical lessons. But as much as they need visibility to make their voices heard to influence decisions and policies that shape their everyday lives and livelihoods, the support we can offer them gathering, systematizing, adapting, and applying their traditional ecological knowledge can foster positive change on the ground.

Therefore, complementary studies are necessary to endorse local organizations in designing and implementing sustainable strategies for fisheries management and conservation.

We take care of the things we value. We value and relate to what we can recognize and distinguish. The beings and the elements we can no longer name vanish before our eyes. Biodiversity extinction also takes place when nature fades away from our language. Therefore, ethnoclassification and ethno-nomenclature are key to helping us protect the names, signification and environmental knowledge treasured in our words. Furthermore, this approach to study Indigenous knowledge, using the loss of fish as unifying threat, allowed us to unveil their integrated understanding of the natural, cultural, and spiritual dimensions of reality, giving us the basic tools to foster biocultural diversity conservation from a holistic perspective.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Comité de Ética del Instituto de Investigación de la Universidad Tecnológica Indoamérica. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. Permission was obtained from the individual(s) and minor(s)' legal guardian/next of kin for the publication of any potentially identifiable images or data included in this article. The animal study was reviewed and approved by Comité de Ética del Instituto de Investigación de la Universidad Tecnológica Indoamérica.

AUTHOR CONTRIBUTIONS

All the authors collaborated in the conception and design of the work, and during data collection. IJ-N and LG-F helped with curating field data, with the interpretation of the results, and with the revision of the manuscript. CC-M helped with digitalization, curation and data analysis, and with the revision of the manuscript. YV-C contributed with data analysis and interpretation, and wrote the first draft of the manuscript. IT obtained the funding for the project, formed the research team, wrote the final manuscript, prepared the figures, and lead the revision.

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REFERENCES

Aigo, J., and Ladio, A. (2016). Traditional mapuche ecological knowledge in Patagonia, Argentina: fishes and other living beings inhabiting continental waters, as a reflection of processes of change. *J. Ethnobiol. Ethnomed.* 12:56. doi: 10.1186/s13002-016-0130-y

Albuja, L. (2011). *Lista de Mamíferos Actuales del Ecuador*. Quito: Escuela Politécnica Nacional.

Albuquerque, U. P., Ramos, M., de Lucena, R. F., and Alencar, N. (2014). "Methods and techniques used to collect ethnobiological data," in *Methods and Techniques in Ethnobiology and Ethnoecology*, eds U. Albuquerque, L. Cruz da Cunha, R. de Lucena, and R. Alves (New York, NY: Humana Press), 15–38. doi: 10.1007/978-1-4614-8636-7_2

Alves, R. R. (2012). Relationships between fauna and people and the role of ethnozoology in animal conservation. *Ethnobiol. Conserv.* 1, 1–69. doi: 10.15451/ec2012-8-1.2-1-69

Alves, R. R., and Souto, W. M. (2011). Ethnozoology in Brazil: current status and perspectives. *J. Ethnobiol. Ethnomed.* 7:22. doi: 10.1186/1746-4269-7-22

Angarita-Baéz, J. A., Pérez-Miñana, E., Beltrán Vargas, J. E., Ruiz Agudelo, C. A., Paez Ortiz, A., Palacios, E., et al. (2017). Assessing and mapping cultural ecosystem services at community level in the Colombian Amazon. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manage.* 13, 280–296. doi: 10.1080/21513732.2017.1345981

Antonelli, A., Ariza, M., Albert, J., Andermann, T., Azevedo, J., Bacon, C., et al. (2018). Conceptual and empirical advances in neotropical biodiversity research. *PeerJ* 6:e5644. doi: 10.7717/peerj.5644

Argueta, A., Sanabria-Diago, O. L., Cano-Contreras, E. J., and Medinaceli, A. (2018). Código de ética para la investigación etnobiológica en América Latina. *Ethnoscientia* 3, 1–6. doi: 10.18542/ethnoscientia.v3i2.10239

Armbruster, J. W. (2005). The loricariid catfish genus *Lasiancistrus* (Siluriformes) with descriptions of two new species. *Neotrop. Ichthyol.* 3, 549–569. doi: 10.1590/S1679-62252005000400013

Barbosa-Filho, M. L. V., Ramires, M., Mourão, J., de Souza Rosa, R., Alves, R. R. N., and Costa-Neto, E. M. (2021). Ethnotaxonomy of sharks by expert fishers from South Bahia, Brazil: implications for fisheries management and conservation. *Ethnobiol. Conserv.* 10:2. doi: 10.15451/ec2021-08-10.02-1-12

Barriga, R. (2012). Lista de peces de agua dulce e intermareales del Ecuador. *Rev. Politécnica* 30, 83–119.

Begossi, A., and Garavello, J. C. (1990). Notes on the ethnoichthyology of fishermen from the Tocantins River (Brazil). *Acta Amazon.* 20, 341–351. doi: 10.1590/1809-43921990201351

Benone, N. L., Leal, C. G., dos Santos, L. L., Mendes, T. P., Heino, J., and de Assis Montag, L. F. (2020). Unravelling patterns of taxonomic and functional diversity of Amazon stream fish. *Aquat. Sci.* 82:75. doi: 10.1007/s00027-020-00749-5

Berlin, B. (1973). Folk systematics in relation to biological classification and nomenclature. *Annu. Rev. Ecol. Evol. Syst.* 4, 259–271. doi: 10.1146/annurev.es.04.110173.001355

Berlin, B. (1992). *Ethnobiological Classification - Principles of Categorization of Plants and Animals in Traditional Societies*. Princeton, NJ: Princeton University Press.

Berlin, B. (2014). "The substance and evolution of ethnobiological categories," in *Ethnobiological Classification*, ed. B. Berlin (Princeton, NJ: Princeton University Press), 260–290. doi: 10.1515/9781400862597.260

Berlin, B., and Berlin, E. A. (1983). "Adaptation and ethnozoological classification: theoretical implications of animal resources and diet of the Aguaruna and Huambisa," in *Adaptive Responses of Native Amazonians*, eds B. Berlin and E. A. Berlin (New York, NY: Academic Press), 301–325. doi: 10.1016/b978-0-12-321250-4.50014-2

Boster, J. S., and Johnson, J. C. (1989). Form or function: a comparison of expert and novice judgments of similarity among fish. *Am. Anthropol.* 91, 866–889. doi: 10.1525/aa.1989.91.4.02a00040

Carrillo-Moreno, C. (2017). "¡Ésta es la laguna de limoncocha!: significados desde una perspectiva comunitaria," in *Naturaleza y Cultura: un Acercamiento Desde la Investigación*, eds A. Krainer and A. Chaves (Quito: FLACSO Sede Ecuador), 15–46.

Carvalho, A. P. C., Collins, R. A., Martínez, J. G., Farías, I. P., and Hrbek, T. (2018). From shallow to deep divergences: mixed messages from Amazon Basin cichlids. *Hydrobiologia* 832, 317–329. doi: 10.1007/s10750-018-3790-x

Castillo, T. I., Brancolini, F., Saigo, M., Correa, J. R., and Baigún, C. (2018). Ethnoichthyology of artisanal fisheries from the lower la Plata river basin (Argentina). *J. Ethnobiol.* 38, 406–423. doi: 10.2993/0278-0771-38.3.406

Castro, M. S., Martins, I. M., and Hanazaki, N. (2016). Trophic relationships between people and resources: fish consumption in an artisanal fishers neighborhood in Southern Brazil. *Ethnobiol. Conserv.* 5:4. doi: 10.15451/ec2016-7-5.4-1-16

Cevallos, S. (2020). Extractivism, pandemics and collective rights: the case of the indigenous peoples of the Yasuní (Ecuadorian Amazon). *Rev. Catalana Dret Ambient.* 11, 1–31. doi: 10.17345/rcda2920

Chernoff, B., and Machado-Allison, A. (1990). Characid fishes of the genus *Ceratobranchia*, with descriptions of new species from Venezuela and Peru. *Proc. Acad. Natl. Sci. Phila.* 142, 261–290.

Clément, D. (1995). Why is taxonomy utilitarian? *J. Ethnobiol.* 15, 1–44.

Costa-Neto, E. M., and Marques, J. G. W. (2000). A etnotaxonomia de recursos ictiofaunísticos pelos pescadores da comunidade de Siribinha, norte do estado da Bahia, Brasil. *Biociências* 8, 61–76.

de Melo, F. A. G., and Buckup, P. A. (2006). *Astyanax henseli*, a new name for *Tetragonopterus aeneus* Hensel, 1870 from southern Brazil (Teleostei: Characiformes). *Neotrop. Ichthyol.* 4, 45–52. doi: 10.1590/S1679-62252006000100003

Ellen, R. F. (1986). Ethnobiology, cognition and the structure of prehension: some general theoretical notes. *J. Ethnobiol.* 6, 83–98.

Ferreira, E. N., Mourão, J., Rocha, P. D., Nascimento, D. M., da, S. Q., and Bezerra, D. M. M. (2009). Folk classification of the crabs and swimming crabs (Crustacea–Brachyura) of the Mamanguape river estuary, Northeastern–Brazil. *J. Ethnobiol. Ethnomed.* 5:22. doi: 10.1186/1746-4269-5-22

Forth, G. (2017). 'Fish' and 'Non-Fish' in Lio and Nage: folk-Intermediates and folk-generics in the fish classification of two eastern Indonesian peoples. *Ethnobiol. Lett.* 8, 61–69. doi: 10.14237/ebl.8.1.2017.900

GADMCA (2014). *Actualización Plan de Desarrollo y Ordenamiento Territorial 2011-2025*. Arajuno: Gobierno Autónomo Descentralizado Municipal.

Gèry, J. (1977). *Characoids of the World*. Neptune City, NJ: TFH Publications Inc.

Gollin, L. X., McMillen, H., and Wilcox, B. (2004). Participant-observation and pile sorting: methods for eliciting local understandings and valuations of plants as a first step towards informed community participation in environment and health initiatives in Hawai'i. *Appl. Environ. Educ. Commun*. 3, 259–267. doi: 10.1080/15330150490882001

Hunn, E. (2014). To know them is to love them. *Ethnobiol. Lett.* 5, 146–150. doi: 10.14237/ebl.5.2014.297

IGM (2020). *Base Arajuno, Escala 1:50.000*. Available Online at: http://www.geoportaligm.gob.ec/portal/index.php/descargas/cartografia-de-libre-acceso/ [accessed November 15, 2021].

Jácome-Negrete, I. (2012). Etnoictiología Kichwa de los bagres del género *Pseudoplatystoma* (Siluriformes: Pimelodidae) en la Amazonía Central del Ecuador. *Rev. Amazon. Cienc. Tecnol.* 1, 36–50.

Jácome-Negrete, I. (2013). Etnoictiología Kichwa de las lagunas de la cuenca baja del río Curaray (Amazonia), Ecuador. *Biota Colomb.* 14, 5–24.

Jácome-Negrete, I. (2021). *Sacha Runa Yachay Kamu: Manual de Etnobiología Ecuatoriana*. Quito: Gráficas Iberia.

Jácome-Negrete, I., and Guarderas-Flores, L. (2015). Nomenclatura y clasificación kichwa de los peces lacustres en la Amazonía central de Ecuador. *Etnobiología* 13, 63–71.

Jensen, A. A. (1985). *Sistemas Indígenas de Classificação de Aves: Aspectos Comparativos, Ecológicos e Evolutivos*. Doctoral thesis. Campinas: Universidade Estadual de Campinas.

Jézéquel, C., Tedesco, P. A., Darwall, W., Dias, M. S., Frederico, R. G., Hidalgo, M., et al. (2020). Freshwater fish diversity hotspots for conservation priorities in the Amazon Basin. *Conserv. Biol.* 34, 956–965. doi: 10.1111/cobi.13466

Jimbo-Campoverde, M. A. (2019). *Caracterización de la Nacionalidad Kichwa Para el Fomento del Turismo Comunitario, Cantón Arajuno, Provincia de Pastaza*. Bachelor's thesis. Quito: Universidad Central del Ecuador.

Kakudidi, E. K. (2004). Folk plant classification by communities around Kibale National Park, western Uganda. *Afr. J. Ecol.* 42, 57–63. doi: 10.1111/j.1365-2028.2004.00462.x

Kullander, S. O. (1986). *Cichlid Fishes of the Amazon River Drainage of Peru*. Stockholm: Swedish Museum of Natural History.

Lahe-Deklin, F., and Si, A. (2014). Ex-situ documentation of ethnobiology. *Lang. Doc. Conserv*. 8, 788–809.

Lepofsky, D. (2009). The past, present, and future of traditional resource and environmental management. *J. Ethnobiol.* 29, 161–166. doi: 10.2993/0278-0771-29.2.161

Levi-Strauss, C., Jacobson, C., and Schoepf, B. G. (1963). *Structural Anthropology*. New York, NY: Basic Books.

Ljusenius, Å., Lovatelli, A., and Qabeel, B. (2020). The international year of artisanal fisheries and aquaculture is coming up in 2022. *FAO Aquac. Newsl.* 62, 13–15.

Loh, J., and Harmon, D. (2005). A global index of biocultural diversity. *Ecol. Indic.* 5, 231–241. doi: 10.1016/j.ecolind.2005.02.005

Lujan, N., German, D. P., and Winemiller, K. O. (2011). Do wood-grazing fishes partition their niche?: morphological and isotopic evidence for trophic segregation in Neotropical Loricariidae. *Funct. Ecol.* 25, 1327–1338. doi: 10.1016/j.ympev.2008.08.013

Lujan, N., Meza-Vargas, V., Astudillo-Clavijo, V., Barriga-Salazar, R., and López-Fernández, H. (2015). Multilocus molecular phylogeny for *Chaetostoma* clade genera and species with a review of *Chaetostoma* (Siluriformes: Loricariidae) from the Central Andes. *Copeia* 103, 664–701. doi: 10.1643/CI-14-194

MAE (2012). *Sistema de Clasificación de los Ecosistemas del Ecuador Continental. Subsecretaría de Patrimonio Natural*. Quito: Ministerio del Ambiente Ecuador.

Marques, J. G. W. (1991). *Aspectos Ecológicos na Etnoictiologia dos Pescadores do Complexo Estuarino-Lagunar Mandau-Manguaba, Alagoas*. Doctoral thesis. Campinas: Universidade Federal de Alagoas.

Medinaceli, A. (2018). Taking an early step in ethnobiological research: a proposal for obtaining prior and informed consent from indigenous peoples. *Ethnobiol. Lett.* 9, 76–85. doi: 10.14237/ebl.9.1.2018.1054

Mertens, F., Fillion, M., Saint-Charles, J., Mongeau, P., Távora, R., Passos, C. J. S., et al. (2015). The role of strong-tie social networks in mediating food security of fish resources by a traditional riverine community in the Brazilian Amazon. *Ecol. Soc.* 20:18.

Ministerio del Ambiente, Agua y Transición Ecológica (2021). *Mapa Interactivo*. Available Online at: http://ide.ambiente.gob.ec/mapainteractivo/ [accessed November 26, 2021].

Montenegro, S. C. S. (2001). *A Conexão Homem/Camarão (Macrobrachium carcinus e M. acanthurus) no Baixo São Francisco Alagoano: Uma Abordagem Etnoecológica*. Doctoral thesis. São Carlos: Universidade Federal de São Carlos.

Mourão, J., and Barbosa Filho, M. L. V. (2018). "Ethnotaxomy as a methodological tool for studies of the ichthyofauna and its conservation implications: a review," in *Ethnozoology Animals in our Lives*, eds R. R. Nóbrega Alves and U. P. Albuquerque (Cambridge, MA: Academic Press), 71–94. doi: 10.1016/b978-0-12-809913-1.00006-5

Mourão, J., and Nordi, N. (2002). Comparação entre as taxonomias folk e científica para Peixes do Estuário do Rio Mamanguape, Paraíba-Brasil. *Interciencia* 27, 607–612.

Pauly, D., Watson, R., and Alder, J. (2005). Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 360, 5–12. doi: 10.1098/rstb.2004.1574

Paz, V. A., and Begossi, A. (1996). Ethnoichthyology of galviboa fishermen of sepetiba bay, Brazil. *J. Ethnobiol.* 16, 157–168.

Pereyra, P. E. R., Hallwass, G., Poesch, M., and Silvano, R. A. M. (2021). 'Taking fishers' knowledge to the lab': an interdisciplinary approach to understand fish trophic relationships in the Brazilian Amazon. *Front. Ecol. Evol.* 9:723026. doi: 10.3389/fevo.2021.723026

Pinto, M. F., Mourão, J., and Alves, R. R. (2013). Ethnotaxonomical considerations and usage of ichthyofauna in a fishing community in Ceará state, Northeast Brazil. *J. Ethnobiol. Ethnomed.* 9, 17–25. doi: 10.1186/1746-4269-9-17

Pinto, M. F., Mourão, J., and Alves, R. R. (2016). How do artisanal fishermen name fish? An Ethnotaxonomic study in Northeastern Brazil. *J. Ethnobiol.* 36, 348–381. doi: 10.2993/0278-0771-36.2.348

Pinto, M. F., Oliveira, T. P. R., Rocha, L. A., and Alves, R. R. N. (2018). "People and fishery resources: a multidimensional approach," in *Ethnozoology animals in our lives*, eds R. R. Nóbrega Alves and U. P. Albuquerque (Cambridge, MA: Academic Press), 119–149. doi: 10.1016/B978-0-12-809913-1.00008-9

Posey, D. A. (1985). Indigenous management of tropical forest ecosystems: the case of the Kayapó Indians of the Brazilian Amazon. *Agrofor. Syst.* 3, 139–158. doi: 10.1007/BF00122640

Previero, M., Minte-Vera, C. V., and Moura, R. L. D. (2013). Fisheries monitoring in Babel: fish ethnotaxonomy in a hotspot of common names. *Neotrop. Ichthyol.* 11, 467–476. doi: 10.1590/S1679-62252013000200016

Provenzano, F., and Barriga-Salazar, R. (2018). Species of *Ancistrus* (Siluriformes, Loricariidae) from Ecuador, with the description of a new species from the Amazon River Basin. *Zootaxa* 4527, 211–238. doi: 10.11646/zootaxa.4527.2.4

Raisg (2021). *Datos Cartográficos*. Available Online at: https://www.amazoniasocioambiental.org/es/mapas/#!/descargas [accessed November, 26, 2021].

Ramires, M., Clauzet, M., Barrella, W., Rotundo, M. M., Silvano, R. A. M., and Begossi, A. (2015). Fishers' knowledge about fish trophic interactions in the southeastern Brazilian coast. *J. Ethnobiol. Ethnomed.* 11:19. doi: 10.1186/s13002-015-0012-8

Rebelo, S. R., Freitas, E. C., and Mota Soares, M. G. (2010). Fish diet from Manacapuru Big Lake complex (Amazon): a approach starting from the traditional knowledge. *Biota Neotrop.* 10, 39–44. doi: 10.1590/S1676-06032010000300003

Santos, C. A. B., and Alves, R. R. (2016). Ethnoichthyology of the Indigenous Truká people, Northeast Brazil. *J. Ethnobiol. Ethnomed.* 12:1. doi: 10.1186/s13002-015-0076-5

Santos-Fita, D., and Costa-Neto, E. M. (2009). "Sistemas de clasificación etnozoológicos," in *Manual de Etnozoología: Una Guía Teórico-Práctica Para Investigar la Interconexión del ser Humano con los Animales*, eds E. M. Costa-Neto, D. Santos-Fita, and M. Vargas Clavijo (Almenara: Tundra Ediciones), 67–94.

Sieber, S. S., da Silva, T. C., de Oliveira Campos, L. Z., Zank, S., and Albuquerque, U. P. (2014). "Participatory methods in ethnobiological and ethnoecological research," in *Methods and Techniques in Ethnobiology and Ethnoecology*, eds U. P. Albuquerque, L. V. F. C. da Cunha, R. F. P. De Lucena, and R. R. N. Alves (New York, NY: Humana Press), 39–58. doi: 10.1007/978-1-4614-8636-7_3

Silvano, R. A., MacCord, P. F., Lima, R. V., and Begossi, A. (2006). When does this fish spawn? Fishermen's local knowledge of migration and reproduction of Brazilian coastal fishes. *Environ. Biol. Fishes* 76, 371–386. doi: 10.1007/s10641-006-9043-2

Tobes, I., Gaspar, S., Peláez-Rodríguez, M., and Miranda, R. (2016). Spatial distribution patterns of fish assemblages relative to macroinvertebrates and environmental conditions in Andean piedmont streams of the Colombian Amazon. *Inland Waters* 6, 89–104. doi: 10.3390/w13081038

Tobes, I., Ramos-Merchante, A., Araujo-Flores, J., Pino-del-Carpio, A., Ortega, H., and Miranda, R. (2021). Fish ecology of the alto Madre de Dios river basin (Peru): notes on electrofishing surveys, elevation, palm swamp and headwater fishes. *Water* 13:1038. doi: 10.5268/IW-6.1.750

Toledo, V. M., and Alarcón-Cháires, P. (2012). La etnoecología hoy: panorama, avances, desafíos. *Etnoecológica* 9, 1–16. doi: 10.2307/j.ctv16b78qv.3

Vacacela, R. (2007). *Sumac Causai - Vida en Armonía. Instituto Quichua de Biotecnología Sacha Supai*. Quito: Ediciones Abya-Yala.

Val, A. L., Almeida-Val, V. M., Fearnside, P. M., dos Santos, G. M., Piedade, M. T. F., Junk, W., et al. (2017). "Amazonia: water resources and sustainability," in *Waters of Brazil*, eds C. de Mattos Bicudo, J. Galizia Tundisi, and S. Cortesão Barnsley (Cham: Springer), doi: 10.1007/978-3-319-41372-3_6

Valdiviezo-Rivera, J., Carrillo-Moreno, C., Madera Arends, R., and Albarracín Rodas, M. E. (2012). *Guía de Peces de Limoncocha*. Quito: Universidad Internacional SEK.

van der Sleen, P., and Albert, J. S. (2017). *Field Guide to the Fishes of the Amazon, Orinoco, and Guianas*. Princeton, NJ: Princeton University Press.

Vari, R. P., and Harold, A. S. (2001). *Phylogenetic Study of the Neotropical Fish Genera Creagrutus Giinther and Piabina Reinhardt (Teleostei: Ostariophysi: Characiformes), with a Revision of the Cis-Andean Species*. Washington, DC: Smithsonian Institution Press.

Vasco, C., and Sirén, A. (2019). Determinants of wild fish consumption in Indigenous communities in the Ecuadorian Amazon. *Soc. Nat. Resour.* 32, 21–33. doi: 10.1080/08941920.2018.1475587

Weckmüller, H., Barriocanal, C., Maneja, R., and Boada, M. (2019). Factors affecting traditional medicinal plant knowledge of the Waorani, Ecuador. *Sustainability* 11:4460. doi: 10.3390/su11164460

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Octopus Fishing and New Information on Ecology and Fishing of the Shallow-Water Octopus *Callistoctopus furvus* (Gould, 1852) Based on the Local Ecological Knowledge of Octopus Fishers in the Marine Ecoregions of Brazil

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Studies that compile local ecological knowledge (LEK) on some of the various species of living beings observe biological data and are notably fundamental for effectively managing fisheries, supporting management strategies for protected areas, species conservation, and other factors. In this study, ethnoecological approaches were used to focus on the octopus *Callistoctopus furvus* (Gould, 1852), recently re-described and re-presented to the academic community more than a century after its discovery. The LEK of octopus fishers from different marine ecoregions of Brazil was compared to identify the distribution limits of the species along the Brazilian coast. Semi-structured interviews were conducted in 16 municipalities across four marine ecoregions located between the states of Ceará (northern limit) and Santa Catarina (southern limit), between March 2018 and August 2019. The results of the 187 interviews indicated a traditionality of fishing among artisanal octopus fishers, who are mostly men, although some are women who also share information on the fishing of *C. furvus* and hold leadership positions in the fishing colony. Cronbach's alpha was used to analyze reliability of the form used in the interviews. A logistic regression model with binomial distribution was used to assess whether the probability of capturing the "eastern octopus" was associated with some of the interview variables. A cluster analysis based only on the respondents who caught the "eastern octopus" indicated the formation of groups and revealed greater dissimilarities among the fishers from the southeastern marine ecoregion of Brazil due to the fishing method used in the region. Heat maps showed that most of the information on the species was obtained in the eastern marine ecoregion of Brazil. The occurrence of the "eastern octopus" was recorded in all the studied Brazilian marine ecoregions. Moreover, this study revealed the relevant contribution of fishers' knowledge to the distribution diagnosis of species with scarce scientific information.

Keywords: ethnoknowledge, marine protected areas, reef environments, artisanal fishing, Western Atlantic Ocean

INTRODUCTION

The Indo-Pacific "spotted octopuses" were originally classified as *Octopus macropus* (Risso, 1826), but from 2005 after taxonomic revision (Norman and Hochberg, 2005), they were reclassified in another genus and became scientifically known as *Callistoctopus macropus* (Risso, 1826). Among the characteristics that allowed its reclassification, the one that stands out the most is its "reddish brownish" chromatic pattern, displaying, when disturbed, the characteristic white spots (Jereb et al., 2014). There are several very similar species in the Indian Ocean and the western Pacific Ocean. The most recent reviews consider that the species *C. macropus* lives in the Mediterranean and the northeast coast of the Atlantic (NW Africa), with some presence on the American and Caribbean coast (Jereb et al., 2014). According to Norman (2000), it is a complex of very similar species, where probably the true identity of American populations needs to be clarified.

In a study carried out by Jesus et al. (2015) a specimen of this other genus of octopus was captured in the region of southern Bahia (Brazil), *Callistoctopus* sp., the "eastern octopus." Given this, and the need to clarify the taxonomic status of the species known locally (South of Bahia state) as "eastern octopus" (*Callistoctopus* sp.), Jesus et al. (2021a,b) presented a neotype and redescribed the octopus species *Callistoctopus furvus* (Gould, 1852), along with morphological and genetic characteristics, after more than 150 years without any scientific publications about it. Despite the recent taxonomic confirmation of *C. furvus*, there are still gaps in information regarding the species.

It is a fact that the worldwide interest in adopting interdisciplinary approaches in the study of the multifaceted relationships between society and its landscapes is increasing every day. In this sense, studies with ethnoecological approaches have been gaining great notoriety. In general, the concept of Ethnoecology can be understood as a branch of ethnoscience related to the study of the knowledge of human groups in relation to their practices about something, as well as about their beliefs and interactions with the environment and its ecosystems (Barrera-Bassols and Toledo, 2005; Zappes et al., 2018). Studies compiling the local ecological knowledge (LEK) on the different species of living beings, complement the biological data and have been fundamental for the effective management of fisheries, strengthening of strategies for the management of protected areas, species conservation, nutritional importance and medicinal use (Begossi and Silvano, 2008; Prabhakar and Roy, 2009; Castilho et al., 2013; Chakraborty et al., 2015; Nascimento et al., 2020).

Mollusks are poorly studied ethnoecologically. Although there is still little information about this group, most are related to management strategies for their artisanal fisheries (Cidreira-Neto et al., 2019). Some ethnoecology works involving bivalve mollusks focus on their medicinal use to cure a number of diseases, such as rheumatism, calcium metabolism, heart disease, conjunctivitis, dizziness, nervousness, dehydration, and various gastrointestinal disorders (Prabhakar and Roy, 2009), as well as the its nutritional importance (Chakraborty et al., 2015). However, regarding ethnoknowledge about cephalopod mollusks, there are information gaps (e.g., distribution, habitat, availability, and socioeconomic importance), which need to be filled. In a study with ethnoecological approaches to the octopus *Octopus insularis* (Leite and Haimovici, 2006) in southern Bahia, Martins et al. (2011) suggested the need for further studies of the octopus species that occurred in that region. This is because in their work on the ethnoecological aspects of octopus fishing in the community of Coroa Vermelha—Santa Cruz Cabrália, Bahia (Brazil), these same authors indicated that octopus fishers reported that in that region there was also another species of octopus that was not commercialized. In this regard, the use of traditional knowledge of extractive communities associated with data collected through scientific methodology can help create management plans and programs to support artisanal fishing (Freitas et al., 2012), as well as characterize a species with limited scientific records of its capture. The local knowledge of fishers, here understood as synonymous with the term ethnoecology (Hanazaki, 2003) can contribute to scientific knowledge and promote cooperation and dialogue between fishers and scientists (Silvano and Begossi, 2005).

It is currently known that the octopus species *C. furvus* occurs along the Brazilian coast, with records of its occurrence in Colombia and Mexico (Cedillo-Robles and Pliego-Cardenas, 2018). Thus, our objective was to analyze the ethnoknowledge of fishermen about octopus fishing, focusing on the species *C. furvus*. In this way, we present initial ethnoecological information on the fishing of the "eastern octopus" species *Callistoctopus furvus*, which has recently been re-described (Jesus et al., 2021b), and compare the LEK of artisanal octopus fishers in four Brazilian marine ecoregions.

MATERIALS AND METHODS

Study Area

The study was carried out in reef environments in the coastal marine zone of Brazil, between the states of Ceará—CE (northeast region) and Santa Catarina—SC (southern region) and the island of Fernando de Noronha—PE (northeast region). According to Spalding et al. (2007), the Brazilian coast comprises the biogeographic domains known as Tropical Atlantic and Temperate South America. The Fernando de Noronha and Atol das Rocas ecoregion is characterized by volcanic islands. The emerged portion of Fernando de Noronha is represented by 21 islands, islets and rocks, featuring algal and coral reefs (Mohr et al., 2009). Atoll das Rocas is a region bathed by the south equatorial current, originating on the coast of Africa. Its formation predominates calcareous algae and colonial mollusks, associated with true corals and foraminifera (Mohr et al., 2009). Northeast Brazil is characterized by dunes, estuaries and reefs in fringing and coral reefs (Leão, 1996). In the Eastern ecoregion of Brazil, there is the Banco dos Abrolhos, an extension of the continental shelf with waters rarely greater than 30 m in depth, representing the largest and richest area of coral reef in the South Atlantic (Moura et al., 2013). It is the most oligotrophic of Brazilian coastal waters (Ekau and Knoppers, 1999). Finally, the Southeastern Brazil ecoregion has colder waters and upwellings, being a region with higher primary productivity (Coelho-Souza et al., 2012).

Considering the need for criteria, requirements, and other conditions to obtain information on ethnoconservation and the occurrence of the octopus *C. furvus* along the Brazilian coast, collection points were established in six marine protected areas (MPAs) and 16 municipalities surrounding these MPAs located in four Brazilian marine ecoregions (BME) (Spalding et al., 2007), as shown in **Figure 1**.

The definition of collection points in the MPA is due to the fact that, as it is a species with few records, the MPAs, theoretically, could harbor some population of the species. Therefore, MPAs with different types of uses were chosen, as well as areas without protection. The North limit was defined because there was a record in Fernando de Noronha (Leite and Haimovici, 2006) and the South limit because one of the divers consulted in the first phase of the study (*ad hoc*) confirmed the presence of the species in the State of Santa Catarina.

The study area was defined after the initial phase of research through expert consultations (see more in Jesus et al., 2021a), by which marine protected areas (MPAs) were defined with different use types and surrounding areas located in distinct marine ecoregions (**Table 1**). These locations were included because they are potential occurrence sites of the species *C. furvus* (**Figure 2**).

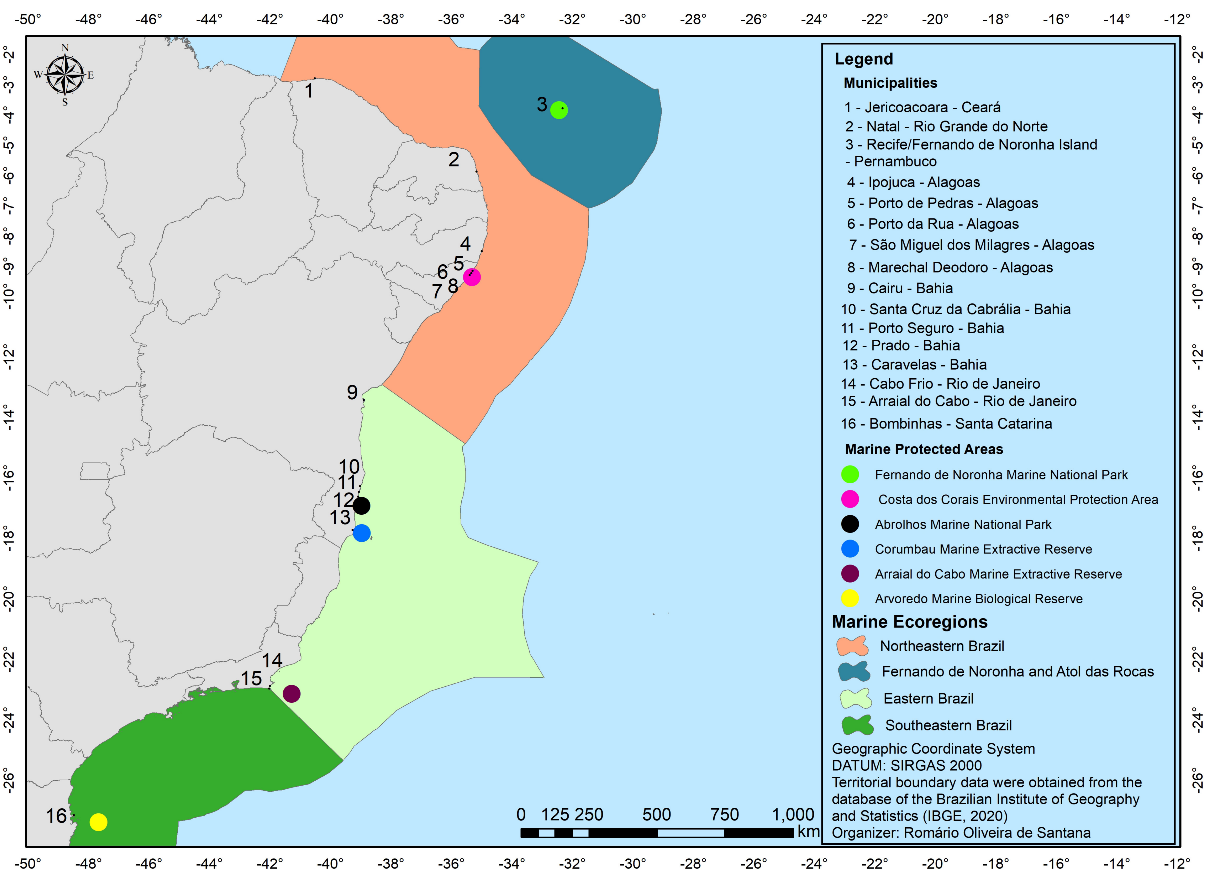

FIGURE 1 | Study area showing the limits of occurrence of *Callistoctopus furvus* on the Brazilian coast: northern limit (1), southern limit (16), and Fernando de Noronha island (3); the colored and numbered points from 1 to 16 correspond to the municipalities surrounding the marine protected areas (MPAs), which were visited throughout the study period, identified in the image with colored dots; the outlined areas along the Brazilian coast indicate the Brazilian marine ecoregions, in which these municipalities and MPAs are located.

TABLE 1 | Marine protected areas in which the study was developed, comprising the marine ecoregions of Fernando de Noronha and Atol das Rocas, northeastern Brazil, eastern Brazil, and southeastern Brazil.

Marine protected area	Legal diploma of creation	MPA class (SNUC/IUCN)	Marine ecoregions
Costa dos Corais Environmental Protected Areas	Decree of October 23, 1997	Sustainable use/V	Northeastern Brazil
Fernando de Noronha Marine National Park	Decree n° 96,693 of September 14, 1988	Full protection/II	Fernando de Noronha and Atol das Rocas
Abrolhos Marine National Park	Decree n° 88,218 of April 6, 1983	Full Protection/II	Eastern Brazil
Arraial do Cabo Marine Extractive Reserve	Decree of January 3, 1997	Sustainable use/V	Eastern Brazil
Corumbau Marine Extractive Reserve	Decree of September 21, 2000	Sustainable Use/VI	Eastern Brazil
Arvoredo Marine Biological Reserve	Decree n° 99,142 of March 12, 1990	Full protection/I	Southeastern Brazil

SNUC, National System of Conservation Units; IUCN, International Union for Conservation of Nature.

FIGURE 2 | "Eastern octopus" (*Callistoctopus furvus* Gould, 1852) found in the coastal reef of Cairu, Bahia, Brazil, photograph (Jesus et al., 2021b).

Data Collection

Data were collected between March 2018 and August 2019, initially by using behavioral components such as Rapport (Petit, 1987) in the previously delimited areas to establish a relationship of trust and respect between the researcher and the interviewed fishers, thus facilitating the exchange of information. Techniques used in social research were also applied, such as simple observation and semi-structured interviews (Minayo, 2016) with a script of closed-ended questions, and visual stimulation through photographs (Garcia, 2006; Monteiro et al., 2006a,b) and guided tours (Petit, 1987).

The semi-structured interviews were conducted to obtain all the details on the method of catching the octopus, the period during which fishing occurs (day/night), length of fishing activities, tide regimes, fishing gear used, fishing frequency, frequency of occurrence of the "eastern octopus" in the fishing region, consumption, trade, knowledge of the species that occur in the location, differences between males and females (sexual dimorphism), color pattern, size and weight requirements for capture/consumption, and sale (see **Supplementary Material 1**). During the interviews, the respondent had access to a set of 12 photographs (with images of *O. insularis*, *O. vulgaris* and *Callistoctopus* spp.), and the interviewer asked the respondent to inform which octopuses occurred in that region and how they differentiated them. The interview involved the use of fishers' LEK to discover, define distribution, and characterize the species of octopus *Callistoctopus furvus* on the Brazilian coast. Participant anonymity and confidentiality of information were guaranteed and specified in informed consent form No. 2,593,218 approved by the Research Ethics Committee of the Universidade Estadual de Santa Cruz.

The fishers who participated in the form-based interviews were initially contacted through fishing associations and colonies.

Permission to carry out this study in Protected Areas was obtained from the Sistema de Autorização e Informação em Biodiversidade (Biodiversity Authorization and Information system) ("SISBio"), under Protocol No. 60468-2.

Data Analysis

First, general octopus fishing data were analyzed (n = 187). The internal consistency (reliability) of the form questions was verified using Cronbach's alpha coefficient (Cronbach, 1951). This coefficient verifies the interrelationship of form items and varies from 0 to 1; the closer to the unit, the better the consistency of the form. Form questions with little variance are removed from the analysis since they decrease the value of the coefficient. According to the literature, values above 0.70 are considered appropriate (Cortina, 1993; Tavakol and Dennick, 2011), while values above 0.90 may suggest redundancy (Streiner, 2003).

Based on the coefficient alpha, the variables that remained and contributed to the alpha result were considered. These variables were used for principal component analysis (PCA) to verify the response pattern of respondents considering the marine ecoregions of their municipalities, namely (i) northeastern Brazil, (ii) Fernando de Noronha and Atol das Rocas, (iii) eastern Brazil, or (iv) southeastern Brazil, according to the classification of Spalding et al. (2007). This analysis was carried out to verify which octopus fishing variables (in general) are associated with which Brazilian marine ecoregion.

A logistic regression model (LRM) was used to evaluate whether the probability (1 = yes; 0 = no) of catching the "eastern octopus" is associated with some of the interview variables. A binomial model with logit link was used.

A second set of analyses was performed considering only the respondents who captured the "eastern octopus" ($n = 50$). Since not all respondents answered all the questions, the data matrix was incomplete. To circumvent this problem, an imputation method was used for missing data. The *mice* package was used to implement a method for handling missing data. The function creates multiple imputations (substitution values) for missing multivariate data. The algorithm can impute combinations of continuous categorical, binary, unordered categorical, and ordered categorical data (for more information, see van Buuren and Groothuis-Oudshoorn, 2019). Specifically in this study, the values are unordered categorical values.

Once the new matrix was complete (with imputed data), a Cronbach's analysis was performed again, as described above. Subsequently, the dissimilarity pattern of the respondent answers in the different locations was verified using cluster analysis (dendrogram) with the *hclust* function and the "average" method. This analysis was used to verify if the formation of groups of respondents occurs within the Brazilian marine ecoregions, considering all the information from fishers about the species *C. furvus*. The optimal number of clusters was verified using the *NbClust* function. The cophenetic correlation coefficient (CCC; Rohlf, 1970) was used to verify the extent to which the observed dendrogram appropriately represented the data. This correlation ranges from 0 to 1; the closer to the unit value, the more fitting the dendrogram. All these analyses were performed in R software (R Core Team, 2020) with the packages *psych*, *MASS*, *cluster*, *vegan*, *labdsv*, *BiodiversityR*, *ggplot2*, *NbClust*, *FactoMineR*, *missMDA*, and *ggfortify*.

The data obtained from the interviews were also the basis for generating heat maps using kernel density estimation, in ArcGIS 10.5 software (Environmental Systems Research Institute [ESRI], 2016). This tool was used to identify the concentration of information on the artisanal fishing of octopus and fishers' LEK on the species *C. furvus* by marine ecoregion. This concentration of information was categorized into three classes, namely low (green), medium (yellow), high (red).

RESULTS

In all, 187 interviews were conducted with questions about octopus fishing traditionality, fishing effort, and sale (**Supplementary Material 1**). Ecological factors of fishing the octopus *C. furvus* were only presented considering the answers of fishers ($n = 50$) who, at some point in their fishing activity, caught one or more specimens of the octopus *C. furvus* since its capture is not frequent.

General Factors of Octopus Fishing

Cronbach's alpha was 0.81 [alpha = 0.81; confidence interval (95%) = 0.78–0.85; $n = 187$; mean inter-item correlation = 0.21]. Only one variable was removed ("consumes"), as there was no response variation. **Table 2** shows the test statistics and alpha value for the case of the individual removal of each variable. Some of the variables were negatively correlated with the total scale.

As shown in **Table 2**, the second column indicates the behavior of Cronbach's alpha in response to the removal of each variable from the analysis. The individual removal of the variables did not produce any significant increases in the alpha value. Therefore, Cronbach's alpha value is satisfactory, the variables are adequate, and the consistency indicator is reliable. As such, the form questions are reliable for assessing fishers' knowledge about octopus fishing.

The first axis of the PCA accounts for more than 36% of the data variation, while the second axis accounts for more than 11% (**Figure 3**). The variables "instrument," "level_tide," "moon_interferes," "phase," "hours," and "kilos" characterized the fishers of the southeastern Brazilian marine ecoregion and reflected the fishing system developed in the region, which is

TABLE 2 | Cronbach's alpha statistics for the form applied to octopus fishers ($n = 187$) along the Brazilian coast (standardized alpha = 0.81).

Variable	Correlation (+ or –)	Alpha when item is removed	Mean inter-item correlation	Correlation of the item with total value
Learned	+	0.83	0.23	0.38
Instrument	+	0.78	0.19	0.86
Dimorphism	+	0.82	0.23	0.23
Frequency	–	0.82	0.23	0.23
Period	–	0.82	0.23	0.16
Influence_tide	+	0.81	0.22	0.48
Level_tide	+	0.79	0.19	0.83
Moon_interferes	+	0.79	0.19	0.81
Phase	+	0.79	0.19	0.83
Alone	–	0.83	0.24	0.20
Hours	+	0.78	0.19	0.82
Kilos	+	0.78	0.20	0.77
Smallest	+	0.78	0.20	0.75
Largest	+	0.80	0.21	0.57
Member	+	0.82	0.23	0.17
Main_income	+	0.82	0.23	0.23
Sale	–	0.82	0.23	0.22

Learned, with whom the fisher learned to fish; instrument, fishing gear used; sex, differentiation between male and female; frequency, frequency of octopus fishing; period, the fishing period; influence_tide, whether fishing is influenced by the tide; level_tide, fishing tide level; moon_interferes, whether the moon interferes with fishing; phase, fishing moon phase; alone, whether he or she fishes alone; hours, fishing times; kilos, amount of fish; smallest, smallest captured octopus; largest, largest captured octopus; member, whether member of a fishing colony or association; main_income, whether octopus is the main source of income; sale, whether all octopuses captured are sold.

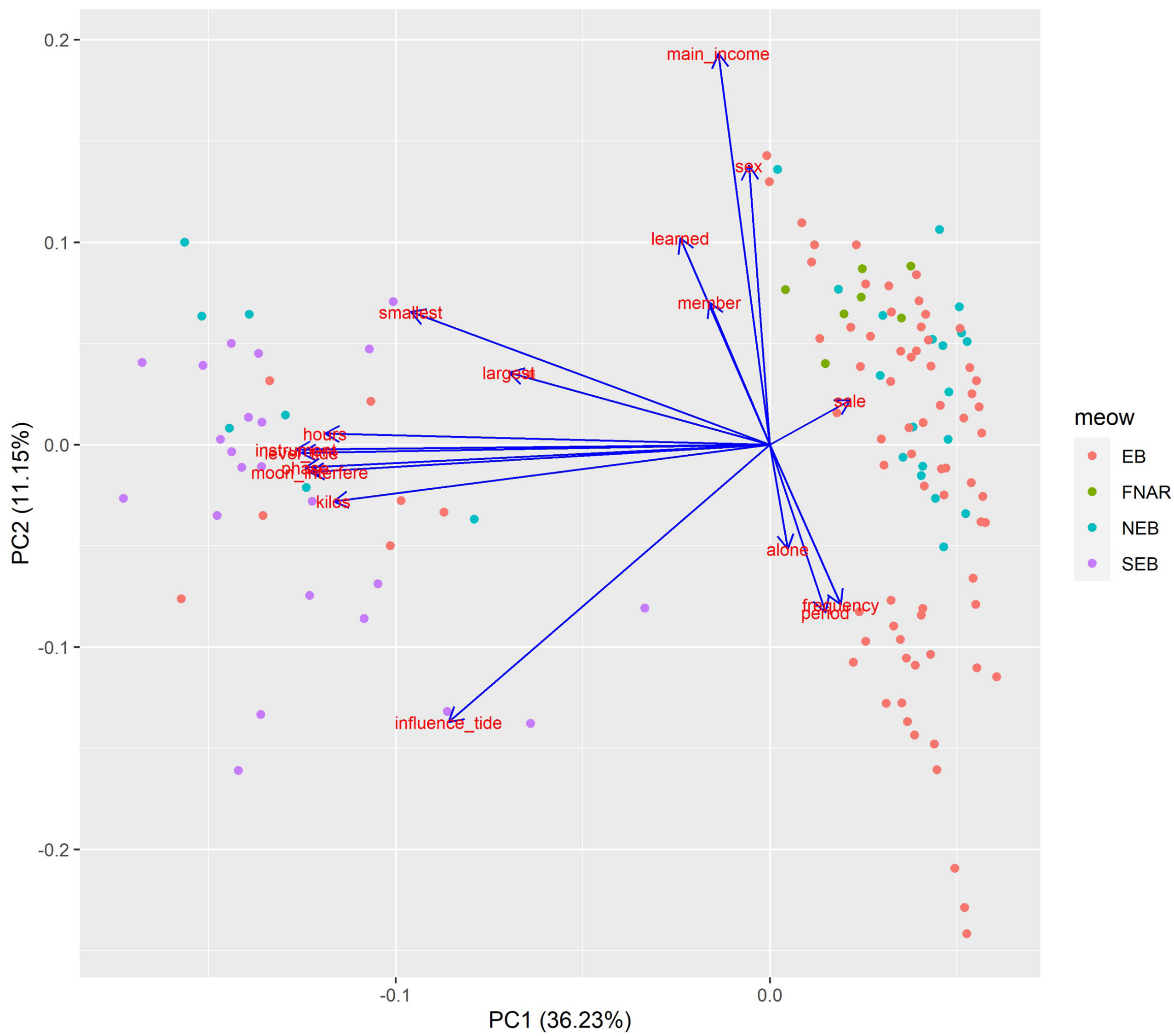

FIGURE 3 | Principal component analysis illustrating the pattern of octopus fishers interviewed along the Brazilian coast, considering the marine ecoregions of the Brazilian coast, according to Spalding et al. (2007): EB, eastern Brazil; FNAR, Fernando de Noronha and Atol das Rocas; NEB, northeastern Brazil; SEB, southeastern Brazil. Description of variables, as in **Table 2**.

predominantly industrial, in contrast to the system in the other national regions (notably artisanal).

Fishing along the coast of Brazil has traditional characteristics since around 45% of the interviewed octopus fishers learned to fish with their parents and/or grandparents. This inherited ecological knowledge was predominantly observed in the northeastern and eastern ecoregions of Brazil, where the artisanal mode of octopus fishing is adopted by 69% of the interviewed fishers.

In all the interviews, the respondents reported that octopuses are captured using a trap ("covo" or pot—industrial fishing) or instrument ("bicheiro" or hook—artisanal fishing). The capture of octopuses using longline pots submerged in water attached to ropes was reported by approximately 27% of fishers.

Notably, this type of fishing was mentioned during the interviews conducted in the localities surrounding the Arraial do Cabo Marine Extractive Reserve (RJ) and the Arvoredo Marine Biological Reserve (SC), located in the southeastern marine ecoregion of Brazil, where octopus fishing takes place at an industrial scale using longline pots (**Supplementary Figure 1**).

Octopus fishing with a hook ("bicheiro," **Supplementary Figure 2**), which is like an iron rebar with a hook at the end, was reported by 79% of respondents. This is the main form of octopus fishing in the other localities, distributed across the three marine ecoregions, Fernando de Noronha and Atol das Rocas, northeastern Brazil, and eastern Brazil. Around 60% of respondents do not consider sexual dimorphism a relevant characteristic for octopus fishing. Among the fishers who have already caught the "eastern octopus" at some point in their fishing activity, around 49.7% said that their fishing region has more than one species of octopus. In general, the fishers mentioned that they can differentiate the species by observing the size and thickness of the arms (longer and thinner for *C. furvus*), smaller head size, body color and type of substrate in which the species is found, namely the stone octopus (*O. insularis*) and sand octopus (*C. furvus*).

In the regions of industrial octopus fishing using longline pots, the tide regime, moon phase, or any traditionality characteristics do not influence the activity. In contrast, artisanal octopus fishing, which is carried out by around 87.16% of the respondents, is directly influenced by the tide regime and moon phases. Fishing occurs fortnightly, at low spring tides and during the "full moon" and "new moon" phases.

Although none of the interviewed fishers catch octopuses exclusively, around 97.3% fish during the day. However, the respondents who fish octopuses at night reported that both the stone octopus and the sand octopus ("eastern octopus") are captured "opportunistically," that is, occasionally, when they are trying to capture another type of fish, usually during lobster fishing.

In regions where octopuses are caught using longline pots, the pots are placed 1–2 km away from the shores of the Marine Extractive Reserve of Arraial do Cabo (RJ), and most of the fishers (65%) do not fish alone. Similarly, artisanal fishers go out in pairs or trios to fish octopuses and optimize foraging time.

According to 57.75% of these artisanal fishers, each fishing session lasts around 3 h and occurs on the reef plateau of coastal reef environments. To maximize the productivity of this activity, 59.4% of fishers go out in search of octopuses with at least one fishing partner. In this joint fishing effort, 78% of fishers catch, on average, 10 kg of octopuses per session.

This number increases considerably (two to four tons) in industrial-scale fishing with longline pots (**Figure 4**), in which around 20 thousand pots (per vessel) are thrown in the sea to capture octopuses, as reported by fishers working in the regions surrounding the Arvoredo Marine Biological Reserve (SC) and the Arraial do Cabo Marine Extractive Reserve (RJ). Regarding average catch size/weight, most of the fishers (64%) generally catch octopuses weighing more than 500 g.

Based on the data obtained from the interviews conducted in the states of Ceará (CE), Rio de Janeiro (RJ), and Santa Catarina (SC), the octopuses caught with longline pots are larger than the octopuses caught in artisanal fishing, although they never exceed 4 kg/individual. This includes the southeastern marine ecoregion of Brazil, where the species of octopus captured is *O. vulgaris* (Cuvier, 1797), which can reach a body weight of 5 kg (Perales-Raya et al., 2014). According to these fishers, the largest octopus they ever captured weighed around 3 kg. Approximately 50.3% of artisanal octopus fishers reported that the largest specimen they caught themselves weighed around 1.9 kg.

Although 90.4% of respondents are members of a fishing colony or association, 79% reported that not every octopus is sold or consumed; when the captured animal is considered small, fishers use it as bait. Part of what is caught is consumed by the fishers or sold by intermediaries, directly to businesses (restaurants, inns, hotels, and beach stands), or final consumers. However, for 96.26% of these fishers, octopus fishing is not their main source of income.

Fishing and Ecology of *Callistoctopus furvus*

Although the octopus *C. furvus* is part of a cryptic species complex, its morphological characteristics are unique and specific when compared to the other two octopus species, namely *Octopus vulgaris* and *O. insularis*, which are common on the Brazilian coast. In this regard, data on the ecological factors of the species *C. furvus* were collected only from octopus fishers, divers, and underwater fishers, who reported having sighted or fished this species at some point during their fishing activity in the region where they operate. Thus, fishers working in localities in the states of CE, SC, and RN did not answer these specific questions, as the species *C. furvus* was not recognized in those regions.

When asked about the capture of *C. furvus,* 67.1% of the respondents answered that, although they were familiar with the octopus species due to sightings of some specimen during underwater activities, they had never caught any individuals. Therefore, the interviews on the ecological factors and fishing of *C. furvus* were conducted with 32.9% of the fishers (n = 50), who had already caught this octopus at some point during their fishing activity.

The LRM indicated that the variables "learned" (the person with whom the fishers learned to catch octopus) and "alone" (if

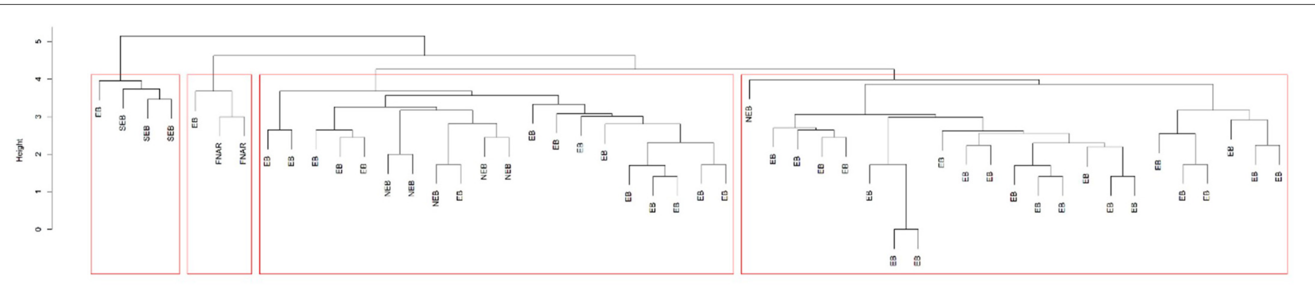

FIGURE 4 | Dendrogram showing dissimilarity among fishers of the "eastern octopus" *Callistoctopus furvus* in the marine ecoregions of the Brazilian coast. EB, eastern Brazil; FNAR, Fernando de Noronha and Atol das Rocas; NEB, northeastern Brazil; SEB, southeastern Brazil.

they fish alone) are associated with "eastern octopus" fishing. That is, fishers who learned to fish with their parents or grandparents are more likely to fish this species than fishers who learned with friends or alone. Similarly, fishers who fish with a fishing partner are more likely to catch the species than if they were alone (**Table 3**).

Cronbach's alpha for data of the "eastern octopus" fisher was 0.75 (alpha = 0.75; confidence interval (95%) = 0.66–0.85; n = 50; mean inter-item correlation = 0.14). Two variables were removed ("consumption" and "arms") because the answers did not change in relation to consumption or the size and thickness of the arms, which hold the greatest commercial interest. **Table 4** shows the test statistics and alpha value for the case of the individual removal of each variable. As in the previous analysis, some of the variables were negatively correlated with the total scale. The individual removal of the variables did not produce any significant increases in the alpha value. Therefore, Cronbach's alpha value is satisfactory.

The dendrogram with the dissimilarities among the "eastern octopus" fishers shows the formation of four groups (**Figure 4**). Fishers from the southeastern ecoregion of Brazil "SEB" differed and formed a group. The second group was formed by fishers from the Fernando de Noronha and Atol das Rocas ecoregion "FNAR." Both groups are accompanied by an individual from the eastern ecoregion of Brazil "EB." The third group was formed by individuals from the eastern ecoregion of Brazil "EB" and northeastern ecoregion of Brazil "NEB." Finally, the fourth group was formed almost exclusively by individuals from the "EB" ecoregion, and only one fisher from the "NEB" fell into this group. This result highlights the different fishing characteristics along the coast, such as the predominance of "SEB" fishers involved in industrial fishing and the predominance of small-scale fishers in the other ecoregions. The CCC showed a good fit (0.78), which indicates the consistency of the clustering pattern of these characteristics.

According to 70% of respondents, *C. furvus* is a large octopus when compared to the other octopus species they capture (*Octopus insularis* Leite et al., 2008 and *O. vulgaris*), and may even reach a total length of 3 m, according to some fishers. The presentation of images during the interview (**Supplementary Figure 3**) revealed that the fishers of the eastern ecoregion of Brazil use the term "common octopus" to refer to both the species *O. insularis* and *O. vulgaris*; moreover, they differentiate them as female octopuses (wider animal with short arms) and male octopuses (slimmer animal with long, robust arms), respectively.

For 100% of respondents, *C. furvus* has no commercial value since the most widely commercialized part of this fish are the arms. Although *C. furvus* is larger and heavier than the common octopus, it can have long and very thin, fragile arms that often break with simple handling. The maximum weight reported by fishers was about 1.5 kg.

According to 76% of respondents, *C. furvus* is commonly found in shallow water less than 5 m deep. However, the largest specimens are usually found during the night. *C. furvus* has an orange-red coloration (**Figure 2**) with white spots scattered throughout its body. Although these white spots are common characteristics of species in the cryptic species complex, this feature does not particularly draw the attention of the fishers since they believe "all octopuses change color when they want to flee." For all the interviewed fishers, the length and thickness of the arms are considered when they determine whether it belongs to another octopus species. For 90.9% of the fishers, "habitat" is the main difference between the species of that region, that is, they believe there are two species of octopus, namely the stone octopus or common octopus, which is *O. insularis*, and the sand octopus, which is *C. furvus*.

TABLE 3 | Result of the logistic regression model with the variables that may be associated with fishing of the "eastern Octopus" (*C. furvus*).

Coefficients	Estimate	Standard error	*z*-value	P
MunicipalityBombinhas	1.149e + 01	1.590e + 04	0.001	0.99
MunicipalityCabo Frio	–4.895e + 00	1.236e + 04	0.000	0.99
MunicipalityCairu	–4.205e + 01	9.456e + 03	–0.004	0.99
MunicipalityCaravelas	–5.308e + 01	1.860e + 04	–0.003	0.99
MunicipalityNoronha	–5.328e + 01	1.860e + 04	–0.003	0.99
MunicipalityIpojuca	–5.412e + 01	1.860e + 04	–0.003	0.99
MunicipalityJericoacoara	–1.851e + 00	1.526e + 04	0.000	0.99
MunicipalityMarechal Deodoro	–5.290e + 01	1.860e + 04	–0.003	0.99
MunicipalityNatal	–7.222e + 01	1.914e + 04	–0.004	0.99
MunicipalityPorto da Rua	–5.465e + 01	1.860e + 04	–0.003	0.99
MunicipalityPorto de Pedras	–7.476e + 01	2.243e + 04	–0.003	0.99
MunicipalityPorto Seguro	–5.412e + 01	1.860e + 04	–0.003	0.99
MunicipalityPrado	–5.511e + 01	1.860e + 04	–0.003	0.99
MunicipalitySão Miguel dos Milagres	–5.428e + 01	1.860e + 04	–0.003	0.99
Learned2	–3.183e + 00	9.556e-01	–3.331	0.00***
Learned3	–3.435e + 00	9.630e-01	–3.568	0.00***
Instrument2	6.428e + 00	9.454e + 03	0.001	0.99
Sex2	1.659e-01	6.729e-01	0.247	0.80
Frequency2	1.752e-02	2.657e + 00	0.007	0.99
Frequency3	2.118e + 00	7.083e + 03	0.000	0.99
Period2	1.365e + 00	2.027e + 00	0.673	0.50
Influence_tide2	1.394e + 00	1.360e + 00	1.025	0.30
Level_tide2	–3.875e + 01	9.161e + 03	–0.004	0.99
Moon_interferes2	–1.039e + 00	6.511e + 03	0.000	0.99
Phase2	–3.748e + 01	8.171e + 03	–0.005	0.99
Alone2	2.440e + 00	1.127e + 00	2.165	0.03*
Alone3	2.638e + 00	1.220e + 00	2.162	0.03*
Hours2	1.082e + 00	1.863e + 00	0.581	0.56
Hours3	9.506e-02	9.099e + 03	0.000	0.99
Kilos2	–7.848e-01	1.067e + 04	0.000	0.99
Kilos3	1.772e + 00	1.287e + 04	0.000	0.99
Smallest2	–7.147e-01	9.373e-01	–0.763	0.44
Smallest3	–7.587e-01	2.216e + 00	–0.342	0.73
Largest2	1.072e + 00	6.903e-01	1.553	0.12
Largest3	4.896e-01	8.783e-01	0.557	0.58
Member2	4.915e-02	1.776e + 00	0.028	0.98
Main_income2	3.960e + 01	9.239e + 03	0.004	0.99
Sale2	4.750e-01	7.470e-01	0.636	0.52

The variable "learned" indicate that the levels "learned2" (= friends) and "learned3" (= alone) are negatively associated with fishing of the "eastern octopus," based on level 1 (parent/grandparents) as reference. The variable "alone" indicates that the levels "alone2" (= no) and "alone3" (sometimes) are negatively related to fishing the species, based on level 1 (= yes) as reference. These results can be interpreted as a possible consequence of the LEK passed from generation to generation (parents/grandparents to children/grandchildren) and the sharing of this knowledge with the fishing partner.

**Significance < 0.05; ***significance < 0.001.*

TABLE 4 | Cronbach's alpha statistics for the questionnaire applied to the fishers of the "eastern octopus" (*n* = 50) along the Brazilian coast (standardized alpha = 0.75).

Variable	Correlation (+ or -)	Alpha when item is removed	Mean inter-item correlation	Correlation of item with total value
Learned	+	0.77	0.15	0.05
Instrument	+	0.75	0.13	0.51
Sex	+	0.76	0.15	0.09
Frequence	+	0.76	0.15	0.09
Period	−	0.75	0.14	0.33
Influence_tide	−	0.73	0.14	0.61
Level_tide	+	0.75	0.14	0.30
Moon_interferes	+	0.75	0.13	0.41
Phase	+	0.75	0.14	0.25
Alone	−	0.74	0.14	0.48
Hours	+	0.74	0.13	0.56
Kilos	+	0.74	0.13	0.48
Smallest	+	0.73	0.13	0.60
Largest	+	0.74	0.14	0.48
Member	+	0.75	0.15	0.29
Main_income	+	0.72	0.13	0.79
Sale	+	0.76	0.15	0.09
Where	+	0.75	0.14	0.40
Depth	+	0.73	0.13	0.63
Largest_furvus	−	0.76	0.15	0.20
When	+	0.71	0.13	0.75
How_many_furvus	−	0.73	0.13	0.68
Season	−	0.79	0.15	0.20
Factor	+	0.75	0.14	0.33
Habitat	+	0.75	0.14	0.49
Color	+	0.77	0.15	0.32

Learned, with whom the fisher learned to fish; instrument, fishing gear used; sex, differentiation between male and female; frequency, frequency of octopus fishing; period, the fishing period; influence_tide, whether fishing is influenced by tide; level_tide, fishing tide level; moon_interferes, whether the moon intereferes with fishing; phase, fishing moon phase; alone, whether he or she fishes alone; hours, fishing times; kilos, amount of fish; smallest, smallest captured octopus; largest, largest captured octopus; member, whether member of a fishing colony or association; main_income, whether octopus is the main source of income; sale, whether all octopuses captured are sold; where, fishing location; depth: fishing depth; largest_furvus, largest captured "eastern octopus"; when, capture season; how_many_furvus, number of "eastern octopus" captured on the best day; season, season of the year of catches; factor, factor considered to differentiate "eastern octopus" from common octopus; habitat, habitat of the "eastern octopus"; color, difference in color between the "eastern octopus" and the common octopus.

In the region of Cairu, (BA) this octopus occurs throughout the year, regardless of season or wind regime, and is often spotted by fishers who catch lobster at night. In the town of Garapuá, near Morro de São Paulo (Cairu district), fishers reported that the species *C. furvus* is very difficult to find and has not been captured for more than 5/10 years. However, recently (November 2020), one specimen was captured in the Garapuá reef environments. This indicates the species also occurs in this region and the possible reason for the absence of records is that the fishers catch octopus during the day, and they do not have the habit of catching lobsters.

In the eastern ecoregion, the Corumbau Extractive Marine Reserve, the species is known although it is infrequent and rarely caught. As in the region of Porto Seguro, it is associated with the "eastern" wind regime that usually occurs between May and August. In contrast, in the Lagos region (Rio de Janeiro), sightings, when they occur, are usually in the summer.

Compared to the common octopus, the "eastern octopus" is apparently less abundant since approximately 62% of the fishers caught less than three specimens in their best fishing sessions. The same species was also caught in coastal reefs less than 5 nautical miles from the coast, according to 74% of the respondents.

Based on the classification of Marine Ecoregions of the World (Spalding et al., 2007), it was also observed that the LEK of artisanal octopus fishers in eastern Brazil is more varied in terms of information than that of the fishers in the southern limit of the eastern ecoregion of Brazil and the southeastern ecoregion of Brazil, who use longline pots. All the information obtained through interviews was organized according to the marine ecoregion in which it was collected, as shown in **Figure 5**.

DISCUSSION

Studies addressing ethnoknowledge and LEK have been essential to aggregate information about resources that have often not been identified by researchers (Neis et al., 1999; Jesus et al., 2021a,b). Traditional communities, such as artisanal fishers, have comprehensive knowledge of the different resources they exploit and can provide valuable information in management scenarios with data-poor fisheries (Sáenz-Arroyo et al., 2005; Ramires et al., 2007; Leeney and Poncelet, 2015; Bezerra et al., 2021). In the present study, the knowledge of the fishers was used to investigate their historical perceptions of octopus fishing, complemented with information on the species *C. furvus*, and, consequently, obtain data to characterize ethnoecologically this octopus species in the different marine ecoregions of Brazil.

The classification of Marine Ecoregions of the World was based on taxonomic configurations of various marine groups, influenced by evolutionary history and geographical isolation (Spalding et al., 2007), resulting in three levels of organization: realms, provinces, and ecoregions. Each ecoregion has a relatively homogeneous species composition, which differs from adjacent systems. This condition would theoretically explain the possibility that Mexico, Colombia, and Brazil share the same genetic lineage of the octopus *C. furvus* (Jesus et al., 2021b) since they are in the same realm (Tropical Atlantic). Following this same line of reasoning, the MPA and surrounding localities from which most of the information was obtained on general octopus fishing and ecological factors of the octopus *C. furvus*, are in the same marine ecoregion (eastern Brazil), as shown in the heat maps.

Although they have distinct geographical characteristics, the species *C. furvus* was reported in all ecoregions; moreover, its occurrence in the southern limit of the Eastern Brazil marine ecoregion was associated with the phenomenon of upwelling (Jesus et al., 2021a). These observations also involved analyzing the dendrogram with the dissimilarities among fishers of the eastern octopus (*C. furvus*), which revealed different fishing characteristics along the coast, namely the predominance of

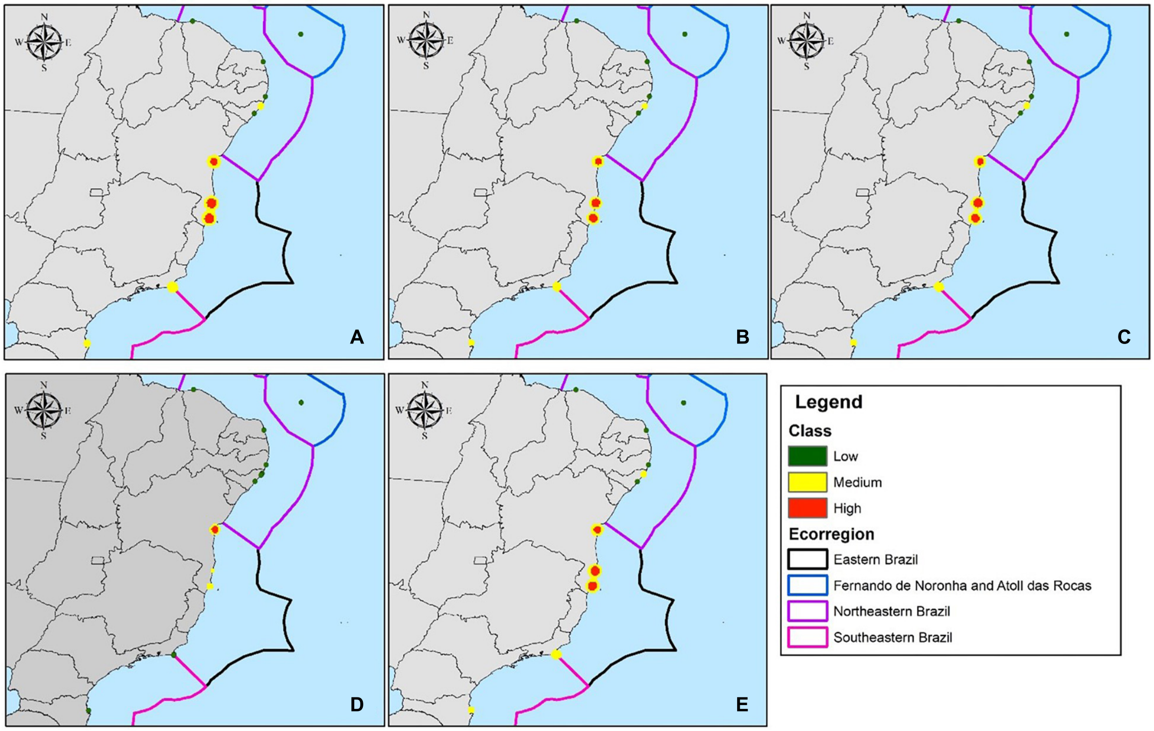

FIGURE 5 | Heat maps indicating the concentration of information obtained on octopus fishing and the ecological factors of *Callistoctopus furvus*, in each of the four Brazilian marine ecoregions included in this study. The information is presented in five categories: **(A)** general factors of octopus fishing; **(B)** seasonality; **(C)** fishing effort; **(D)** sale; and **(E)** factors of *C. furvus* fishing. The marine ecoregion with the highest concentration of information in the five categories was eastern Brazil, high class, in red.

"SEB" fishers in industrial fishing and the predominance of small-scale fishers in the other ecoregions.

Some gaps regarding the fishers of the Southeastern marine ecoregion indicate the need for more research to clarify the possible occurrence of *C. furvus* in this region, especially considering that this species was only recorded once outside the Atlantic Tropical realm (Jesus et al., 2021a,b), which starts in Florida (United States) and extends up to a part of southeastern Brazil. The upwelling phenomenon in the southern limit of the Tropical Atlantic realm (Spalding et al., 2007), associated with the movement of marine currents (Brazil current), can theoretically explain the occurrence of the species *C. furvus* in the realm and adjacent ecoregion (Temperate South America realm and the Southeastern ecoregion of Brazil, respectively).

Notably, fishers have detailed ecological knowledge about resources on a local geographical scale (Johannes, 1998). For example, they may remember particularly good catches from a productive day (Daw, 2010). According to the artisanal fishers, the average amount of common octopuses caught at the end of each fishing session is currently around 10 kg even when they fish in pairs or trios to optimize fishing effort. Therefore, the fishing of this resource is a secondary source of income since it does not meet the demands of the fishing market, as also reported by Jesus et al. (2015).

In the Northeastern and Eastern marine ecoregions of Brazil, the octopus *O. insularis* is predominantly captured by artisanal fishers, as reported by 79% of the respondents; moreover, fishing is directly influenced by the tidal regime and moon phases and occurs fortnightly at low spring tides and during the "full moon" and "new moon" phases, as previously reported by other researchers (Mendes, 2002; Martins et al., 2011; Haimovici et al., 2014; Jesus et al., 2015). Although *O. vulgaris* occurs in all the studied marine ecoregions, since it is commonly found in deeper waters, it is predominantly captured on an industrial scale with longline pots in the southern limit of the Eastern and Southeastern marine ecoregions of Brazil.

Notably, the eastern octopus, also known as "sand octopus" or "cheetah octopus" (*chita*, in Portuguese; Jesus et al., 2021a) *C. furvus*, is difficult to find; moreover, scientific reports of its capture are scarce (Leite and Haimovici, 2006; Jesus et al., 2015, 2021a,b; Cedillo-Robles and Pliego-Cardenas, 2018). It has long, thin arms and apparently inhabits shallow waters with higher temperatures when compared to *O. vulgaris*. Although its occurrence has been recorded, niche overlap was not observed in areas predominantly close to reef environments with the species *O. insularis*, which also occurs in the studied reef environments. *C. furvus* is an octopus with reportedly nocturnal habits and a different escape strategy than that of the two other species mentioned above.

According to the fishers' LEK in Eastern ecoregion of Brazil, when *C. furvus* feel threatened, they bury themselves in the sand rather than "release" ink to "throw off the predator." This is a common behavior among octopus species, including *O. insularis* and *O. vulgaris*. This behavior helps them distinguish these two other species, which are also called "stone octopus" by the fishers of this same ecoregion since they are commonly caught in existing burrows in reef environments.

Traditionality in relation to octopus fishing in general and the fishing of *C. furvus* was analyzed using the logistic regression model. Among other factors, this analysis revealed that the "eastern octopus" was more commonly captured among the fishers who learned to fish from their parents or grandparents than among those who were taught by friends or who learned alone. This finding reinforces the idea that the information shared between different generations can provide reliable data on occurrence sites (Reis-Filho et al., 2016); moreover, this LEK may play an important role in the development of measures to protect vulnerable stages of life history (Herbst and Hanazaki, 2014).

Interviews using quantitative methodological approaches can contribute to the available data by providing insight into the decline of some species over time (Santos et al., 2016) and accurate capture data even after decades (e.g., Sáenz-Arroyo and Revollo-Fernández, 2016; Thurstan et al., 2016). However, survey strategies that target the conservation of endangered and widely distributed species can be challenging and costly to develop and require long-lasting research programs (Wiley and Simpfendorfer, 2010). In this regard, unconventional data sources are convenient to infer, for example, long-term abundance trends for target species (Pitcher and Lam, 2010), as in the case of alternative approaches, namely LEK and citizen science (Jesus et al., 2021a), which generate results in a short period.

Despite their remarkable economic importance and although the phylum Mollusca, which includes octopuses, is the second-largest group of invertebrate animals (Haszprunar, 2001), these representatives are not among the groups of aquatic invertebrate animals on the list of endangered species (ICMBio, 2018). As a result, studies conducted on the ecology and artisanal fishing of octopus in Brazil indicate that the standardization goal of this type of fishing in the northeast region, for example, should be to protect the species and its environment and make it compatible with a small-scale fishing modality for recreational purposes (Leite et al., 2008). Thus, some conservationist measures, such as establishing standard measures for making and using hooks (used for octopus fishing), prohibiting, and supervising the use of chemicals for removing octopuses from burrows, establishing minimum catch size and weight, and curbing trap fishing (Leite et al., 2008; Haimovici et al., 2014), can support the management of octopus fishing.

Given the absence of a global and/or national regulation for artisanal octopus fishing, the species *Octopus* spp. are being commercially exploited according to normative instructions that regulate octopus fishing with long-line pots in the northeastern, southeastern, and southern regions of Brazil. In this regard, Ordinance SAP/MAP N° 328, of December 31, 2020, proposes a public consultation to change the minimum permitted depth and disposal of octopus (*Octopus* spp.) fishing gear. These guidelines were originally established in the normative instruction of the Special Secretariat for Aquaculture and Fisheries of the Presidency of the Republic No. 26 of December 19, 2008, by means of criteria and procedures for managing operations related to octopus (*Octopus* spp.) fishing in the marine waters of the southeastern and southern Brazil.

However, fisheries involving the capture of species of the genus *Callistoctopus* have been reported as exceptional (Leite and Haimovici, 2006) or sporadic (Haimovici et al., 2014), which exempts them from any use and management rules applicable to the capture and conservation of the species *Octopus* spp. In this context and based on the ethnoecological information about the octopus species *C. furvus* obtained in this study, the species may not be suffering fishing pressure since it has no commercial value and is rarely used in the sampled area, even for subsistence consumption.

However, the scarce occurrence of *C. furvus* on the Brazilian coast may be related to species recolonization as it was first recorded in Brazil in the nineteenth century, followed by new records in the twenty-first century (Mendes, 2002; Martins et al., 2011; Jesus et al., 2015), resulting in its redescription (Jesus et al., 2021b).

CONCLUSION

Although data obtained from LEK and the perception of fishers require careful analysis, these data proved efficient and reiterated their value as a source of information. Grouped data obtained through interviews and presented in heat maps indicated that most of the answers on the ecological factors of *C. furvus* were provided by artisanal fishers in the Eastern marine ecoregion of Brazil who learned their craft from parents and/or grandparents. A comparison of the frequency of occurrence of *C. furvus* in relation to *O. insularis* and *O. vulgaris* (species also occurring in the study area) showed that *C. furvus* was less abundant than the other two species, although it has different habits.

Based on the information presented here, studies with behavioral approaches should be carried out to complement current data and adapt conservation strategies for the species *Callistoctopus furvus*.

DATA AVAILABILITY STATEMENT

Copies of the interviews were deposited in the collection of the Laboratório de Etnoconservação e Áreas Protegidas of the Universidade Estadual de Santa Cruz (BA), Ilhéus, Brazil. Any requests to access the datasets for this article should be directed towards the corresponding author(s).

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Research Ethics Committee of the Universidade Estadual de Santa Cruz Authorization No. 2,593,218. The patients/participants provided their written informed consent to participate in this study. The animal study was reviewed and approved by Sistema de Autorização e Informação em Biodiversidade (SISBIO) Protocol No. 60468-2.

AUTHOR CONTRIBUTIONS

MJ and AS conceived of the presented idea. MJ carried out the data collection and wrote the first draft of the manuscript. MJ, CZ, and RS carried out the data analysis. MJ, CZ, RS, and AS reviewed and final wrote of the manuscript. AS supervised. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.788879/full#supplementary-material

REFERENCES

Barrera-Bassols, N., and Toledo, V. (2005). Ethnoecology of the yucatec maya: symbolism, knowledge and management of natural resources. *J. Latin Am. Geogr.* 4, 9–41. doi: 10.1353/lag.2005.0021

Begossi, A., and Silvano, R. A. M. (2008). Ecology and ethnoecology of dusky grouper [garoupa, *Epinephelus marginatus* (Lowe, 1834)] along the coast of Brazil. *J. Ethnobiol. Ethnomed.* 4:20. doi: 10.1186/1746-4269-4-20

Bezerra, I. M., Hostim-Silva, M., Teixeira, J. L. S., Hackradt, C. W., Félix- Hackradt, F. C., and Schiavetti, A. (2021). Spatial and temporal patterns of spawning aggregations of fish from the Epinephelidae and Lutjanidae families: an analysis by the local ecological knowledge of fishermen in the Tropical Southwestern Atlantic. *Fish. Res.* 239:105937. doi: 10.1016/j.fishres.2021.105937

Castilho, L. C., Martinez, R. A., Giné, G. A., Ribeiro, G. C., and Schiavetti, A. (2013). The thin-spined porcupine, *Chaetomys subspinosus* (Rodentia: erethizontidae), within protected areas in the Atlantic Forest, Brazil: local knowledge and threats. *Trop. Conserv. Sci.* 6, 796–810. doi: 10.1177/194008291300600607

Cedillo-Robles, C., and Pliego-Cardenas, R. (2018). "Shallow water octopuses from off Mexico," in *Cephalopod Research Across Scales: From Molecules to Ecosystems*, ed. H. Judkins (St Petersburg, FL: Cephalopod International Advisory Council), 246.

Chakraborty, D., Mukheriee, M., and Maity, J. (2015). Ethno-medicinal importance of viviparous gastropod, *Bellamya bengalensis* (Lamarck, 1822) in terms of estimation of its proximate protein and amino acid composition. *Int. J. Sci. Res.* 4, 178–180.

Cidreira-Neto, I. R. G., Fragoso, M. L. B., and Rodrigues, G. G. (2019). Pesca artesanal do marisco no litoral paraibano: relações socioambientais e tecnologias sociais. *Rev. Geogr.* 36, 97–109.

Coelho-Souza, S. A., López, M. S., Guimarães, J. R. D., Coutinho, R., and Candella, R. N. (2012). Biophysical interactions in the cabo frio upwelling system, Southeastern Brazil. *Braz. J. Oceanogr.* 60, 353–365. doi: 10.1590/s1679-87592012000300008

Cortina, J. M. (1993). What is coefficient alpha? an examination of theory and applications. *J. Appl. Psychol.* 78, 98–104. doi: 10.1037/0021-9010.78.1.98

Cronbach, L. J. (1951). Coefficient alpha and the internal structure of tests. *Psychometrika* 16, 297–334. doi: 10.1016/0020-7489(93)90092-9

Daw, T. (2010). Shifting baselines and memory illusions: what should we worry about when inferring trends from resource user interviews? *Anim. Conserv.* 13, 534–535. doi: 10.1111/j.1469-1795.2010.00418.x

Ekau, W., and Knoppers, B. (1999). An introduction to the pelagic system of the NorthEast and East Brazilian shelf. *Arch. Fish. Mar. Res.* 47, 113–132.

Environmental Systems Research Institute [ESRI] (2016). *ARCGIS Desktop: Release 10.5*. Redlands, CA: Environmental Systems Research Institute.

Freitas, S. T., Pamplin, P. A. Z., Legat, J., Fogaça, F. H. S., Barros, R. F. M. (2012). Conhecimento tradicional das marisqueiras de Barra Grande, área de proteção ambiental do delta do Rio Parnaíba, Piauí, Brasil. *Ambiente Sociedade* 15, 91–112. doi: 10.1590/s1414-753x2012000200006

Garcia, G. F. C. (2006). The mother – child nexus. Knowledge and valuation of wild food plants in Wayanad, Western Ghats, India. *J. Ethnobiol. Ethnomed.* 2:39. doi: 10.1186/1746-4269-2-39

Haimovici, M., Andriguetto Filho, J. M., and Sunye, P. S. (2014). *A Pesca Marinha e Estuarina no Brasil: Estudos de Caso Multidisciplinares*. Rio Grande: Editora da FURG, 191.

Hanazaki, N. (2003). Comunidades, conservação e manejo: o papel do conhecimento ecológico local. *Biotemas Florianópolis* 16, 23–47.

Haszprunar, G. (2001). *"Mollusca (Molluscs)". Encyclopedia of Life Sciences*. Hoboekn, NJ: John Wiley & Sons Ltd.

Herbst, D., and Hanazaki, N. (2014). Local ecological knowledge of fishers about the life cycle and temporal patterns in the migration of mullet (*Mugil liza*) in Southern Brazil. *Neotrop. Ichthyol.* 12, 879–890. doi: 10.1590/1982-0224-20130156

ICMBio (2018). *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume VII – Invertebrados*. Brasília: ICMBIO, 730.

Jereb, P., Roper, C. F. E., Norman, M. D., and Finn, J. K. (2014). *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Octopods and Vampire Squids, FAO Species Catalogue for Fishery Purposes*. Rome: FAO.

Jesus, M. D., Gouveia, M. T., de, J., Zapelini, C., and Schiavetti, A. (2015). Pesca artesanal e cadeia produtiva de *Octopus insularis*: o caso dos ambientes recifais do sul da Bahia, Brasil. *Gaia Sci.* 9, 195–204.

Jesus, M. D., Zapelini, C., and Schiavetti, A. (2021a). Can citizen science help delimit the geographical distribution of a species? The case of the *Callistoctopus* sp. ("eastern octopus") on the Brazilian coast. *Ethnobiol. Conserv.* 10:03. doi: 10.15451/ec2020-09-10.03-1-15

Jesus, M. D., Sales, J. B. L., Martins, R. S., Ready, J. S., Costa, T. A. S., Ablett, J. D., et al. (2021b). Traditional knowledge aids description when resolving the taxonomic status of unsettled species using classical and molecular taxonomy: the case of the shallow-water octopus *Callistoctopus furvus* (Gould, 1852) from the Western Atlantic Ocean. *Front. Mar. Sci.* 7:595244. doi: 10.3389/fmars.2020.595244

Johannes, K. (1998). The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol. Evol.* 13, 243–246. doi: 10.1016/s0169-5347(98)01384-6

Leão, Z. M. A. N. (1996). The coral reefs of Bahia: morphology, destruction and the major environmental impacts. *An. Acad. Bras. Ci.* 68, 439–452.

Leeney, R. H., and Poncelet, P. (2015). Using fishers' ecological knowledge to assess the status and cultural importance of sawfish in Guinea-Bissau. *Aquat. Conserv.* 25, 411–430. doi: 10.1002/aqc.2419

Leite, T. S., and Haimovici, M. (2006). "Presente conhecimento da biodiversidade e habitat dos polvos (Cephalopoda: família Octopodidae) de águas rasas das ilhas oceânicas do nordeste brasileiro," in *Ilhas Oceânicas Brasileiras – da Pesquisa ao Manejo*, eds R. J. V. Alves and J. W. A. Castro (Brasília: Ministério do Meio Ambiente), 199–214.

Leite, T. S., Haimovici, M., and Oliveira, J. E. L. (2008). Uma proposta de manejo para a pesca do polvo Octopus insularis Leite & Haimovici, 2008 (Mollusca: Cephalopoda) no arquipélago de Fernando de Noronha, Brasil. *Arq. Ciên. Mar* 41, 81–89.

Martins, V. S., Schiavetti, A., and Souto, F. J. B. (2011). Ethnoecological knowledge of the artisan fishermen of octopi (*Octopus* spp.) in the community of Coroa Vermelha (Santa Cruz Cabrália, Bahia). *An. Acad. Bras. Ci.* 83, 513–522. doi: 10.1590/S0001-37652011000200011

Mendes, L. P. (2002). *Etnoecologia dos Pescadores e Marisqueiras da vila de Garapuá. Monografia*. Salvador: Universidade Federal da Bahia, 97.

Minayo, M. C. D. S. (2016). *Pesquisa Social: Teoria, Método e Criatividade*. Petrópolis, RJ: Vozes.

Mohr, L. V., Castro, J. W. A., Costa, P. M. S., and Alves, R. J. V. (2009). *Ilhas Oceânicas Brasileiras: da Pesquisa ao Manejo – Volume II*. Brasília: MMA/Secretaria de Biodiversidade e Florestas, 502.

Monteiro, J. M., Albuquerque, U. P., Lins-Neto, E. M. F., Araújo, E. L., and Amorim, E. L. C. (2006a). Use patterns and knowledge of medicinal species among two rural communities in Brazil's semi-arid Northeastern region. *J. Ethnopharmacol.* 105, 173–186. doi: 10.1016/j.jep.2005.10.016

Monteiro, J. M., Almeida, C. F., Albuquerque, U. P., Lucena, R. F., Florentino, A. T., and Oliveira, R. L. (2006b). Use and traditional management of *Anadenanthera colubrina* (Vell.) Brenan in the semi-arid region of northeastern Brazil. *J. Ethnobiol. Ethnomed.* 2:6. doi: 10.1186/1746-4269-2-6

Moura, R. L., Secchin, N. A., Amado-Filho, G. M., Francini-Filho, R. B., Freitas, M. O., Minte-Vera, C. V., et al. (2013). Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. *Cont. Shelf Res.* 70, 109–117. doi: 10.1016/j.csr.2013.04.036

Nascimento, M. G. P., Santos, K. P. P., De Lima, E. F., Da Silva Meireles, V. D. J., De Andrade, I. M., and De Barros, R. F. M. (2020). Conhecimento ecológico local dos pescadores artesanais da apa do delta do Rio Parnaíba, Piauí, Brasil. *Rev. Gestão Sustentabilidade Ambiental* 9, 275–296. doi: 10.19177/rgsa.v9e42020275-296

Neis, B., Schneider, D. C., Felt, L., Haedrich, R. L., Fischer, J., and Hutchings, J. A. (1999). Fisheries assessment: what can be learned from interviewing resource users? *Can. J. Fish. Aquat. Sci.* 56, 1949–1963. doi: 10.1007/s13280-013-0460-0

Norman, M. D. (2000). *Cephalopods: A World Guide*. Hackenheim: ConchBooks.

Norman, M. D., and Hochberg, F. G. (2005). The current state of octopus taxonomy. *Phuket Mar. Biol. Center Res. Bull.* 66, 127–154.

Perales-Raya, C., Almansa, E., Bartolomé, A., Felipe, B. C., Iglesias, J., Sánchez, F. J., et al. (2014). Age validation in octopus vulgaris beaks across the full ontogenetic range: beaks as recorders of life events in octopuses. *J. Shellfish Res.* 33, 481–493. doi: 10.2983/035.033.0217

Petit, A. (1987). Claude Bernard and the history of science. *Isis* 78, 201–219. doi: 10.1086/354390

Pitcher, T. J., and Lam, M. E. (2010). Fishful thinking: rhetoric, reality, and the sea before us. *Ecol. Soc.* 15:12.

Prabhakar, A. K., and Roy, S. P. (2009). Ethno-medicinal uses of some shell fishes by people of Kosi river basin of North-Bihar, India. *Stud. Ethno Med.* 3, 1–4. doi: 10.1080/09735070.2009.11886329

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ramires, M., Molina, S. M. G., and Hanazaki, N. (2007). Etnoecologia caiçara: o conhecimento dos pescadores artesanais sobre aspectos ecológicos da pesca. *Biotemas* 20, 101–113.

Reis-Filho, J. A., Freitas, R. H., Loiola, M., Leite, L., Soeiro, G., Oliveira, H. H., et al. (2016). Traditional fisher perceptions on the regional disappearance of the largetooth sawfish *Pristis pristis* from the central coast of Brazil. *Endanger. Species Res.* 29, 189–200. doi: 10.3354/esr00711

Rohlf, F. J. (1970). Adaptative hierarchical clustering schemes. *Syst. Biol.* 16, 58–82. doi: 10.2307/2412027

Sáenz-Arroyo, A., and Revollo-Fernández, D. (2016). Local ecological knowledge concurs with fishing statistics: an example from the abalone fishery in Baja California, Mexico. *Mar. Policy* 71, 217–221. doi: 10.1016/j.marpol.2016.06.006

Sáenz-Arroyo, A., Roberts, C. M., Torre, J., Carino-Olvera, M., and Enríquez-Andrade, R. R. (2005). Rapidly shifting environmental baselines among fishers of the Gulf of California. *Proc. R. Soc. Lond. B Biol. Sci.* 272, 1957–1962. doi: 10.1098/rspb.2005.3175

Santos, A. A., Santos, E. M., and Santos, C. A. B. (2016). Crenças e percepções sobre *Philodryas olferssi* (Lichtenstein, 1823), em Ribeira do Amparo, sertão da Bahia. *Rev. Ibero Am. Ci. Ambientais* 7, 16–26. doi: 10.6008/spc2179-6858.2016.003.0002

Silvano, R. A. M., and Begossi, A. (2005). Local knowledge on a cosmopolitan fish ethnoecology of *Pomatotus saltatrix* (Pomatomidae) in Brazil and Australia. *Fish. Res.* 71, 43–59. doi: 10.1016/j.fishres.2004.07.007

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., et al. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57, 573–583. doi: 10.1641/B570707

Streiner, D. (2003). Starting at the beginning: an introduction to coefficient alpha and internal consistency. *J. Pers. Assess.* 80, 99–103. doi: 10.1207/S15327752JPA8001_18

Tavakol, M., and Dennick, R. (2011). Making sense of Cronbach's alpha. *Int. J. Med. Educ.* 2, 53–55. doi: 10.5116/ijme.4dfb.8dfd

Thurstan, R. H., Buckley, S. M., Ortiz, J. C., and Pandolfi, J. M. (2016). Setting the record straight: assessing the reliability of retrospective accounts of change. *Conserv. Lett.* 9, 98–105. doi: 10.1111/conl.12184

van Buuren, S., and Groothuis-Oudshoorn, K. (2011). *mice: Multivariate Imputation by Chained Equations in R. Journal of Statistical Software*, Vol. 45 (Los Angeles, CA: Foundation for Open Access Statistics), 1–67. Available online at: https://www.jstatsoft.org/v45/i03/

Wiley, T. R., and Simpfendorfer, C. A. (2010). Using public encounter data to direct recovery efforts for the endangered smalltooth sawfish *Pristis pectinata*. *Endanger. Species Res.* 12, 179–191. doi: 10.3354/esr00303

Zappes, C. A., Da Costa Oliveira, P., and Di Beneditto, A. P. M. (2018). Percepção de pescadores do norte fluminense sobre a viabilidade da pesca artesanal com a implantação de megaempreendimento portuário. *Boletim Instituto Pesca* 42, 73–88. doi: 10.20950/1678.2305.2016v42n1p73

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Biocultural Drivers Responsible for the Occurrence of a Cassava Bacterial Pathogen in Small-Scale Farms of Colombian Caribbean

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Cassava (*Manihot esculenta* Crantz) is a primary crop for food security of millions of people worldwide. In Colombia, the Caribbean region contributes about half of the national cassava production, despite major socioeconomic constraints such as unequal land property, omnipresence of middlemen, low and unstable prices, armed conflict, climate change and phytosanitary issues. Among the latter is Cassava Bacterial Blight (CBB), a disease caused by the bacterial pathogen *Xanthomonas phaseoli* pv. *manihotis* (*Xpm*) that leads to irreversible damage to plants, impeding growth and productivity. In 2016, we analyzed the role of sociocultural and agricultural practices on CBB prevalence in small-scale fields of a village of the Colombian Caribbean region, where farmers live almost exclusively from the sale of their cassava production. Semi-structured interviews (48) were conducted with all farmers who cultivated cassava to document individual sociodemographic characteristics, cassava farming practices, and perceptions about CBB occurrence. Cassava Bacterial Blight was diagnosed in the field and the presence of *Xpm* was further confirmed upon laboratory analysis of collected diseased leaf samples. Our data show that (i) according to the risks perceived by farmers, CBB is the main disease affecting cassava crops in the village and it could indeed be detected in about half of the fields visited; (ii) CBB occurrence depends strongly on land property issues, likely because of an inadequate phytosanitary control during acquisition of cuttings when farmers are forced to rent the land; and (iii) there is a strong positive correlation between the use of commercial fertilizers and the occurrence of CBB in the village of Villa López.

Keywords: agricultural practices, cassava bacterial blight (CBB), fertilizer use, land property, *Xanthomonas phaseoli* pv. *manihotis*, circulation of propagative propagules, seed system

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INTRODUCTION

Agriculture today is faced with a double challenge: coping with the impacts of climate change and reducing chemical inputs. It will become even more difficult to overcome these challenges, knowing that pest attacks are projected to decrease the yield of major grain crops by 10 to 25% per degree Celsius of warming (Deutsch et al., 2018). Root crops are particularly concerned by yield reduction compared to cereals under drought conditions (Daryanto et al., 2017). Phytosanitary problems in a context of climate change could potentially deprive humanity of up to 82% of the attainable yield (Chakraborty and Newton, 2011). It is estimated that each year already, approximately 16% of global harvest is lost due to plant diseases (Strange and Scott, 2005). Economic losses caused by plant pathogens may affect food security, especially in food-deficit regions with fast-growing populations such as countries in Latin America, Sub-Saharan Africa, and the Indo-Gangetic Plain (Savary et al., 2019).

Cassava (*Manihot esculenta* Crantz) is extensively cultivated all over the tropics; its tuberous root is a major source of carbohydrates for hundreds of millions of people worldwide (Lebot, 2009). Because of its tolerance to heat and water stress, cassava is thought to be resilient to climate change (Jarvis et al., 2012; El-Sharkawy, 2014), and hence is considered a strategic food, especially in a context of human adaptation to climate change (Burns et al., 2010). In Colombia, cassava is one of the most cultivated food crops, with a production of approximately two million tons per year (FAOSTAT, 2019), ensuring the subsistence of farmer families that cultivate it. The Caribbean region contributes to about 50% of Colombian production (Departamento Nacional de Estadística [DANE], 2017), mainly through small-scale cultivation by local communities who not only use it as part of their traditional diets, but also as a source of income (Aguilera-Díaz, 2012).

Cassava is susceptible to several pests and diseases during its cycle that could significantly reduce its yields (Center for Agriculture and Bioscience International [CABI], 2021) bringing socioeconomic problems to small-scale farmers who depend on the crop for survival. Among the main diseases affecting cassava production is Cassava Bacterial Blight (CBB), which is caused by *Xanthomonas phaseoli* pv. *manihotis* (*Xpm*). *Xpm* is a systemic Gram-negative bacterium that penetrates host leaves through natural openings or wounds, and can move into distal leaves and stems upon colonization of the plant vascular system. The most severe symptoms include leaf wilting, vascular necrosis of the stem, and shoot dieback causing irreversible damage that impedes cassava's growth and productivity (Zárate-Chaves et al., 2021). Dispersal of the pathogen within and among fields is thought to occur mainly through agricultural practices. Cassava is propagated clonally through stem cuttings. The pathogen can be spread when contaminated tools are used to prepare stem cuttings at planting time, and to cut stems when the roots are harvested. Exchanges of infected stem cuttings can disperse the pathogen among fields (Lozano, 1986; Boher and Verdier, 1994; Zárate-Chaves et al., 2021). At a small-scale, within fields or between adjacent fields, the bacterium can be dispersed naturally via rain and wind (Lozano, 1986).

This bacterium was first reported in Brazil in 1912 (Lozano, 1986), and in Colombia in 1971 (Lozano and Sequeira, 1974). In Colombian Caribbean, a high genetic diversity of *Xpm* has been reported, in comparison with other regions where the disease is present. This higher diversity can be explained by the wide range of environmental conditions in which the crop is cultivated (Restrepo and Verdier, 1997; Restrepo et al., 2004). The frequencies and variation of *Xpm* haplotypes have changed dramatically over time in different regions of Colombia, suggesting that populations may evolve rapidly (Restrepo et al., 2000, 2004) and possibly migrate within and between regions (Restrepo and Verdier, 1997).

The relative impact of farming practices and social drivers on CBB occurrence have not yet been clearly determined. Here, we investigate the role of local knowledge (i.e., perception of CBB), agronomic practices (i.e., fertilizer use, diversity of cultivated cassava varieties, circulation of plant propagative material) and socioeconomic factors (i.e., land tenure) on the occurrence of CBB, at the scale of a village in the Caribbean region of Colombia.

MATERIALS AND METHODS

Study Area

We chose to work in the Caribbean region of Colombia, because the cassava market is highly dynamic in this region and some localities, such as Chinú play a central role in cassava farmers meetings of cassava farmers during which propagative material may be exchanged. In addition, in this region *Xpm* is highly diverse (Trujillo et al., 2014), but to our knowledge, there have been no deliberate efforts to control CBB. The village of Villa López was selected because (i) its reasonably small size and concentrated habitat facilitate study; (ii) its main economic activity has relied on cassava production for at least three generations; and (iii) farmers expressed concern about the increasing incidence of CBB in their fields. Villa López is part of the municipality of San Juan de Betulia (Department of Sucre, Colombia), and is located at 9° 18' 14.7" N and 75° 13' 49.6" W, four kilometers away from the center of the municipality of San Juan de Betulia (**Figure 1**).

In 2016, when field study was conducted, almost all the families living in Villa López received income from the cassava value chain, as transporters, harvesters or merchants. Out of the 115 families, 48 families grew cassava as their main source of income. All farmers were men; these 48 farmers represent the totality of cassava growers living in this locality. The economy of other villages around Villa López also relies on cassava production (Agronet, 2020). A number of fields around Villa López are cultivated by farmers living in these villages such as Corozal, Las Cruces and Sabaneta, all 2-7 km away. Thirty-nine out of 48 men cultivating cassava were born in Villa López; the others were born in nearby municipalities and, in most cases, arrived after marrying women from this village.

Interviews

Of the 115 families living in Villa López between September and December 2016, we interviewed all the people who cultivated cassava during this period: 48 male farmers who cultivated 40 fields (**Table 1**). The number of fields does not correspond to the number of farmers because (1) two producers did not cultivate during that time because last season they did not have good results in selling their cassava production in the preceding season, (2) three farmers cultivate more than one field, and (3) twelve interviewed farmers (30 to 60 years old) shared the same collective field as they are part of a local association of

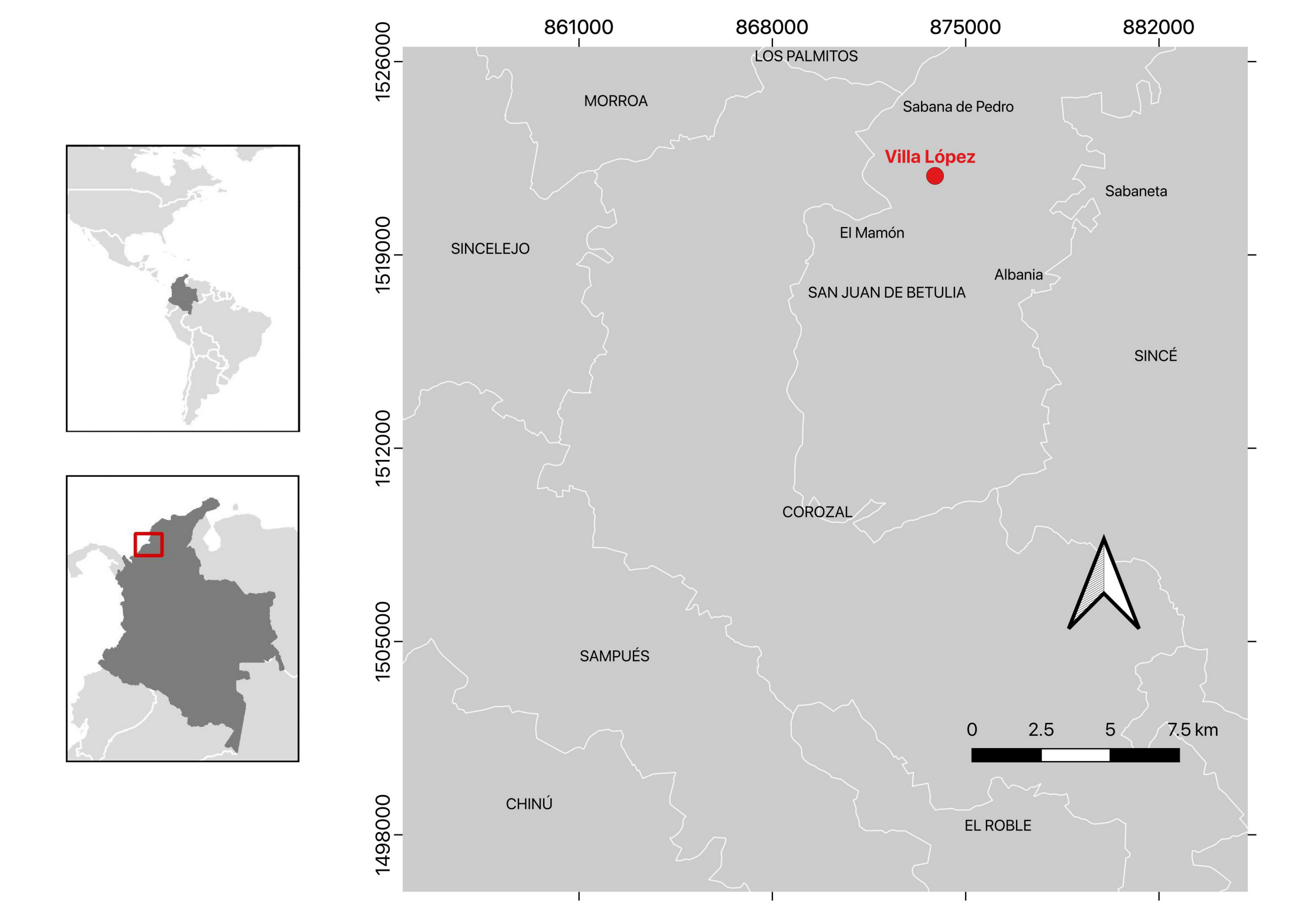

FIGURE 1 | Location of the village Villa López in the Caribbean region, Colombia, and of the localities mentioned in the text. WGS 84.

cassava producers named "Asoproagrovilo" (Cassava Producers' Association of Villa López).

Semi-structured interviews (77 questions) conducted at the farmer's home and then in the field (**Supplementary Materials 1, 2**) sought information about (1) sociodemographic characteristics of each farmer (i.e., gender, age, life history), (2) identification of cassava diseases, presence of CBB, the farmers' perception about its occurrence in the field, (3) cassava management practices [i.e., planting techniques, use of agrochemicals (fertilizers, insecticides and herbicides)], (4) the diversity of cassava varieties planted and their characteristics based on local knowledge, (5) general information about each field (i.e., associated crops within the same field and in neighboring fields, farming calendar, crop rotation, associated land user rights and history), and (6) the origin of planting material (i.e., characteristics and circulation networks of cuttings). To analyze the origin of cassava stems for cuttings, we asked whether farmers (1) recycled stem cuttings from their own fields, or (2) if they received cuttings from other farmers (i.e., identity and localization of the donors; terms of the transaction: gift or purchase). In statistical analyses, the farmer association was considered as a single farmer, characterized by their collective way of managing their field.

TABLE 1 | Farmers interviewed and fields visited in Villa López.

Number of fields per farmer	Number of farmers interviewed	Number of fields visited
0	3	0
1	30	30
2	1	2
3	2	6
1 field of the association	12	2
Total	**48**	**40**

Identification of Cassava Bacterial Blight

In each of the visited fields, the fields were surveyed for CBB-like symptoms: two apparently diseased leaves of up to five plants of each variety were sampled per field. Each sampled plant was documented and georeferenced. The isolation of strains of *Xpm* and PCR validation were performed as described by Trujillo et al. (2014). Leaf samples were sterilized with a 1% sodium hypochlorite solution and rinsed with sterile water. Subsequently, the tissue sample was macerated in a salt solution and drops of diluted macerate were plated onto LPGA medium (5g/L yeast extract, 5g/L peptone, 5g/L glucose, and 15g/L agar) and incubated at 28°C for 48 h. Bacterial colonies with typical *Xpm* morphology were selected and further validated through a PCR-based molecular diagnostic assay (Bernal-Galeano et al., 2018).

Statistical Analysis of Factors Explaining the Occurrence of Cassava Bacterial Blight

To identify factors that could explain the occurrence of CBB at the scale of individual fields, we assessed the impact of five qualitative explanatory variables on the occurrence of CBB (**Supplementary Data 1**): (1) land tenure (owned or rented), (2) cultivation time in the same field (3 consecutive years or fewer, versus 4 consecutive years or longer), (3) use of fertilizers (yes or no), (4) origin of the plant material (three modalities: acquired from other farmers, recycled from the same field, recycled from another field cultivated by the same farmer), (5) whether sampling occurred before or after harvest of the fields' cassava; and two quantitative variables: (6) the number of varieties of cassava cultivated in the field, (7) the number of other farmers who provided planting material for the focal field, (8) the proportion of external donors living in villages other than Villa López.

The date of collection was included, because CBB symptoms became increasingly visible over the plant's growth. Sampling took place in October (before harvest) and November (after harvest on plants left over because the farmers wanted to select these plants to provide vegetative propagules). Although the interviews asked about all agrochemicals used during the crop cycle, for the statistical analysis we only considered fertilizers because herbicides were used by few farmers and insecticides were used by almost all farmers. Thirty-eight fields had no missing data (the two missing ones were harvested before we sampled).

Prior to any analysis, we checked for multicollinearity using Pearson coefficient (**Supplementary Figure 1**). Two variables were removed from the analysis because they were strongly correlated with another variable: "cultivation time" (correlated to "land tenure", r^2 = 0.63) and "number of donors" (correlated with both "land tenure," r^2 = 0.40 and "cultivation time," r^2 = 0.51), resulting in six possible explanatory variables. We performed logistic generalized linear models, with CBB occurrence explained as a function of each possible combination of the six candidate explanatory variables (2^6 = 64 models investigated). Models were ranked according to Akaike's information criterion modified for small samples (AICc, Burnham and Anderson, 2002). We measured the relative importance of each variable, by summing the Akaike weights of the models including this variable. Since each variable was present in exactly half of the models, variables with importance > 0.5 are the most relevant. Model comparison was implemented in the R package MuMIn (Bartoń, 2019).

For the two best models, Likelihood Ratio Tests (LRT) were performed comparing these models and those including all but one of each of the explanatory variables. Explanatory variables that combined high importance and significant LRT tests were considered as relevant.

RESULTS

Cassava, A Traditional Staple Crop in Villa López

Most Villa López farmers grew cassava in a single field averaging one hectare in size. Out of 40 visited fields, 28 were rented. Farmers usually rented their lands for six months or for a year through informal contracts. Farmers reported that they selected their field based on previous experience about soil characteristics, proximity to their home and cost of rental. Most fields were located within a 7 km radius of the center of the village. Landowners generally lived in the larger nearby municipalities, especially San Juan de Betulia and Corozal.

In 2016, cassava cultivation was the main source of income for the inhabitants of Villa López. Men were generally in charge of economic activities such as cassava selling or cattle breeding, while women were in charge of housekeeping. Growing cassava has been part of their daily life: 94% (45/48) of the consulted farmers had cultivated cassava for more than five years, and 92% (44/48) reported that their parents and grandparents had also cultivated cassava.

Cassava was grown in thirty-six fields out of the 40 visited, in association with either maize (*Zea mays*), yam (*Dioscorea* spp.), pumpkin (*Cucurbita maxima*), watermelon (*Citrullus lanatus*), sesame (*Sesamum orientale*) or beans (*Phaseolus vulgaris*). Normally, cassava was planted first, along with pumpkin or watermelon seeds if these are available, then maize, and finally yams. When the cassava was harvested, maize was usually sown again, accompanied by sesame. All these plants are part of their traditional food system and were available to be harvested throughout the year, favoring self-sustainability.

To supplement soil nutrition, 45% (18/40) of the visited fields used commercial NPK fertilizers. Prior to sowing cassava, the substrate of 14 fields (35%) was prepared by ploughing with a tractor and the technique locally named "aporque." It consists in accumulating soil at the base of the stem cutting, thus forming a small mound. In Villa López, both the use of mechanical plough and investment in external labor were limited, since profits from the sale of cassava production were small.

During the growth of the crop, the farmers mentioned that one of the most frequent problems was weed invasion. Most farmers weeded exclusively manually, since weed growth can be controlled by ground-covering associated crops, such as pumpkins or watermelons. About 20% of the fields were treated with herbicides.

During the growing season, most farmers applied insecticides (38 out of 40 fields), despite their high costs at the local market. Most of them (82% of fields) applied organophosphate insecticides, including Lorsban® and Roxion®. Questionnaires showed that these insecticides were applied mostly to prevent or control other pests and diseases during the cassava crop cycle. Usually, the doses applied were decided by trial and error, based on farmers' previous experience or on advice received from those who sell the agrochemicals. As a preventive treatment against CBB, prior to planting, farmers soaked stem cuttings in copper oxychloride (17,5% of fields), and in organophosphate insecticides such as Lorsban® and Roxion® (32,5% of fields). Stem cuttings were not treated prior to planting in the other fields (50%). In two fields (5%) were used copper oxychloride and organophosphate insecticides at the same time.

Although most cassava plants were harvested at the end of October, the cultivation cycle can last from 6 to 12 months, depending on climatic variations, variety characteristics and market opportunities. During the harvest period, the intermediaries in charge of marketing at departmental and regional levels occasionally visited farmers to evaluate the yield and the qualities of the soil and the crop (plant health and size), so as to negotiate prices with farmers. Farmers reported that this informal market dynamic and the large number of levels of middlemen in the value chain contribute to lower prices and incomes.

Origins of the Cassava Cuttings

Farmers planted cassava during the March to June rainy season. They preferred to plant five days after the full moon, because they thought that this practice prevents plant rotting. Cassava was mainly propagated clonally through stem cuttings; we observed only a single volunteer plant issued from sexual reproduction in one field. Because cassava is generally harvested in October and planted in March, farmers had to store their own planting material for several months, or requested some from other farmers before planting. If farmers were able to use their own plant material, they might collect it either from the same previously cultivated field, or from a different field. In this case, they selected cassava cuttings considering the characteristics of the adult plants and the soil moisture.

According to farmers, the plant material that would be planted during the next cultivation cycle could be conserved either as stems under the shade of trees, or as living plants. If stored as stems, farmers reported that they needed to be watered daily for at least two weeks. Farmers said that the wound to the stem made during cutting was healed by the plant's natural latex. Just before planting, stems were cut with a machete into 30 cm long cuttings.

In 70% of the surveyed fields (28 out of 40), farmers kept a few living plants as planting stock. However, according to the interviews, this stored plant material was often left aside, either because farmers could not exploit the same field for the next cropping cycle, or because the plant material dried out due to delayed rainy seasons.

Even when farmers keep cassava planting material in their fields or under trees, they may still face a shortage of stems and need to request cuttings, just before the sowing period, from someone else living in or outside the village. Seventy-seven donors of cassava cuttings were identified in our surveys (**Figure 2**). A total of 304 actions of "seed" transfer were identified. The majority (74%) were undertaken by people from Villa López who exchanged seeds with their neighbors in the same village. Forty-five of the 48 local farmers were identified as having provided plant material to someone else (in 88% of cases not from the same family) in the preceding year (2015). The remaining providers of plant material are settled in the surrounding villages, especially San Juan de Betulia (whose farmers provide 86% of the actions of seed transfer from outside the village).

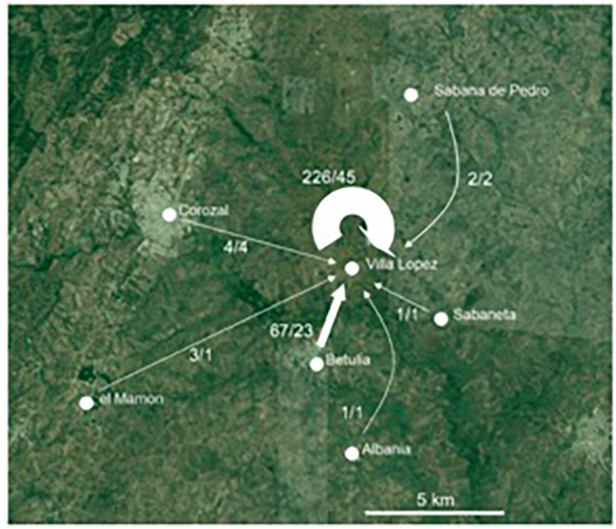

FIGURE 2 | Cassava stem cuttings circulation among farmers from Villa López and from neighboring villages. A transaction is described as cuttings of a given variety provided by a farmer to a farmer from Villa López. The size of the arrow is proportional to the number of transactions and the direction of the arrows shows the provenance of cuttings planted in Villa López (from donors to receivers). Numbers: the number of incoming transactions/number of donors from each neighboring village. This figure only focuses on stem cuttings received in Villa López, since they may imply the transfer of *Xpm* in the village.

Sociocultural Drivers of Cassava Bacterial Blight Occurrence in Villa López

Cassava Bacterial Blight (CBB) is known popularly by the common name "quema" (burning), because leaves look as though they are burnt when attacked by the pathogen (**Figure 3**). All consulted farmers declared to knowing the disease. They acknowledged that CBB occurs during rainy seasons, and that its characteristic symptom is a leaf blight starting from the apical part of the plant and progressing toward its base.

Perception of CBB occurrence as an importance risk in Villa López was relatively high, as 65% of the interviewees quoted CBB as a problem. However, out of the 26 fields that the farmers thought to be infected by CBB, only 16 actually had fields with infected plants, based on our field observations and further confirmed by molecular diagnostic-based analysis. Conversely, we found CBB in three fields where farmers initially thought that it was not present. To sum up, we observed that farmers made mistakes in reporting the presence of CBB in 32.5% of the fields when it was not present (ten instances), or the inverse (three instances).

Nineteen fields out of 40 were infected by CBB. Among all fields, 28 were rented (70%). Rented fields showed a higher prevalence of CBB than owned fields (respectively, 16/28 and

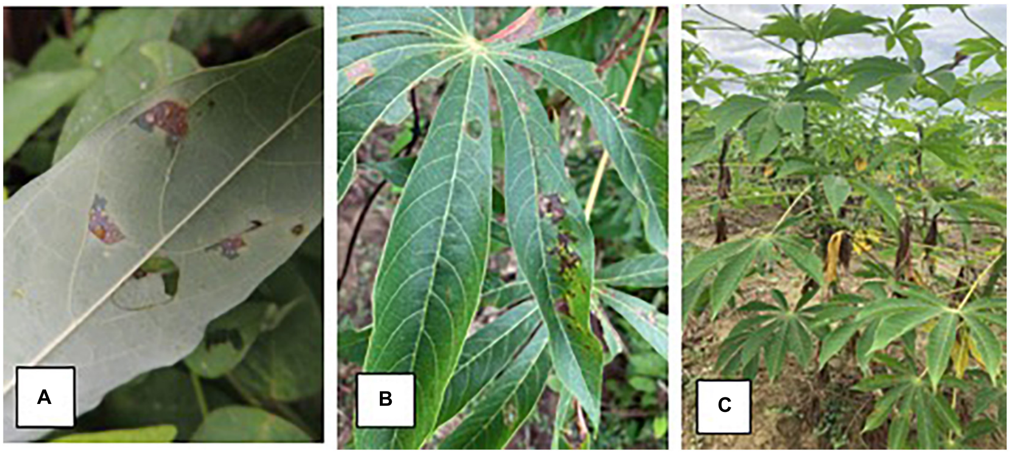

FIGURE 3 | Symptoms of Cassava Bacterial Blight in Villa López. **(A)** Angular leaf spot with water soaking on the leaf underside, **(B)** leaf blight symptom, and **(C)** wilting leaves on 7-month-old cassava.

TABLE 2 | Sum of Akaike weights of the models for each variable.

Variable	Variable importance	Interpretation
Fertilizer use	0.77	Fertilizer use increases the probability of occurrence of CBB
Land tenure	0.73	Farmers who rent their field are more prone to CBB infection than those who own their field
External donors	0.44	Weak effect. Farmers requesting cuttings from farmers outside the village seem to have more CBB than those receiving cuttings from other farmers living within Villa López
Origin of planting material	0.30	Very weak effect
Cassava diversity	0.29	Very weak effect
Sampling date	0.23	Very weak effect

The last column indicates in which way the important variables affect the occurrence of CBB.

3/12 fields infected; odds-ratio = 4; **Figure 4**). Among all fields, commercial fertilizers were applied in 18 (45%). Fertilized fields showed a higher prevalence of CBB than unfertilized fields (respectively, 11/18 and 8/22 fields infected; odds-ratio = 2.75; **Figure 4**).

To try to find variables explaining for the occurrence of *Xpm* in fields, we evaluated 64 linear models, including or excluding each of the six explanatory variables. No model showed a strong superiority in explaining *Xpm* occurrence; however, over all models, fertilizer use and land tenure were the variables showing the greatest importance (**Table 2**).

LRT tests indeed confirmed that both these variables added explanatory power to the best model ($P < 0.05$ for both). The proportion of external donors and the origin of the planting material showed lower importance (i.e., these variables only contributed to models that sum an Akaike weight of < 50%). They were included in the second-best model, with LRT tests returning *P*-values just below 0.05 (0.047 and 0.048). These two variables may play a role in CBB occurrence, but our dataset seems too small to confirm this. The other most relevant models (*i.e.,* those within two AICc points of the best model) are listed in **Supplementary Figure 2** and **Supplementary Table 1** illustrates the Akaike weights of each of the 64 possible models and the variables included for each of them. Neither the diversity of cassava (measured by the number of planted varieties), nor the sampling date (before or after the harvest) significantly impacted CBB occurrence: these variables showed low importance and did not appear in the few most likely models.

Figure 5 shows the spatial distribution of infected fields as a function of land tenure. Indeed, 16 out of the 19 identified infected fields were rented parcels.

DISCUSSION

Farmers' Perception of Cassava Bacterial Blight

All farmers declared knowing CBB and name it *quema*, which means *burn* and is reminiscent of some leaf wilting symptoms observed at late stages. However, considering that cassava is subjected to various abiotic and biotic stresses, most of which occur in Latin America, the identification of CBB is not straightforward, since different stresses may lead to similar symptoms. In addition, CBB symptoms may vary according to the susceptibility of the host and the time of infection (Álvarez and Llano, 2002).

In 2016, the harvest in this village started in October, approximately at the same time when CBB symptoms appeared in the infected plants. We observed no significant effect of collection time (before or after harvest) on the occurrence of CBB. The symptoms were weak at all times (October through November), suggesting that the yield may not have been strongly impacted by CBB this particular year. According to Lozano (1986), CBB

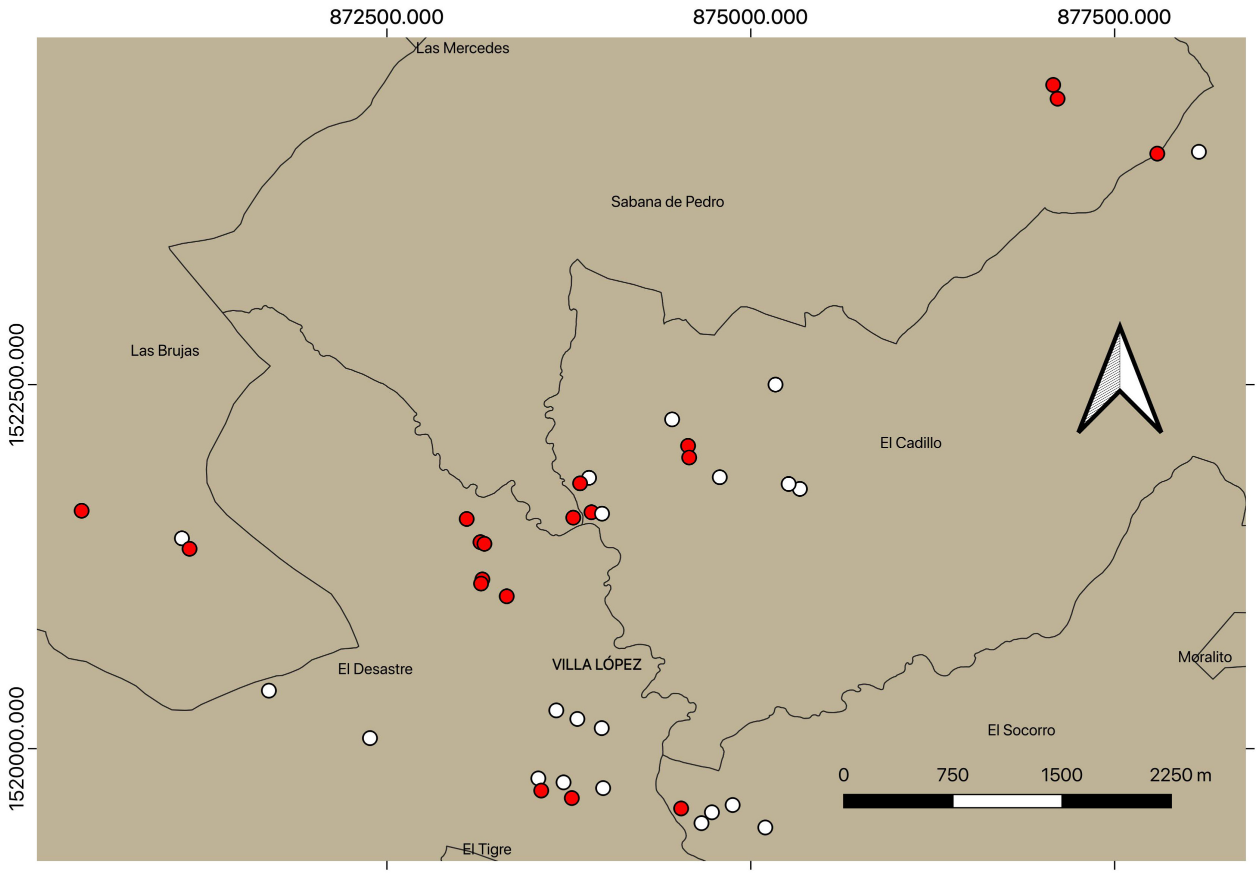

FIGURE 4 | Distribution map of the 40 cassava fields sampled in Villa López and infected by Cassava Bacterial Blight. Fields infected with CBB are depicted in red (n = 19), and uninfected fields appear in white (n = 21). WGS 84.

can be responsible for the loss of up to 80% of the yield in wet years in tropical countries. However, the few years preceding our sampling were particularly dry years in the Caribbean region (IDEAM, 2020), and this may have led to a reduced impact of the disease. In addition, it should be noted that the most frequently cultivated varieties in Villa López, namely *venezolana* and *chirosa*, have a short cultivation cycle (six months), which gives little time for the bacteria to develop.

The Fields of Land Renters Are More Likely to Be Infected by *Xanthomonas phaseoli* pv. *manihotis*

National statistics about land use in the department of Sucre show that most rural areas are dedicated to extensive livestock production, progressively replacing food crops at the local scale (Departamento Nacional de Estadística [DANE], 2017). Because of competition with land for grazing, land for cultivation is scarce, and local farmers are constrained to work in small areas (about one hectare). Those who do not own land have to rent small fields, where they cultivate cassava for sale. In Villa López, cassava cultivated in fields owned by the farmer are less infected by CBB than in fields rented by the farmer (odds-ratio = 0.25).

When fields are rented over short periods, i.e., less than a year, farmers cannot conserve stem cuttings for the next cropping season. In consequence, they must optimize planting with the material available at the local cuttings market, either with farmers from Villa López or from neighboring villages; they do not have the option to control for the disease when choosing cuttings. Inadequate control and management of the propagative material before planting seems a key factor for CBB propagation (Mansfield et al., 2012). However, in the Villa López informal propagule network, control of propagule quality would be difficult to achieve without diagnostic tools, because plants may host the pathogen asymptomatically until the beginning of the rainy season (Wydra and Verdier, 2002). Thus, it is necessary to carry out control practices in each cassava cultivation stage to avoid spread of the pathogen. Crop rotation could be employed as a strategy to avoid the permanence of the pathogen in the crop's environment.

Fertilizer Use Increases the Probability of Occurrence of Cassava Bacterial Blight

Fertilizers used by Villa López farmers can supplement soil nutrition, but may also increase plant susceptibility to disease (Long et al., 2000; Veresogloua et al., 2013). Our data show

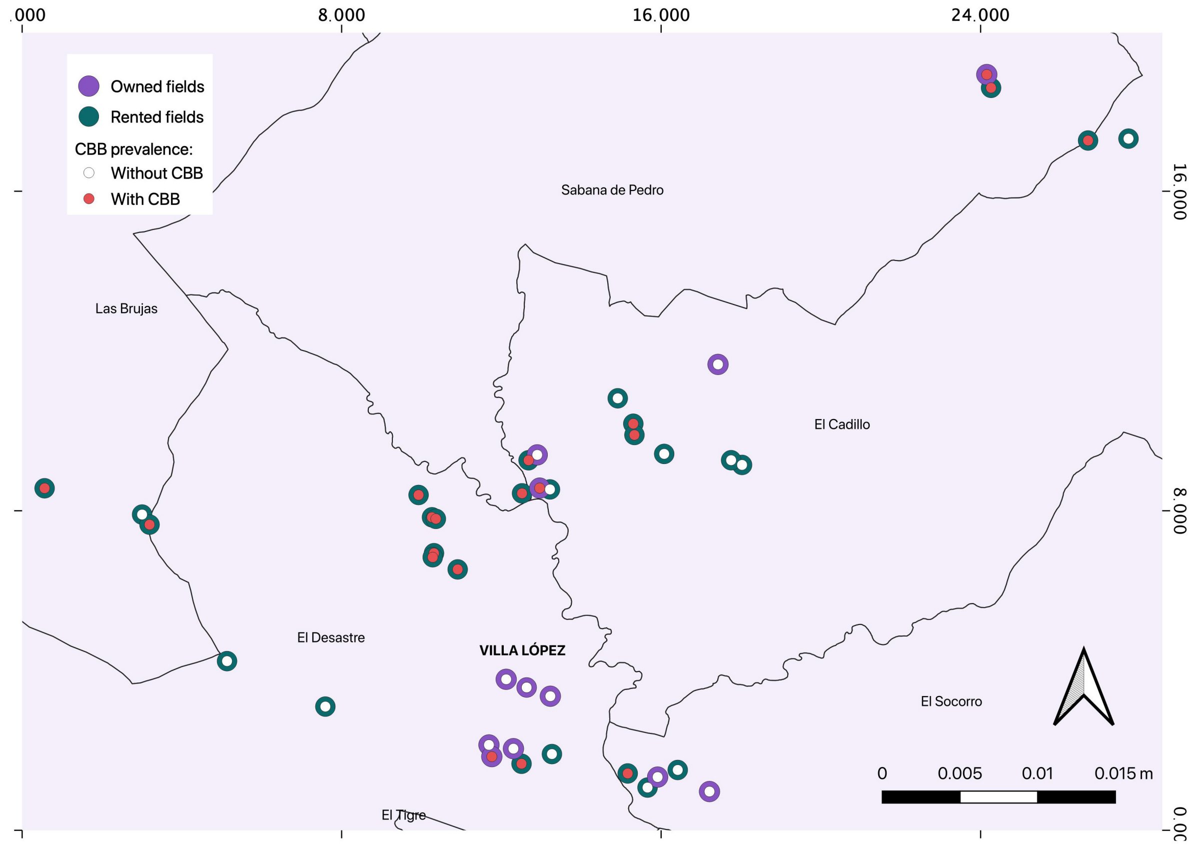

FIGURE 5 | Map of the distribution of Cassava Bacterial Blight occurrence as a function of land tenure. WGS 84.

that the application of fertilizers significantly increased the probability of CBB occurrence (odds-ratio = 2.75; see **Table 2**). Fertilizers for instance increase the production of young cassava tissues, which are highly susceptible to CBB (Lozano, 1986). These young shoots can be quickly infected during the rainy season while natural infection is limited on mature tissues. In addition, for some plant-pathogen combinations, it has been shown that increased nitrogen supply can increase disease susceptibility (Dordas, 2008). Nitrogen fertilization has been shown to either increase or decrease susceptibility to various diseases in different agrosystems; the response notably depends on the form and amount of nitrogen applied (Mur et al., 2017; Sun et al., 2020). For example, nitrogen can impact some resistance genes in rice, resulting in higher susceptibility to fungal blast disease (Ballini et al., 2013). Effects of nitrogen fertilization have not been studied for CBB. However, the effect of nutrients may vary depending on the environment and on deficiencies or toxicities of some elements (Dordas, 2008).

Influence of Other Agricultural Practices on Cassava Bacterial Blight Occurrence

The cultivation of cassava remains a traditional activity for the inhabitants of Villa López. Methods for cassava production have been adapted to respond to the demands of commercialization in nearby rapidly growing cities such as Sincelejo and Cartagena. However, despite market pressures favoring an intensive agriculture, traditional family farming practices are still preserved, because cassava is also cultivated as a staple crop. Therefore, farmers cultivate following natural rain and drought cycles to optimize water use, they plant and harvest according to the moon cycles, and cultivate associated crops to provide household food needs. Intercropping may reduce CBB intensity in Villa López since it can act as a physical barrier and limit the dispersal of the bacterial pathogen within the field by rain and wind (Wydra and Verdier, 2002; Zinsou et al., 2004), but we were unable to test this here.

Another benefit of polycultures in cassava crops is the control of weeds owing to agroecological competition dynamics (Weerarathne et al., 2017). The establishment of polycultures probably plays a major role in controlling the proliferation of weeds in Villa López, and this, in addition to the increasing costs of agrochemicals, may explain the low use of herbicides in the village's fields. Spread of weeds decreases yields directly. By creating microclimates that favor the development of diseases and the proliferation of possible vectors, weeds can also increase the risk of dispersal of diseases and pests (Zandjanakou-Tachin et al., 2007; Uzokwe et al., 2016). For this reason, weed control is determinant in avoiding spread of bacterial blights (Sikirou and Wydra, 2008).

Furthermore, over the growing season, cassava can be impacted by a multitude of pests and/or diseases. The large majority of farmers used insecticides to control them, including as a preventive measure against CBB, even though the literature says there is no effective chemical treatment for it (Trujillo et al., 2014). Some reports indicate that copper-based treatments can be successful in managing bacterial diseases (Sundin et al., 2016). However, as farmers plant cassava at the beginning of the rainy season, the efficiency of such treatment is likely to be diminished due to leaching of cooper. Following strategies suggested by local institutions (Álvarez and Llano, 2002), about half of the farmers in Villa López applied copper oxychloride on stem cuttings before planting, to protect them from penetration of pathogens and rotting agents during growth. However, this superficial treatment of stem cuttings cannot kill bacteria located in the vascular tissues, and thus has little effect on limiting CBB occurrence.

CONCLUSION

Cassava has been the main livelihood and source of income for the inhabitants of Villa López for at least four generations. Although according to farmers' perceptions, CBB is the main disease affecting crops in the locality—especially because there is no effective control method—yields were not impacted during the year of our study because the rainy season came close to harvest and the disease appeared at a time when the root was already of marketable size.

Inadequate management and control of stem cuttings seems to be a determining factor for the spread of CBB, and this could be related to land tenure problems, since farmers must plant in rented locations and continually move to new fields, limiting crop rotation and the monitoring of phytosanitary problems of previous cycles. These circumstances promote the circulation of cuttings infected by the pathogen but showing no symptoms permitting its detection.

In addition, we observed a strong correlation between the application of commercial agrochemicals, essentially NPK fertilizers, and the occurrence of the disease in Villa López. Experimental studies are needed to confirm the impact of application of these products on the spread of CBB.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary Material**.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Universidad de los Andes. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

DP, AD, and SC conducted the field work. CV and BS conducted the lab work. AD and DP performed all the statistical analysis. All authors wrote the first draft of the manuscript, and contributed to subsequent versions and revisions.

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SUPPLEMENTARY MATERIAL

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REFERENCES

Agronet (2020). *Estadística del Cultivo de la Yuca. Evaluaciones Agropecuarias Municipales.* Available online at: https://www.agronet.gov.co/estadistica/Paginas/home.aspx?cod=4 (accessed October 15, 2021).

Aguilera-Díaz, M. (2012). *La yuca en el Caribe colombiano: Del cultivo ancestral a agroindustrial. Documentos de Trabajo Sobre Economía Regional y Urbana*. Bogotá: Banco de la República.

Álvarez, E., and Llano, G. (2002). "Enfermedades del cultivo de la yuca y métodos de control," in *La yuca en el Tercer Milenio: Sistemas Modernos de Producción, Procesamiento, Utilización y Comercialización*, eds B. Ospina and H. Ceballos (Cali: CIAT), 131–147.

Ballini, E., Nguyen, T. T., and Morel, J. B. (2013). Diversity and genetics of nitrogen-induced susceptibility to the blast fungus in rice and wheat. *Rice* 6:32.

Bartoń, K. (2019). *MuMIn: Multi-Model Inference. R package version 1.43.6*. Available online at: https://cran.r-project.org/web/packages/MuMIn/index.html (accessed September 20, 2019).

Bernal-Galeano, V., Ochoa, J. C., Trujillo, C., Rache, L., Bernal, A., and López, C. (2018). Development of a multiplex nested PCR method for detection of *Xanthomonas axonopodis* pv. *manihotis* in cassava. *Trop. Plant Pathol.* 43, 341–350. doi: 10.1007/s40858-018-0214-4

Boher, B., and Verdier, V. (1994). Cassava bacterial blight in Africa: the state of knowledge and implications for designing control strategies. *African Crop Sci. J.* 2, 505–509.

Burnham, K. P., and Anderson, D. R. (2002). *Model Selection and Multimodel Inference*, 2nd Edn. Berlin: Springer.

Burns, A., Gleadow, R., Cliff, J., Zacarias, A., and Cavagnaro, T. (2010). Cassava: the drought, war and famine crop in a changing world. *Sustainability* 2, 3572–3607. doi: 10.3390/su2113572

Center for Agriculture and Bioscience International [CABI] (2021). *Invasive Species Compendium [dataset]*. Available online at: https://www.cabi.org/isc/datasheet/56952 (accessed 15 Dec, 2021).

Chakraborty, S., and Newton, A. C. (2011). Climate change, plant diseases and food security: an overview. *Plant Pathol.* 60, 2–14. doi: 10.1111/j.1365-3059.2010.02411.x

Departamento Nacional de Estadística [DANE] (2017). *Tercer Censo Nacional Agropecuario*. Available online at: https://geoportal.dane.gov.co/geocna/index.html# (accessed May 16, 2019).

Daryanto, S., Wang, L., and Jacinthe, P. A. (2017). Global synthesis of drought effects on cereal, legume, tuber and root crops production: a review. *Agric. Water Manage.* 179, 18–33. doi: 10.1016/j.agwat.2016.04.022

Deutsch, C. A., Tewksbury, J. J., Tigchelaar, M., Battisti, D. S., Merrill, S. C., Huey, R. B., et al. (2018). Increase in crop losses to insect pests in a warming climate. *Science* 361, 916–919. doi: 10.1126/science.aat3466

Dordas, C. (2008). Role of nutrients in controlling plant diseases in sustainable agriculture. a review. *Agron. Sustain. Dev.* 28, 33–46. doi: 10.1051/agro:2007051

El-Sharkawy, M. A. (2014). Global warming: causes and impacts on agroecosystems productivity and food security with emphasis on cassava comparative advantage in the tropics/subtropics. *Photosynthetica* 52, 161–178. doi: 10.1007/s11099-014-0028-7

FAOSTAT (2019). *Food and agriculture data, Food and Agriculture Organization of the United Nations (FAO)*. Available online at: http://www.fao.org/faostat/en/#data/QC/metadata (accessed 13 May, 2019).

Jarvis, A., Ramirez-Villegas, J., Herrera-Campo, B. V., and Navarro-Racines, C. (2012). Is cassava the answer to African climate change adaptation? *Trop. Plant Biol.* 5, 9–29. doi: 10.1007/s12042-012-9096-7

Lebot, V. (2009). *Tropical Root and Tuber Crops: Cassava, Sweet Potatoes, Yams and Aroids*. Wallingford: CABI.

Long, D. H., Lee, F. N., and TeBeest, D. O. (2000). Effect of nitrogen fertilization on disease progress of rice blast on susceptible and resistant cultivars. *Plant Dis.* 84, 403–409. doi: 10.1094/PDIS.2000.84.4.403

Lozano, J. C. (1986). Cassava bacterial blight: a manageable disease. *Plant Dis.* 70, 1089–1093. doi: 10.1094/PD-70-1089

Lozano, J. C., and Sequeira, L. (1974). Bacterial blight of cassava in Colombia: II: epidemiology. *Phytopathology* 64, 83–88. doi: 10.1094/phyto-64-83

Mansfield, J., Genin, S., Magori, S., Citovsky, V., Sriariyanum, M., Ronald, P., et al. (2012). Top 10 plant pathogenic bacteria in molecular plant pathology. *Mol. Plant Pathol.* 13, 614–629. doi: 10.1111/j.1364-3703.2012.00804.x

Mur, L., Simpson, C., Kumari, A., Gupta, A. K., and Gupta, K. J. (2017). Moving nitrogen to the centre of plant defence against pathogens. *Ann. Bot.* 119, 703–709. doi: 10.1093/aob/mcw179

Restrepo, S., Velez, C. M., Duque, M. C., and Verdier, V. (2004). Genetic structure and population dynamics of *Xanthomonas axonopodis* pv. *manihotis* in Colombia from 1995 to 1999. *Appl. Environ. Microbiol.* 70, 255–261. doi: 10.1128/AEM.70.1.255-261.2004

Restrepo, S., Vélez, C. M., and Verdier, V. (2000). Measuring the genetic diversity of *Xanthomonas axonopodis* pv. *manihotis* within different fields in Colombia. *Phytopathology* 90, 683–690. doi: 10.1094/PHYTO.2000.90.7.683

Restrepo, S., and Verdier, V. (1997). Geographical differentiation of the population of *Xanthomonas axonopodis* pv. *manihotis* in Colombia. *Appl. Environ. Microbiol.* 63, 4427–4434. doi: 10.1128/AEM.64.3.1166a-1166a.1998

Savary, S., Willocquet, L., Pethybridge, S. J., Esker, P., McRoberts, N., and Nelson, A. (2019). The global burden of pathogens and pests on major food crops. *Nat. Ecol. Evol.* 3, 430–439. doi: 10.1038/s41559-018-0793-y

Sikirou, R., and Wydra, K. (2008). Effect of intercropping cowpea with maize or cassava on cowpea bacterial blight and yield. *J. Plant Dis. Prot.* 115, 145–151. doi: 10.1007/BF03356262

Strange, R. N., and Scott, P. R. (2005). Plant disease: a threat to global food security. *Annu. Rev. Phytopathol.* 43, 83–116. doi: 10.1146/annurev.phyto.43.113004.133839

Sun, Y., Wang, M., Mur, L. A. J., Shen, Q., and Guo, S. (2020). Unravelling the roles of nitrogen nutrition in plant disease defences. *Int. J. Mol. Sci.* 21:572. doi: 10.3390/ijms21020572

Sundin, G. W., Castiblanco, L. F., Yuan, X., Zeng, Q., and Yang, C. H. (2016). Bacterial disease management: challenges, experience, innovation and future prospects. *Mol. Plant Pathol.* 17, 1506–1518. doi: 10.1111/mpp.12436

Trujillo, C. A., Ochoa, J. C., Mideros, M. F., Restrepo, S., López, C., and Bernal, A. (2014). A complex population structure of the cassava pathogen *Xanthomonas axonopodis* pv. *manihotis* in recent years in the Caribbean region of Colombia. *Microb. Ecol.* 68, 155–167. doi: 10.1007/s00248-014-0411-8

Uzokwe, V., Mlay, D. P., Masunga, H. R., Kanju, E., Odeh, I. O. A., and Onyeka, J. (2016). Combating viral mosaic disease of cassava in the Lake Zone of Tanzania by intercropping with legumes. *Crop Prot.* 84, 69–80. doi: 10.1016/j.cropro.2016.02.013

Veresogloua, S. D., Bartoab, E. K., Menexescand, G. M., and Rillig, C. (2013). Fertilization affects severity of disease caused by fungal plant pathogens. *Plant Pathol.* 62, 961–969. doi: 10.1111/ppa.12014

Weerarathne, L. V. Y., Marambe, B., and Chauhan, B. S. (2017). Does intercropping play a role in alleviating weeds in cassava as a non-chemical tool of weed management? – A review. *Crop Prot.* 95, 81–88. doi: 10.1016/j.cropro.2016.08.028

Wydra, K., and Verdier, V. (2002). Occurrence of cassava diseases in relation to environmental, agronomic and plant characteristics. *Agric. Ecosyst. Environ.* 93, 211–226. doi: 10.1016/S0167-8809(01)00349-8

Zandjanakou-Tachin, M., Fanou, A., Le Gall, P., and Wydra, K. (2007). Detection, survival and transmission of *Xanthomonas axonopodis* pv. *manihotis* and *X. axonopodis* pv. *vignicola*, causal agents of cassava and cowpea bacterial blight, respectively, in/by Insect Vectors. *Phytopathology* 155, 159–169. doi: 10.1111/j.1439-0434.2007.01210.x

Zárate-Chaves, C. A., Gómez de la Cruz, D., Verdier, V., López, C. E., Bernal, A., and Szurek, B. (2021). Cassava diseases caused by *Xanthomonas phaseoli* pv. *manihotis* and *Xanthomonas cassavae*. *Mol. Plant Pathol.* 22, 1520–1537. doi: 10.1111/mpp.13094

Zinsou, V., Wydra, K., Ahohuendo, B., and Hau, B. (2004). Effect of soil amendments, intercropping and planting time in combination on the severity of cassava bacterial blight and yield in two ecozones of West Africa. *Plant Pathol.* 53, 585–595. doi: 10.1111/j.0032-0862.2004.01056.x

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Customary Rights and Freshwater Ecology in Pluralistic Societies on the Monsoonal Island of Sumba (Eastern Indonesia)

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This article evaluates the ways water is made and unmade on Sumba Island when subjected to tensions between Indigenous and off-island political ecologies. Located in the eastern Indian Ocean, Sumba has a semi-arid, monsoonal climate with an uplifted coral reef geological structure where a spatially and temporally dynamic hydrological system shapes people's access to freshwater. Customary adat societies on the island have histories of struggling to maintain the integrity of their own political ecologies, further increasing the precarity of their access to freshwater. The topic of the research reported on in this paper was determined through collaboration with members of the Kodi community in western Sumba who urged the author to study the problem of water. This article highlights ongoing threats to the further degradation of local societies' rights to control their customary territories and freshwater within them by summarizing the phenomena of water grabbing in Indonesia. Zooming in on three projects that manifest as water grabs, this article finds, respectively, that water grabbing occurs under the guise of forest protection and production, behind the veil of philanthropy, and for economic development with military backing. In all three cases, water grabs take place in the context of a decentralizing nation-state where the ways adat is understood and the ways laws regarding it have been interpreted and enacted have changed through time and have varied between communities, partly in relation to the societies' proximity to centers of colonial and postcolonial power as well as the development of activities in their territories. On Sumba the content of adat and relationships among distinct adat societies evolves on a bioculturally diverse island that is home to numerous Indigenous ethnolinguistic communities. Consequently, people's responses to interventions into their political ecologies vary. More broadly, the context for this study is the intersections of water grabbing and social change during the Reformasi, the post-Suharto era of decentralization in Indonesia.

Keywords: freshwater ecology, water grabbing, adat (customary practices), traditional ecological knowledge, Sumba, decentralization, political ecology

MAP 1 | Sumba island in the Indo-Australian monsoon zone.

INTRODUCTION: THE GOVERNANCE OF WATER IN PLURAL LEGAL CONTEXTS

Freshwater is made and remade through everyday practices and multiscale processes. Similarly, legitimate and illegitimate authority relative to freshwater are biosocially constructed by multiscale, complex, and sometimes problematic processes. Being socially constructed indicates that legitimacy in the governance, management, and use of freshwater is both collective and subjective. Within every social collective, the existence of multiple subjectivities creates variability in views about authority and power. In today's world, the governance of water is pluralistic at the global scale (Franco et al, 2013) and in the case of Indonesia, also at the national scale (von Benda-Beckmann, 2007). Scaling down, numerous governance regimes impact freshwater tenure and use in regional and local post/neocolonial settings such as on Sumba Island in the Indo-Australian monsoon zone. (**Map 1**) Interactions within a pluralistic context of water tenure, use, and management impact both the freshwater resources and the people who live closest to them.

Governance at all levels has changed radically in Indonesia since the end of the 20th century as the nation moved out of the 31-year-long (1967–1998) Suharto rulership to the post-Suharto *Reformasi* era (1999-now). As relationships between governmental and nongovernmental entities change, the landscape literally changes as well (cf. Prato, 2018). Encounters between customary governments, the Indonesian state, and international organizations create ecological and social ripple effects in freshwater reservoirs. Of particular interest in this paper are those freshwater sites where distinct types (i.e., regimes) of legitimacy intersect. These specific freshwater reservoirs and creeks are medleys of ideas about and practices related to legitimacy in the governance, management, tenure, and use of water.

One transformation in the governance of freshwater resources that has accompanied Indonesia's 23-year long transition from the New Order guided democracy to the Reformasi presidential republic has been an increase in water grabbing through the transfer of ownership and use rights from *adat*[1] customary communities to more powerful persons or entities who are not the multigenerational owners. Thus, whilst governance and tenure[2] related to water have been transforming, the role and status of adat has also been changing.

Adat is a topic of national-level conversation in Indonesia. In discussions about biodiversity and conservation, the

[1]The term "adat" refers to many aspects of Indonesia's "customary" societies including governance, laws, and tenure as well as economics and exchange, internal political organization, intra- and inter-group relations, conflict resolution, ethnoecologies, religion, rituals, ethics, rules, norms, and more. "Customary" in the context of discussion about adat refers to "locally rooted systems. . .devised through time in response to local conditions" (Bettinger et al., 2014, page 200). The ways adat is understood as well as the ways it has operated and changed through time have varied between communities, partly in relation to the societies' proximity to centers of colonial and postcolonial power as well as the development of activities in their territories. The history of adat for Meratus Dayaks (Tsing, 2004), for example, differs from its trajectory in Togean Sama communities (Lowe, 2007). The diversity of adat appears in the social context and changes in it on Sumatra (Fisher et al., 2017), which differ from the multiple adat communities on Seram (Ellen, 2017) and Sumba (Fowler, 2013) and the ways they have changed over time.

[2]Tenure here is understood as the social relations and practices associated with access to and use of resources. Tenure often includes combinations of collective and individual rights that people acquire by way of belonging to kin groups and alliance networks, the latter of which cohere through marriage and exchange practices. For adat communities on Sumba, similar to many other Indonesian adat communities, tenure regulations and practices often include combinations of collective and individual rights that people acquire by way of belonging to kin groups and alliance networks, the latter of which cohere through marriage and exchange practices. Many of Sumba's adat tenure systems are unwritten and verbally transmitted and negotiated.

environment and the economy, development and sustainability, culture and history, and other poignant issues, adat is politicized. The ways this politicization of adat occurs has shifted from an early start in the Dutch colonial period through the Reformasi era. In pre-colonial times, adat was the default—the given, widespread social system. In the colonial period, Dutch colonizers sanctioned customary social systems because they viewed them as conduits through which they could exert their own control over the widely dispersed Indigenous communities living in their East Indies colony (Li, 2001). During the New Order and early Reformasi eras, adat was displaced and invisibilized, but then subsequently revitalized and legitimized (Henley and Davidson, 2008). In the second decade of the twenty-first century, adat has become the subject of advocacy and honor (Bettinger et al., 2014). Now, adat is not only being promoted but also sometimes romanticized by conservationists, developers, aid agencies, scholars, activists, and journalists, in the 21st century.

Why Water Security is a Priority of Scholarship

The critical work of adat activists on Sumba directly involves customary communities' rights related to water and many additional crosscutting elements as we can see in cases from North Kodi, Nihiwatu, and Marosi discussed in this paper. Vel and Makambombu (2019) recommend defending Indigenous Peoples against the appropriation of their resources and advocating for the repatriation of their customary territories (Vel and Makambombu, 2019). I suggest that scholars stand with Indigenous Peoples and take cues from them and their activism in order to recognize which issues are most important points of advocacy in their specific communities.

Water grabbing involves the appropriation by outsiders of Indigenous People's water and land (Rulli, Saviori, D'Ordorico, 2013). Water grabbing potentially restricts local people's access to freshwater and coastal resources and thus threatens water security, particularly in environments where freshwater is already limited, such as in Sumba's semi-arid and arid climate. Moreover, the ways water is managed after it has been grabbed on Sumba and elsewhere has resulted in its overharvesting and pollution (Vel and Makambombu, 2019). Water grabbing frequently is associated with land grabbing (de Bont et al., 2016; Rulli, Saviori, D'Ordorico, 2013) and is an intended or unintended consequence of land grabbing. Land grabbing often leads to both water and food insecurity (Rulli, Saviori, D'Ordorico, 2013; Vel and Makambombu, 2019), especially for subsistence farmers, fishers, and agropastoralists—as most Sumbanese are.

Water grabbing often includes human rights violations when it deprives people of water for bathing and sanitation and the means of producing and processing food. Access to clean water and sanitation are recognized as human rights since the United Nations General Assembly, who governs water-related rights at the global level, and the UN Human Rights Council formalized this in 2010. In addition, the UN has ratified several water treaties among member nations, including the UN Watercourses Convention of 2014, Convention on the Law of the Non-Navigational Uses of International Watercourses, and the Protocol on Water and Health of 1999. Indonesia is not a signatory on any of these three treaties.

The magnitude of water grabbing is tremendous in Indonesia. Indonesia is the country with the highest amount of grabbed rainwater (also known as green water) in the world at 117.40 billion m^3 (Rulli, Saviori, D'Ordorico, 2013). Another 1.19 billion m^3 of irrigation water (also known as blue water[3]) is grabbed in Indonesia. The total amount of grabbed rainwater and irrigation water (118.59 billion m^3) accounts for 39% of the total amount of rainwater (292.35 billion m^3) and irrigation water (11.94 billion m^3) used for food production in Indonesia, which is 304.29 billion m^3.

Within this troubling context, Sumba is in a monsoonal climate where access to water is limited and variable across specific sites depending on micro-level social and ecological conditions. Since water is always entangled in political ecologies that may be transitory, its availability for multispecies' survival is increasingly precarious. Amidst the many entangled political ecological processes that affect freshwater on Sumba is water grabbing, which is the transfer of ownership and use rights (or *de facto* use rights) from Indigenous communities to more powerful persons or entities who are not the customary owners. For many people living on Sumba, water grabbing has the potential to further reduce access to freshwater as well as the quality of existing resources. The already insecure situation with freshwater is being aggravated by water grabbing.

The availability and quality of freshwater in any particular village or region of Sumba, while extremely variable across space and through time due to the island's hydrology and geology as well as weather and climate, limits the wellbeing of the island's residents. Major drainages are dispersed, some are small in size, and some have seasonal flows. Freshwater lakes in western Sumba are scarce and mostly occur in the island's interior with only a few outliers on the northern and southern coastal plains. Some of the lakes in western Sumba are saltwater rather than freshwater.

The types of naturally-occurring sites where Sumba's residents collect freshwater include springs, creeks, small ponds, and micro-reservoirs such as banana plant trunks and tree cavities. People also capture water using rainwater collection systems, dammed streams, cement pools, and wells. Water can be purchased from tanker trucks, but many Sumbanese rely on naturally occurring sources of water. For those who do not live adjacent to a source or purchase their water, accessing water requires walking distances from their homes that vary from less than a kilometer up to 20 km roundtrip.

[3]Anthropologists writing about Sumba define *kabisu* as an exogamous patrilineal clan associated with a particular *tana* (territory) (Onvlee, 1980).

In Nusa Tenggara Timur Province (NTT) where Sumba is situated, 56% of households have to travel more than 1 km to access clean water and 33% of households lack access to clean drinking water altogether. NTT ranks 32nd out of 33 provinces in Indonesia on the Human Development Index, which is the next to worst. Twenty-three percent of NTT Province's residents are impoverished. The western sector of Sumba Island has the highest rate of water insecurity in NTT with more than 40% of households lacking sufficient clean drinking water (Ashmad et al., 2012). South West Sumba District is the second poorest district in NTT. This high degree of poverty is linked to access to clean water, which in turn is a proximal determinant of human health and overall wellbeing (Reading and Wien, 2009) as evident in a study village in South West Sumba where 95% of residents ages 2 months to 80 years suffer from intestinal parasitic infections due to unclean water and lack of sanitary facilities (Sungkar et al., 2015).

Water for Forests in North Kodi

Since the Indonesian government claims ownership of sizeable portions of South West Sumba District, they simultaneously exert dominion over freshwater sources. Water is variably figured in state claims—sometimes as the primary target, other times as a secondary or tertiary object, as an incidental component, or an altogether unmentioned element. As we can see by looking further into the management of state-owned units in the North Kodi Subdistrict, the Indonesian government recognizes (or does not recognize) the freshwater dimension to their operations in South West Sumba in assorted ways. One project in which the state exerts control was inventorying national forests to prepare for reforestation of the landscape. Another space within which the national government exerts control over adat territories is the Rokoraka Forest, which is also known as the Southwest Sumba Protection Forest Management Unit.

The West Sumba District Forestry and Soil Conservation Service (Dinas Perhutanan dan Konservasi Tanah, DPKT) demarcated and categorized the lands in Kodi[4] as part of a regreening/reforestation plan for 1998–1999. The DPKT plan has two layers (*Peta Rencana Penyebaran Kegiatan Penghijauan Tahun Anggaran 1998–1999*). One of the layers partitions North Kodi's lands into Critical Forest (*Hutan Kritis*, K) and Non-Critical Forest (*Hutan Tidak Kritis*, TK). The second layer divides lands into Permanent Production Forest (*Hutan Produksi Tetap*, HP), Limited Production Forest (*Hutan Produksi Terbatas*, HT), and Protection Forest (*Hutan Lindung*, HL). Protection Forests are treed areas maintained for the purposes of water management, flood control, prevention of seawater intrusion, and soil conservation (Head of KPHL for the South West Sumba District, 2015). Permanent Production Forests are timber plantations. Limited Production Forests are managed for multiple goals including timber production but also protection and conservation. The Indonesian Government claims ownership of all of these designated forests.

The forests whose boundaries had already been demarcated (*kawasan hutan yang sudah ditata batasnya*) by 1998 cover a large portion of the area that is now called the North Kodi Subdistrict. This demarcated land in North Kodi includes Critical Forest (K) and Non-Critical Forest (TK) as well as Production Forest (HP). The Critical Forest areas are typified as being covered by the invasive *Imperata cylindrica* grass and affected by erosion. These areas are targeted for soil conservation and reforestation. Additional Non-Critical Forests were outlined for future demarcation in North Kodi. Additional Critical Forests in North Kodi, especially along the coastal margins were not slated for demarcation. This particular way of mapping Sumba performed by the Forestry and Soil Conservation Service was driven by the national government's Basic Long-Term Development Plans (*Pola Dasar Pembangunan Jangka Panjang*), with its first iteration from 1968 to 1993 and its second iteration from 1994 to 2019.

Notable is the absence of Protected Forest and Limited Production Forest in the North Kodi Subdistrict in the 1998–1999 management plan, which was put together at the end of the New Order. A decade-and-a-half into the Reformasi, the 20,646.64-hectare South West Sumba Protection Forest Management Unit (KPHL) was established through a series of decrees from the Indonesian Ministry of Forestry and Plantations (Decree Number 3911 of 2014), the South West Sumba District (a Regulation in 2014), and the Indonesian Ministry of the Environment and Forestry (Decree Number 633 of 2015). KPHL consists of 12,028.41 hectares (58%) of Protection Forest and 8,618.23 hectares (42%) of Permanent Production Forests (Head of KPHL for the Southwest Sumba District, 2015). Landcover in the KPHL is primary dry forests (55%), secondary dry forests (11%), shrublands (27%), savanna (3%), mixed rainfed gardens (2%), and vacant land (0.006%). KPHL crosses the boundaries of the North Kodi, South Wewewa, and East Wewewa Subdistricts within the South West Sumba District. A sector of the KPHL overlaps with a portion of the area of focus in my ethnographic research, that is Bukambero Village in the North Kodi Subdistrict. (My research area also extends into other Villages beyond Bukambero.) Portions of Bukambero Village are located within Rokoraka Matalumbu Forest, which is the name given to a group of forest patches in years prior when the Indonesian Ministry of the Environment and Forestry set up the land unit. Parts of

[4]An older system of mapping and naming the districts and sub-districts of Sumba existed in 1997–98. At that time, Sumba was divided into two Districts/Regencies: West Sumba District/Regency (Kabupaten Sumba Barat) and East Sumba District/Regency. Following the implementation of regional autonomy in 2001, the island was divided into four Districts/Regencies: Sumba Barat Daya (South West Sumba), Sumba Barat (West Sumba), Sumba Tengah (Central Sumba), and Sumba Timur (East Sumba). Redistricting also resulted in the division of the Kodi Sub-district (Kecamatan Kodi) into four subdistricts: Kodi Utara (North Kodi), Kodi Bangedo, Kodi Balaghar, and Kodi. Kodi Utara in South West Sumba, where the author has conducted ethnographic research, has a land area of 245.4 km^2 and a population of 53,345 people according to the 2015 census.

Bukambero Village are located within the Rokoraka's boundaries and part lie just outside of the borders.

The Ministry of the Environment and Forestry identifies customary forms of tenure as a "high threat" (KPHL, 2015, page 91) to the forest because, the KPHL managers write, tenure is based on heritage and also because communities' territories cross into the government's land. The KPHL managers call Bukambero's tenure system "kabisu."[4] Among the 3,626 residents of Bukambero in 2015, 98% are farmers. According to KPHL managers, Bukambero's people identify Wenamaya as the largest kinship group in Bukambero with Watupakadu, Umbu Tanda, and Umbu Tedda as the three subgroups within Wenamaya. Belonging to Wenamaya qualifies descendants to inherit land after they marry. The average landholding in Bukambero is 0.5–1 hectare, according to the KPHL managers, and they worry that economic needs will drive people to encroach upon the forest.

On the one hand, forest managers view tenure and encroachment as threats to the protection of their forest and the production of commodities. On the other hand, they see adat as an asset to forest protection and production. KPHL managers recommend supporting adat because of its "large role in the lives of the people of Bukambero Village [who] highly respect the role of adat institutions and Rato Marapu (i.e., the elders who govern the Indigenous religion)" (KPHL, 2015, page 41). Forest managers appreciate that adat causes people to avoid taboo places, refrain from degrading sacred places within the forest, conserve specific trees such as banyans, and not hunt special birds such as crows and owls. However, managers also worry about adat's limits when people are economically stressed and when traditional seasonal prohibitions on entering the forest and extracting its resources are not enforced. Managers are concerned about the inadequacies of customary forms of conflict resolution and the potential for conflict in the future if Bukambero's residents have differences of opinions among themselves or if they violate the government's regulations related to the state-owned forest. This line of reasoning positions the Indonesian government to take control of monitoring natural resources within the forest's boundaries: in order to avoid conflict or mediate it if and when it arises. It also justifies state agencies' efforts towards claiming the authority to make decisions: in order to regulate people's interactions with places and resources within forest boundaries. These moves are part of the process of water (and land) grabbing, which Franco, Mehta, and Veldwisch (Franco et al, 2013, page 1654) define as "the capturing of control not just of the water itself, but also of the power to decide how this will be used—by whom, when, for how long and for what purposes—in order to control the benefits of use."

While the 2015 management plan for KPHL lists numerous management goals, it clearly highlights the precarity of water resources when it states, "Protected Forests in this area are generally more intended as a buffer for water systems" (KPHL, 2015, page 8). Secondarily, the KPHL managers value the native flora and fauna in the designated area.[5] Additional management goals for the KPHL are to provide ecosystem services, improve community welfare, optimize the production of non-timber forest products, develop ecotourism, ensure forest protection and security, empower communities to protect the forest while they access non-timber forest products, promote other industries, partner with stakeholders, and protect and conserve forests (Head of KPHL for the Southwest Sumba District, 2015). With regard to water resources, forest managers recognize the important functions of the KPHL as a catchment for water emanating from springs and creeks and as a carbon capture site. Forest managers acknowledge the local residents who rely upon water within KPHL for their drinking needs as well as for agricultural activities. Forest managers matter-of-factly describe water scarcity for people living in the area by noting the total absence of constructed reservoirs and wells and by pointing to residents' three options for obtaining water: 1) walking about 3–4 km each way to reach natural springs, 2) capturing rain water, and 3) purchasing tank water (*air tangki*) for Rp200,000 (US$14.00) per 5,000 L. North Kodi offers a case of water grabbing that involves smaller and dispersed volumes of water that vary over time and space in comparison to the more commonly documented cases of water grabbing where powerful entities appropriate large volumes of water (Franco et al., 2013).

[5]The KPHL provides the following selective, shortened list of tree species in its Long Term Forest Management Plan (KPHL, 2015, page 20–21): "Cendana (*Santalum album*), usapi/kesambi (*Schleichera oleosa*), gaharu (*Aquilaria malaccensis*), Hue (*Eucalyptus alba*), Kabesak/Pilang (*Acacia leucophloeae*), Kleo/Laban (*Vitex pubescens*), Matani/Kayu Merah (*Pterocarpus indicus*), Kolaka/Besi (*Parinarium corimbosum*), Ampupu (*Eucalyptus urophylla*), Ajaob/Kasuari/Cemara (*Casuarina junghuhniana*), Kolo (*Erithrena littosperma*), Kelumpang (*Sterculia foetida*), Mbuhung (*Schoutenis ovata*), Munting/Bungur (*Langerstonia speciosa*), Kawak/Jabon (*Anthocepalu cadamba*), Kodal/Eboni (*Diospiros maritima*), Nera/Mindi (*Melia acederachta*), Worak/Kasai (*Pometia tomentosa*), Nunuh/Beringin (*Ficus benjamina*), Lontar(*Borasus flabilifer*); *Rhizophora mucronata*, *Rhizophora appiculata*, *Ceriops tagal*, *Xylocarpus granatum*, *Baringtonia speciosa*, *Avicenia amarin*, and *Bruguera gimnorhyza*."

Medicinal plants occurring in the KPHL include: "pulai (*Alstonia scholaris*); kunjur (*Cassia fistula*); nggai (*Timonius flavescens*); bila (*Clerodendrum speciosum*); hekul/genoak (*Acorus calamus*); guava (*Psidium guajava*); padamu dima (*Jatropha curcas*); mawona/marungga/moringa (*Moringa oleifera*); kuta kalara/sirih hutan (*Piper amboinensis*); winnu/winno (*Arecha pinnata*); tada linnu (*Dysoxylon arborescens*); nittu/hadana/sandalwood (*Santalum album* Linn. Kerr.); turmeric (*Curcuma domestica*); tai kabala (*Chromolaena odorata*); tada kaninggu (*Cinnamomum burmanii*); cat's whiskers (*Orthosiphon stamineus*); waru (*Hibiscus tiliacus*); kadabu/noni (*Morinda* sp.)" (Njurumana and Dwi Prasetyo 2010 cited in KPHL, 2015, page 21).

Gouramy (*Osphronemus gouramy*), swamp eel (*Monopterus albus*), and crayfish (*Cambarus virilis*) are three among many animals living in the creeks within the KPHL (KPHL, 2015, page 21).

Among the non-timber forest products harvested by people who live in and around the KPHL area are: fern fronds (*sayur paku*) from *Diplazium esculentum*, *Sternoclaena palustris*, and *Neprolepis bisserata*; wood ear mushrooms (*jamur kuping*, *Auricularia auricula*), and oyster mushrooms (*jamur payung/tiram*, *Pleurotus ostreatus*), mango (*Mango indica*), jackfruit (*Artocarpus integra*), coconut (*Cocos nucifera*), kesambi (*Schleichera oleosa*), *Eugenia* sp., ginger (*Zingiber* sp.), candlenut (*Aleurites moluccana*), and more (KPHL, 2015).

Forest managers also acknowledge the value of water in the KPHL and the surrounding region for industries and for ecotourism. Forest managers specifically point to Waibuku, Watu Maladong, and Tangung Bulir beaches as attractions in the adjacent Kodi Balaghar Subdistrict and Pabeti Lakira and Dikira waterfalls in East Wewewa Subdistrict. They also mention Weekuri Lake and Mandorak Beach—both of which are in the North Kodi Subdistrict but outside of the KPHL boundaries. KPHL's managers describe the steep cliffs of Mandorak Beach as "exotic" and its white sands as "beautiful." As proof of the potential for North Kodi's bodies of water to drive economic prosperity, KPHL's managers mention that "there is already one investor from France who develops ecotourism," referring to the developer of Mandorak Beach (KPHL, 2015, page 25). Romanticizing freshwater and saltwater resources and celebrating foreign investment encourages tourists to visit and foreigners to claim resources, which could potentially degrade water quality and increase water grabbing. By casting water in this way, KPHL's managers and others who engage in similar discursive practices signal a specific yet widespread morality in which "market value supersedes... cultural and social values" (Franco et al, 2013, page 1663). Elsewhere in the world, water grabbing has resulted from similar processes as Franco et al. (2013) point out for Mozambique when they write, "discourses and policies that favour foreign direct investment over investing in smallholder agriculture encourage local water grabbing processes."

Water (and Land) Grabbing in the Global and National Context

Water grabbing is a worldwide phenomenon that exhibits both global patterns and local specificities. While on Sumba water grabbing takes on its own situated character, it exhibits some of the patterns seen in water grabbing across societies and incidents (Mehta, Veldwisch, and Franco, 2012; Franco et al, 2013). One pattern is the link between water grabbing and land grabbing. A second pattern is that water grabbing is a form of structural violence occurring in the context of structurally inequitable systems, where immensely wealthy people's activities impact the lives of deeply impoverished people. Another pattern is that many water acquiring parties come from places where water resources are limited, exhausted, or impaired (von Braun and Meinzen-Dick, 2009). The water acquirers' places of origin are often in arid or desert regions or where pollution and overpopulation are problems causing parties to seek land and water outside of their borders. Perhaps, because of the patterns mentioned so far, this next pattern is inevitable: water grabbing is often contentious and produces conflict.

Indonesia is both a subject and object of water and land grabbing. As subject, Indonesian parties acquire large tracts in foreign countries. As object, foreign entities acquire land within Indonesia. These parties who acquire land are governments or state-owned entities, private persons or businesses, and also public and private entities in partnership with each other. The parties who acquire land internationally may be motivated by profiting from harvesting resources, such as minerals, oil, and timber, and also by producing agricultural and biofuel commodities to supplement insufficient production in home countries and to profit from trading in marketplaces. Pressures from within the acquirers' countries that influence international purchases are limited land and water supplies, population increases, food security and food crises, and increasing land and water values (von Braun and Meinzen-Dick, 2009). One problem with the acquirers' approach is that the communities who live in the places where land acquisitions are made often face challenges of their own related to water and food security, insufficient production, increasing populations, and changing valuations in addition to social and environmental changes.

In the larger land acquisitions of the 21st century, the land-acquiring agents in Indonesia include both domestic and foreign entities, or partnerships between these two types. Large scale acquisitions of waters and lands within the country of Indonesia are not uncommon. Agribusiness has been on the rise in Indonesia during the 21st century as the demand for globally traded commodities such as oil palm, sugar, and rubber has grown. By 2018, oil palms already covered 11 million hectares and another 20–30 million hectares were planned (Li, 2018). Most oil palms are planted as single-species stands in rural areas where subsistence farmers, fishers, pastoralists, hunters, and collectors live. The development of these oil palm plantations "takes away: customary land, resilient ecologies and diverse rural livelihoods" (Li, 2018, page 328).

Immense inequities are an inherent to the global social structures within which water and land grabs occur. The inequities between the local communities and the land acquirers are evident in the costs of land. Members of the Moi community were paid US $2.50/hectare when Henrison Inti Persada acquired 32,000 hectares of their land in Sorong District of West Papua. Henrison Inti Persada is a subsidiary of the Kayu Lapis Indonesia Group, a securities holding company. In 2010, the Hong Kong-based Noble Group Ltd., which manages supply chains for energy, metal, and mineral commodities, purchased a majority 51% share in Henrison Inti Persada. The Noble Group was listed on the Singapore Stock Exchange in 1997 and in Fortune 500 in 2000. In 2015, the company was valued at US $6 billion, but suffered financial collapse after accounting and debt fraud were revealed, which caused its value to drop to US $80 million. It was delisted from the Singapore Stock Exchange in 2018 and, since then, has been restructuring under the name Noble Group Holdings Ltd. The wealth gap between the Noble Group executives and the Moi community members is vast. Other transactions similarly represent the structure of global society, although the numbers vary widely. A case example is Nihi Sumba, a resort in which an American hotelier invested US $30 million in a district where 29% of the Indigenous People earn less than US $22.00 per month.

Water for Tourists Looking for Waves

"Behind every land grab is a water grab," according to the international nonprofit GRAIN (2012a). On Sumba, where land is the main target in some acquisitions and water in others, the inverse may also be true: behind every water grab is a land grab. Some land purchasers are motivated by the water itself, such as developers who work in the tourism industry. Saltwater and freshwater are both vulnerable in a tourism economy. Agents from the tourism industry seek to establish water-based tourist attractions on the seashore, in front of surf breaks, in sight of waterfalls, and on a saltwater lake. Water draws tourists who wish to recreate and sightsee on Indonesia's outer islands. The tourist industry also consumes water to supply the needs of visitors and to fuel its operations.

The most powerful, monied agents in Sumba's tourist economy who have executed water grabs on Sumba are not Indigenous to the island. Sumba is being promoted as "the next Bali" by proponents for the development of tourism on the island (e.g., McCall, 2015). Bali, in these promoters' materials, has been overrun by tourists and is suffering from the negative effects of its popularity in the form of polluted beaches in overcrowded resorts run by jaded locals. In these narratives, Sumba's "untouched beaches" (Travel and Leisure, 2020) and "magnificently preserved ancient cultures" (Nihi Sumba, 2020b under "Sumba Culture," no page number) promise to fulfill tourists' fantasies about exotic tropical islands and noble savages (Kahn, 2011). A highly lauded success story is Nihi Sumba. Located on a "protected white sandy beachfront" with "superlative waves" that "blend harmoniously with authentic local experiences" (Wonderful Indonesia, 2018), Nihi Sumba has won multiple awards, including Travel and Leisure's Best Hotel in the World for 2016 and 2017. Nihi Sumba attributes much of its success to its location landward of the world's best surf break and to the surrounding "unspoiled natural beauty, and pristine wilderness." This luxury resort appeals to high-end travelers with accommodations ranging from US $895/night for a one-bedroom villa to US $17,445/night for a five-bedroom compound. The entire 27-villa estate can be reserved for US $250,000 per night. In response to the coronavirus pandemic, guests can reserve the whole place for 1 month for US $1 million. This price includes an all-inclusive stay for up to 80 people as well as a 5% donation to The Sumba Foundation and a tour of the Foundation's project sites. Nihi Sumba is an aspirational model for many who wish to develop the tourism industry on Sumba.

The Australian couple Claude and Petra Graves built Nihi Sumba (then called Nihiwatu, which they translate as "Stone"). In 2012, Chris Burch, an American, and James McBride, a South African purchased the resort from the Graves. The original owners of Nihiwatu were "Sumba's ancestors, the 'Marapu,' [who] landed on its secluded beach centuries ago" according to Nihi Sumba's website (Nihi Sumba, 2020a under "About," no page number). On their "About" webpage, Nihi Sumba presents this line of ownership as seamless: the Indigenous People's ancestors were the first to land on the beach. The romantic Australian tourists were the first to have legal title to it.[6] The heroic American and South African hoteliers unproblematically acquired it. Another, different version of the Nihi Sumba story is of its conversion from a historically significant site belonging to the area's customary community to one grabbed and settled (i.e., colonized) by foreigners.

Nihi Sumba has its critics among locals and foreigners. The anthropologists Janet Hoskins (2002), Vel (2008) write about the great inequities in wealth brought to light by Nihi Sumba's luxury. They point to the tremendous gap between the wealth of Indigenous Sumbanese and the wealth of Nihi Sumba's guests as evident in comparisons of the costs of staying at Nihi Sumba compared with the wealth of West Sumba's residents whose average annual income in 2011 was US$424.[7] Twenty-nine percent of people in West Sumba District, where Nihi Sumba is located, live below the poverty line, meaning they earn less than US$22.00 per month.

When Hoskins frames tourism as a manifestation of colonialism and social inequities, she specifically names Nihi Sumba as an actor in Sumba's burgeoning tourism economy (Hoskins, 2002). Hoskins' theorization focuses on cultural tourism and Sumbanese People's interpretation of the tourists' gaze as violent. The association of tourism with violence is logical when viewed within a historical context that extends back to the 18th century when Sumbanese leaders began selling slaves to Dutch East Indies traders and continues through the immigration of Muslim merchants from neighboring islands. From the perspective of Sumbanese witnessing tourists' behaviors, their "attraction to sandy beaches places them in the company of slave raiders, Muslim merchants, surfers, and the violators of many important taboos" (Hoskins, 2002, page 806). One arena where taboos govern people's behaviors is along coastal sites associated with the ancestors' activities. Watu Malondo (Hoskins, 2002) and Halete (Fowler, 2016) are two coastal locations where, when Sumbanese People visit, they follow numerous taboos in alignment with their belief that ancestral spirits reside there. When residents in the area of the resort tell a story about their ancient ancestors coming ashore on Nihiwatu upon their initial migration to the island, they express a feeling that this beach is also a place with heightened significance and special meaning for the people who descend from those early founders. Dispossessing the ancestors' descendants from this special place is a form of colonial violence.

The resort's owners are the legitimate occupiers of Nihiwatu even while being wealthy colonizers. What does Nihi Sumba say to convince people of its legitimacy? Most prominent among the ways Nihi Sumba attempts to earn legitimacy are its economic contributions and its philanthropy. Nihi Sumba's owners cite their contributions to the local economy through hiring local people to staff the resort and to entertain tourists during activities on the hotel's grounds (e.g., surfing, turtle releases) as well as off-site excursions (e.g., on waterfall tours, cultural activities). To complement the resort's operations, Nihi Sumba's first owners created The Sumba Foundation as a private, non-profit, nongovernmental organization. Nihi Sumba funds The Sumba Foundation and raises money from private contributors. The

[6]I do not know the specific type of legal title that Nihi Sumba's owners possess.

[7]The average annual per capita income in South West Sumba District for 2011 was US$209 (Manek et al., 2013). South West Sumba District has the highest poverty rate in East Nusa Tenggara Province.

resort connects its business to the Sumba Foundation's philanthropy to justify the wealth of its owners and clients: "The resort was founded on the trust and cooperation of the local community and today they remain the heart and soul of the experience. Ninety percent of the staff (including those in senior positions) are from the local area and the resort supports local initiatives and enterprise through our continued partnership and collaboration with the Sumba Foundation" (Nihi Sumba, 2020c, no page number).

The Sumba Foundation aims to reduce poverty through investing in health, nutrition, education, housing, farming, and drinking water. One of the Sumba Foundation's projects is developing freshwater infrastructure in the region of Hoba Wawi Village in the Wanokaka Subdistrict of West Sumba District where the resort is located. They have built at least 65 wells that deliver water through gravity and electric pump systems; 250 faucet stations; 76 water tanks; and toilet facilities (Knickerbocker, 2017 and 2018). They have also installed electrical equipment, power lines, and more than 15,000 m of pipelines. These systems provide water for health clinics, schools, and householders. By 2018, The Sumba Foundation was providing water to 6,576 people.

In the Nihi Sumba situation, a foreign-owned business holds title to 270 hectares (667 acres) of former space formerly controlled by adat communities. Demonstrating how water grabs often include land grabs, Nihi Sumba's holdings include a 2.5-km-long beach as well as the land fronting the beach. Most of the resort's villas have private swimming pools as well, which is notable because it increases the volume of water consumed by the hotel and its guests. Maintaining swimming pools requires grabbing more water than if fewer or no swimming pools were located in Hoba Wawi Village. Two nearby waterfalls are enclosed within Nihi Sumba's holdings (Nihi Sumba, 2020d), but whether these are within its resort's boundaries or beyond is unclear. Nevertheless, the resort's physical footprint illustrates that tourists are drawn to places where they have options to indulge in saltwater and/or freshwater.

To complement the water grab that generates additional wealth for the wealthy, the colonizers created a nongovernmental organization that conducts development work in island communities. Does associating a for-profit business with philanthropy legitimize a grab? For off-island sources, it does seem to be effective in boosting a luxury hotel's status among journalists. Many media reports praise the resort for engaging in charity as illustrated by the headline from a Harper's Bazaar Singapore report: "Book Into These Socially-Conscious Luxe Hotels Around the World" with the byline "Get a Tan and Do Some Good" (Rey, 2019, no page number). Among budget-conscious traveling surfers who find their way to Sumba's waves and resent the resort from preventing their access to the infamous Occy's Left break, charity work is no excuse for privatizing a beach and then excluding the locals from it. Yet, for hoteliers and journalists in the travel industry, this business model remains not only unproblematized but highly lauded. Nihi Sumba's "recipe of sustainable luxury, responsibility, philanthropy and community engagement, in a wild seaside setting" (Barker, 2019, no page number) is celebrated. Having acquired land in Costa Rica, Mexico, and Iceland, Burch and McBride are applying the Nihi model to other sites beyond Indonesia. In stark contrast to the ways foreigners view tourism and development, many locals think of tourists as violent predators who use the bodies of kidnapped, enslaved, and murdered Sumbanese as construction materials for their development projects (Hoskins, 2002). Community engagement, philanthropy, and charity are not legitimate it this context where multiple generations of Sumbanese have endured colonialism and where neocolonialism continues to impose itself.

Water (and Land) Grabbing at the Island Level of Sumba

Cases from across Sumba illustrate how water grabbing is part and parcel of land acquisitions. The cases highlighted in this article are a reforestation scheme managed by federal and regional government agencies and two highly expensive resorts financed by private developers. More cases from Sumba could have been featured here; specifically, sugar plantations designed by multinational corporations and renewable energy projects undertaken through partnerships between the Indonesian government and multinational corporations. The water, land, labor, additional construction materials, food for workers, and so forth that are required to produce trees, tourists, sugar, and electricity have driven bureaucrats, designers, investors, and profiteers to acquire resources belonging to Sumba's customary communities. Orchestrating these assets in order to grab water could only occur under certain conditions. Further along in this analysis, I point out connections between water grabbing incidents on Sumba for the purpose of identifying the aspects, forms, and machinations of legitimacy that allow, enable, facilitate, or promote the transfer in ownership of critical amounts of water.

On Sumba, legitimacy is determined within a creolized society (Fowler, 1999) consisting of elements amalgamated from internal and external influences (Kirch, 2000). Disassembling the creole society reveals pre-Austronesian, Austronesian, Dutch colonial, Indonesian, and globalized constituents that are being assembled in collectives that are called by names identifying particular ethnolinguistic terms, such as Umalulu, Lamboya, Kodi, Bukambero, and Wanukaka (AKA Wanokaka). Moreover, components of activities related to development and aide in response to environmental limitations and socioeconomic marginalization are integrated into the creolized society. Freshwater—with all of its tangible and intangible characteristics—is one manifestation of the mélange of political ecological processes that constitute Sumbanese societies.

Looking at multi-scale political economies in relation to rural water grabbing incidents is an "opportunity," as Atalay (2018) writes about urban areas, "to observe better the interaction between micro and macro processes." The conditions under which people interact with freshwater on Sumba Island are impacted by machinations of four types of social actors: Indigenous agropastoralists, resource managers working for Indonesian government agencies, non-Sumbanese investors seeking to capitalize from Sumba's resources, and the staff of nongovernmental organizations and corporations whose operations involve Sumba. Similarities and differences exist in the ways each of these social groups interact with water. The members of these groups are often moving along on separate paths, but they also frequently converge in watered sites or over watery issues. A brief comparison of these groups reveals the following key characteristics. Sumbanese agropastoralists have long historical relationships with water around which they have shaped their customary forms of social organization, religion, tenure, and ecological interactions. Sumbanese agropastoralists engage with water for survival in the course of everyday activities related to subsistence as well as for special occasions related to beliefs and rituals all of which are influenced by internal and external sociopolitical dynamics. Resource managers who work for the Indonesian government engage with water in the process of carrying out their job duties and are directed by the explicit and implicit goals of the Sumbanese and non-Sumbanese Indonesians who legislate, implement, and enforce policies. The resource managers who appear in this study are mostly working for federal agencies who have operations on Sumba related to forests, including forests designated for resource production and protection. Private investors seek to intervene in Sumba's economy for the purpose of generating profit. The ones who are described in this article are people whose interventions affect fresh water, especially those who seek to buy or sell, own or use water and land where water is located. Workers from nongovernmental agencies and corporations aim to develop aspects of Sumbanese people's lives or components of the island's landscape. Their work may be directly focused on water (e.g., well boring, hydropower) or it may be focused on something other than water but that nevertheless impacts water resources (e.g., energy production). An example is the UNDP who partnered with the Indonesian Ministry of Environment and the Development Planning Agency of Eastern Nusa Tenggara Province (BAPPEDA) to develop training manuals for managing water in the context of climate change. In another project, UNDP built micro-hydropower plants in East Sumba in a partnership with Bank NTT. This paper provides details about these social groups' interactions with water and with each other as they occur in specific instances of water grabbing.

Legal Structure for Tenure in Indonesia

Since freshwater resources on Sumba are surrounded by and embedded within land, the legitimacy in claims to use, own, manage, and govern freshwater resources is taken to operate within the same legalistic structure as land does. Land rights in Indonesia derive from the two prevailing systems of national law (*hukum*) and customary law (*adat*). The Indonesian Constitution of 1945 (amended in 2002) and the Basic Agrarian Law of 1960 (BAL) are two foundational national laws that define points related to the use and ownership of water (and land). Article 33 (3) of the Constitution as well as Article 2 of the BAL claims that the Indonesian State has power over land, water, and natural resources. Article 5 of the Constitution states that adat law governs water, land, and air with the caveat that "it is not in conflict with the State's interests based on the unity of the Nation, and with Indonesian Socialism as well as with the regulations stipulated in this Act and with other legislative regulations, all with due regard to the elements based on the Religious Law" (Indonesian Constitution, 1945, no page number).

The BAL established a system of certifying titles to land and registering ownership certificates in local land offices (FAO, 2020) and launched the project to convert all customary land to certified land, a process which is still underway 60 years after the establishment of the policy. Four types of land tenure are made available to Indonesian citizens by the BAL. These are land ownership (*hak milik*); cultivation and exploitation rights on no fewer than 5 hectares of state-owned land for no longer than 25 years (*hak guna usaha*); building rights for no longer than 30 years (*hak guna bangunan*); use and collection rights on state-owned land or land owned by individuals (*hak pakai*). Additional rights recognized by the BAL are the right to clear (*hak membuka tanah*); the right to collect forest products (*hak memungut hasil hutani*); and customary tenure (*adat*) (FAO, 2020). Rent or lease rights (*hak sewa*) are available to citizens as well as non-citizens.

The BAL recognizes adat communities as the legitimate authority to oversee land use and tenure, to administer transfers of land tenure, and to settle conflicts over land. Article 2 of the BAL grants authority to implement the state's policies on state-owned land to adat communities and regional governments. Article 5 of the BAL gives customary tenure rights (*hak ulayat*) to adat communities. However, the Indonesian government retains greater authority over transfers of ownership and rights for developmental purposes. Only Indonesian citizens can possess land ownership rights (*hak milik*). Indonesian citizens can sell, transfer, inherit, and hypothecate *hak milik* lands. Only citizens and approved corporate entities can possess cultivation rights (*hak guna usaha*) and building rights (*hak guna bangunan*). Citizens and resident foreigners or foreigners with in-country representation can rent or lease land (*hak pakai*). Possessors of use rights cannot sell, transfer, or exchange the land. Rent and lease rights (*hak sewa*) are available to citizens, foreigners, Indonesian businesses, and foreign corporate entities. Adat communities govern rights to collect forest products (*hak memungut hasil hutani*) and ownership of customary lands both of which are rights only available to citizens.

The Development of Postcolonial Indonesia

Using the Constitution and the BAL as well as subsequent legislative acts that further elaborated land tenure and rights in Indonesia, the Sukarno (Indonesia's first president after decolonization from 1945 until 1967) and Suharto governments established a system in which national law superseded customary law. Whereas the opening 53 years of the Indonesian nation were characterized by the centralization of power in the Jakarta-based national government, decentralization has been an aim of the subsequent 23 years known as the Reformasi. Much of the Reformasi era legislation related to tenure directs governance to the provincial, regency, district, and local levels. While Article 14(e) of the BAL assigned responsibility to regional governments for water, land, and air (FAO, 2020), Reformasi era legislation has further specified regional responsibilities and thereby officially bolstered the power of provincial agencies. Presidential Decree Number 34 of 2003 assigned the following tasks to regency governments: land use planning; managing land redistribution and compensation for maximum excess land and absentee land; managing neglected lands; managing compensation for lands allocated for development; mediating disputes over cultivated land; mediating communal land conflicts; issuing location permits and land clearing permits; and provisioning land for public interest (FAO, 2020). At the district level, district governments, through their Offices of Land and Property Taxes, have the authority to manage the conversion of collective land ownership to individual land ownership, a process promoted by the BAL. Law 23/2014 outlines the jurisdictions of the central, regional, and local governments in the realms of "marine and fisheries, tourism, agriculture, forestry, trade, and industry" (UU No. 23 Tahun 2014 Ayat 6 Huruf B). The law can, in some ways, be read as granting autonomy to regions in managing governmental affairs. Regional (meaning, provincial) governments have authority within state forest lands (KPH) over harvesting timber and processing non-timber forest products; environmental services; forest protection; watershed management; and rehabilitation of areas outside of forest boundaries; counseling with partner agencies; and "community empowerment." Law 23/2014 also authorizes the co-management of natural resources by the central (federal), regional (provincial), and local (district) governments. However, uncertainties about governance and management are present due to the transitional status of governmental structures. In Nusa Tenggara Timur, the province where Sumba is located, the problems are compounded by "ineffective coordination and lack of capacity development being implemented at the subnational level" (UNDP Indonesia, no date, no page number).

The National Land Agency Regulation Number 5 of 1999 defines the relationships between district governments (*kabupaten*) and adat tenure systems. With this legislation we see how, alongside efforts to decentralize authority and responsibility, legislative acts from the Reformasi era also reinforce the legitimacy of adat. Another prime illustration is the Local Government Act Number 22 of 1999 that supports the authority of adat communities and empowers adat governance in issues related to natural resources (FAO, 2020). In the Reformasi era, governmental entities continue to possess the right to acquire land as provided by the Land Procurement for Development in the Public Interest (or Land Acquisition Act) of 2012. Article 2 of the Land Acquisition Act places these conditions on governmental procurement of land: "Acquisition of land in the public interest must follow the principles of humanity (protection of human dignity), justice (compensation), benefit (to the public), certainty (legal certainty on the availability of land), transparency (access to information), agreement (negotiation between parties), participation (public participation throughout the process), welfare (added value), sustainability and harmony (development can be balanced and aligned with the interests of the public and the state)" (Land Procurement for Development in the Public Interest Article 2 2012, no page number). To address the reality that some land procurements do not conform to these principles, legislation also exists that assigns regional governments as mediators in land conflicts involving adat land owners. Indeed, tensions have occurred between Indonesia's customary communities and agents external to their territories. Such tensions are apparent in the research literature about, for example, agrarian livelihoods (Peluso, Affif, and Rachman, 2008), fire ecologies (Fowler, 2013), forest management (Boedhihartono, 2017), and ocean-based livelihoods (Ramenzoni, 2013).

Generational Shift in Opinions About Relinquishing a Sacred Site

The appropriation of a community's water often causes social conflicts (Dell'Angelo et al., 2018; Rodríguez-Labajos and Martínez-Alier, 2015). To identify a few specific causes of conflicts when tenure over water resources changes, we may consider the case of Marosi Beach where a violent clash occurred between the customary rights bearers and a newer, non-Native permit holder. Marosi Beach is located within Patiala Bawa Village in the Lamboya District of West Sumba. The sandy strand of Marosi Beach is approximately three to 4 km long and is bordered by a biologically rich tidal flat/coral reef, which leads out to abundant ocean fisheries. A small estuary forms where the mouth of a river empties onto the beach.

Lamboya District is home to the group of people who call themselves "Lamboya" and speak the Lamboya language, which belongs to the Central-Eastern Malayo-Polynesian subgroup of Austronesian languages. The Lamboya People are considered to be the first settlers of this area and have lived there for many generations—long enough to have developed their own distinct Lamboya language and identity. Marosi Beach has heightened value for Lamboya People for multiple reasons, and coopting their access to it threatens these values. Marosi is important for religious reasons as it serves as the site for the annual Pasola ritual, which is a key community event (Geirnaert-Martin, 1992). Marosi also holds economic and practical values for Lamboya People and their neighbors deriving from the resources available on the beach, on the coral reefs, and in the fisheries. Lamboya villagers participate in a tourism industry that centers around the notoriety of Marosi Beach especially for surfing and Pasola, and also for swimming and sightseeing. Villagers earn incomes that contribute to their livelihoods by providing homestays for tourists and guiding them around the beach. Children also earn cash by selling coconuts and other novelties to tourists.

In 1994, the company Sutera Marosi Kharisma obtained building rights permits (*hak guna bangunan*) from the Indonesian government that gave them permission to build and operate a business on 50 hectares around and including Marosi Beach for 30 years. Constructing a resort on this site could lead to the exclusion of Lamboya People from the estuary, the beach, and adjacent offshore areas. This means that whatever values the land, the freshwater, and the saltwater at the site have for Lamboya could be reduced or eliminated. Their access to water and land could be restricted. Economically, local small businesses may have difficulty surviving alongside this large company. Ecologically, the resort's construction and the operation of tourism at Marosi has the potential of damaging biodiverse habitats, polluting the water and soil, and creating light and noise pollution. The development of Sutera Marosi Kharisma's resort threatens to physically displace the Indigenous People themselves from their customary lands and waters. Dispossessing the Lamboya of their lands and waters, would desecrate sacred spaces, damage the spiritual system, degrade livelihoods, and violate human rights (Saraswati, 2018).

Sutera Marosi Kharisma's permit grants them the rights to control an area containing land as well as freshwater and saltwater resources. Even though Sutera Marosi Kharisma obtained their permits in 1994, they did not begin construction for another 12 years and this delay in their plans caused major problems once they finally decided to move forward. In 2016, Sutera Marosi Kharisma began establishing their presence in Patiala Bawa Village and reminding the locals that they had permits to create a resort on Marosi Beach. Once Sutera Marosi Kharisma launched their construction project, the necessity for negotiations between the company and the Lamboya emerged. Sutera Marosi Kharisma claimed they had obtained agreement from not only the Indonesian government but also the Lamboya People when they requested the original building permits. The villagers who were politically active in 2016–2018 said that, while back in the early-1990s their parents may have acquiesced to the company's desire to build a resort, they themselves had never agreed to sell the land and did not want the resort to be built on their ancestral territory. By 2018, the negotiations were failing and the relationship between company officials and local villagers had fallen apart.

In 2016, Sutera Marosi Kharisma attempted to acculturate the younger generation of villagers—to change their minds—so they would be in favor of the development of the tourist economy. Company spokespersons said their goal was "…to develop the economy of the region" (Hindarto, 2018, no page number). Sutera Marosi Kharisma promised to share the wealth with villagers by hiring them as construction workers. Villagers posted no construction signs and built fences to keep out the company. The size of the permitted concession, in Sutera Marosi Kharisma's records, was 50 hectares. Residents of Patiala Bawa Village said the company was actually operating in multiple fields across a 200-hectare expanse. Villagers questioned the legality of the company's building permits and demanded that the BPN (*Badan Pertahanan Nasional Republik Indonesia*, Indonesian Land Office) conduct a new survey of the concession. When BPN and employees of Sutera Marosi Kharisma began marking the boundaries, they were confronted by weapon-wielding villagers who protested, threw stones, and prevented company workers from leaving by blocking the exit road. Consequently, the surveyors began taking security guards with them from the police and military. According to news sources, the guards were members of the Indonesian National Armed Forces (CNN Indonesia, 2018) and/or the Mobile Brigade Corps, which is a paramilitary branch of the National Police charged with internal security control (Saraswati, 2018). The guards responded to the Lamboya protestors by throwing tear gas at them and confiscating the mobile phones they were using to videotape and photograph the surveyors and security forces. On 25 April 2018, Poro Duka, a local man in his early 40s, was shot and killed, allegedly by the police and/or security forces, as he protested the company's activities (Saraswati, 2018).

The Marosi case illustrates a situation in which contact between two distinct types of legitimacy—Lamboyan adat and the Indonesian government's—gave rise to serious social conflict. In addition to the friction generated by divergent political ecologies, an additive cause of conflict was the reversal in political sentiment among the Lamboya between 1994 and 2016. Community leaders in the 1990s were willing to consent to non-Native businesses to profit from tourism on their beach, but the subsequent generation of community leaders no longer wanted to authorize that model of tourism. Whereas the older Lamboya regime ceded their territory, the newer one attempted to reclaim their property. The determinants of legitimacy had changed in the transition from the late-New Order to the early-Reformasi era as Lamboya People asserted their customary rights and took action to decolonize.

Communities are sometimes willing to grant permits to outsiders. In some cases, the communities reach consensus about transferring their rights. Yet, the community's sentiment can change over time, as in the situation at Marosi Beach. In tenure dealings, differences in opinions exist within communities, the relative power of the actors involved may influence decisions. For individuals and subgroups within communities who are less powerful, their wishes to consent or not consent to changes in tenurial relations may lead to their loss of access to vital resources and meaningful spaces. This experience with changes in tenure can be a source of stress. In yet other cases, communities, segments of communities, or even individuals within them change their minds.

Local residents prioritize historical and genealogical connections to place and believe that, as descendants of the original settlers to the area, they are the rightful authorities. They believe that, even when they have given a company the right to use water and land, that they should be able to rescind the agreement. More specifically on that point, Lamboya believe that if a permit holder does not use the property for a significant amount of time, then they forfeit their rights and control returns to the previous owners. The Lamboya People considered themselves to be the legitimate rights holders to Marosi because they were actively using the property. Lamboya People's continuous use legitimizes them. Sutera Marosi Kharisma is delegitimized because of its non-use in addition to its non-local identity. To the contrary, the water grabbers and their enablers in the government, military, and police believe that legal documents and federal laws justify their activities. The case of Marosi Beach illustrates that one characteristic of legitimacy is that it has different parameters when looked at from differing perspectives (Pardo and Prato, 2018); specifically at Marosi, from point of view of local community members who live in the sites where water grabs occur versus from the point of view of the people who are acquiring water.

DISCUSSION: MAKING AND REMAKING FRESHWATER IN A CHANGING CONTEXT

When are claims of water grabbing considered to be legitimate or illegitimate, by whom and why? The characteristics of water itself—its ephemerality, changing volumes, movement through landscapes, sources and sinks, mobility—can make it difficult for claims of unjustifiably grabbing it to be seen as legitimate. As Franco et al. (2013) put it, "The fluidity of water (and dislocated effects of water grabbing) and the "invisibility" of customary water rights systems can complicate the task of "framing" water grabbing as really happening and as an injustice warranting a serious and systematic political response." To water's character, these authors add the status of customary water rights as a systemic cause of water grabbing.

In Indonesia customary land rights (*hak ulayat*) are not only visible, they are also guaranteed by the Constitution and subsequent legislation. Moreover, the visibility of customary rights has increased during the Reform Era. Thus, even when customary rights are visible they are not always considered legitimate. And even when customary rights are deemed legitimate in legal documents, the rights holders are not always treated justly. Indeed, national governments might formally recognize customary rights, and yet still the system does not always work in the favor of the rights holders (Franco et al, 2013) partly because absentee national governments cannot properly manage rights that operate at the local level within traditional systems. Exacerbating the problem, systems such as Indonesia's endorse alienation by providing land tenure permitting for non-customary owners in ways that ease the transfer of ownership away from customary communities (Franco et al, 2013). Government's take-over of tenure arrangements may look past local tenure systems and complicate traditional tenure by causing disfunctions within the traditional culture, such as eroding women's rights.

The legal structure within which water grabbing occurs on Sumba is connected to the legal framework for land tenure and rights in Indonesia. Many of the situations where transfers of tenure and access to freshwater occur are plural-legal ones that are "characterised by the coexistence of varied and diverse regulatory frameworks and processes shaping who gets what kind of access to which water resources and for what purposes" (Franco et al, 2013, page 1656). In each of the constituent legal systems, legitimacy and illegitimacy are differentially defined, determined, contested, and negotiated.

When regimes of legitimacy change, freshwater resources also change. Since pre-colonial times, Sumbanese communities have engaged with their neighboring on-island communities as well as with external political ecological entities and forces by responding and adjusting to them, accommodating and resisting, including and excluding, and adopting and rejecting particular components of them. On Sumba, as elsewhere in Indonesia, the environment is a playing field where people work through the legitimacy of the co-existing adat, colonial, postcolonial, and developmentalist political ecologies. This peculiar but not unique set of regimes of legitimacy that operate on Sumba has tangible and intangible effects on customary communities' sovereignty as well as rights and access related to natural resources, including freshwater as has been the subject here in this paper. The political context surrounding freshwater resources influences the barriers to and affordances available for the equitable and sustainable management of water, the protection of water quality, and the conservation of freshwater biota.

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REFERENCES

Ashmad, A., Giroud, S., Blait, B., and Ragalawa, H. (2012). *Gender Issues in Food and Nutrition Security in NTT Province*. Jakarta: Indonesia Country Office, World Food Programme. Available at: https://www.wfp.org/sites/default/files/WFP-Gender%20Rapid%20Assesment.pdf.

Atalay, Z. N. (2018). Legitimacy Crisis: Commonalities and Differencew. *Urbanities* 8 (10), 27–31.

Barker, C. (2019). Fashion Mogul's 'Irrational' Investment Turning Surf Paradise into Luxury Resort Chain. Available at https://www.forbes.com/sites/christianbarker/2019/04/16/fashion-moguls-irrational-investment-turning-surf-paradise-into-luxury-resort-chain/#1399006c359a.

Bettinger, K., Fisher, M., and Miles, W. (2014). The Art of Contestation and Legitimacy: Environment, Customary Communities, and Activism in Indonesia. *Occupy Earth Glob. Environ. Movements* 15, 195–224. doi:10.1108/s2051-503020140000015008

Boedhihartono, A. (2017). Can Community Forests Be Compatible with Biodiversity Conservation in Indonesia? *Land* 6, 21. doi:10.3390/land6010021

CNN Indonesia (2018). Kesaksian Kepala Desa Saat Polisi Tembak Warga Sumba NTT. Available at https://www.cnnindonesia.com/nasional/20180502222056-12-295260/kesaksian-kepala-desa-saat-polisi-tembak-warga-sumba-ntt.

de Bont, C., Veldwisch, G. J., Komakech, H. C., and Vos, J. (2016). The Fluid Nature of Water Grabbing: the On-Going Contestation of Water Distribution between Peasants and Agribusinesses in Nduruma, Tanzania. *Agric. Hum. Values* 33, 641–654. doi:10.1007/s10460-015-9644-5

Dell'Angelo, J., Rulli, M. C., and D'Odorico, P. (2018). The Global Water Grabbing Syndrome. *Ecol. Econ.* 143, 276–285. doi:10.1016/j.ecolecon.2017.06.033

Ellen, R. (2017). "Contingency and Adaptation over Five Decades in Nuaulu Forest-Based Plant Knowledge," in *Indigenous Knowledge: Enhancing its Contribution to Natural Resource Management Edited by Paul Sillitoe* (Wallingford, Oxfordshire: CAB International), 28–39. doi:10.1079/9781780647050.0028

FAO (Food and Agriculture Organization of the United Nations) (2020). Gender and Land Rights Database. Indonesia. Available at http://www.fao.org/gender-landrights-database/country-profiles/countries-list/land-tenure-and-related-institutions/en/?country_iso3=IDN.

Fisher, M. R., Workman, T., Mulyana, A., Moeliono, M., Yuliani, E. L., et al.Balang Institute (2020). Striving for PAR Excellence in Land Use Planning: Multi-Stakeholder Collaboration on Customary Forest Recognition in Bulukumba, South Sulawesi. *Land Use Policy* 99, 102997. doi:10.1016/j.landusepol.2017.09.057

Fowler, C. (2016). *Biosocial Synchrony on Sumba: Multispecies Relationships and Environmental Variations on Sumba*. Lanham: Lexington Press.

Fowler, C. (2013). *Ignition Stories: Indigenous Fire Ecologies in the Indo-Australian Monsoon Zone*. Durham: Carolina Academic Press.

Fowler, C. (1999). *The Creolization of Natives and Exotics: The Changing Symbolic and Functional Character of Culture and Agriculture in Kodi, West Sumba (Indonesia)*. PhD Dissertation. Honolulu: University of Hawai'i at Manoa.

Franco, J., Mehta, L., and Veldwisch, G. J. (2013). The Global Politics of Water Grabbing. *Third World Q.* 34 (9), 1651–1675. doi:10.1080/01436597.2013.843852

Geirnaert-Martin, D. C. (1992). *The Woven Lands of Laboya: Socio-Cosmic Ideas and Values in West Sumba, Eastern Indonesia*. Leiden, Netherlands: The Centre for Non-Western Studies, Leiden University.

GRAIN (Genetic Resources Action International) (2012a). Squeezing Africa Dry: Behind Every Land Grab Is a Water Grab. Available at https://www.grain.org/en/article/4516-squeezing-africa-dry-behind-every-land-grab-is-a-water-grab.

Head of KPHL for the Southwest Sumba District (2015). Long Term Forest Management Plan for the Southwest Sumba Protection Forest Management Unit (KPHL). Available at https://fdokumen.com/document/rencana-pengelolaan-hutan-jangka-kphlsim-dan-mengembangkan-kemitraan-dengan-para.html.

Henley, D., and Davidson, J. S. (2008). In the Name ofAdat: Regional Perspectives on Reform, Tradition, and Democracy in Indonesia. *Mod. Asian Stud.* 42 (4), 815–852. doi:10.1017/s0026749x07003083

Hindarto, S. Y. (2018). *Kronologi Konflik Lahan Tewaskan Warga NTT*. Jakarta, CNN Indonesia. Available at https://www.cnnindonesia.com/nasional/20180430180108-20-294743/kronologi-konflik-lahan-tewaskan-warga-ntt.

Hoskins, J. (2002). Predatory Voyeurs: Tourists and "Tribal Violence" in Remote Indonesia. *Am. Ethnol.* 29 (4), 797–828. doi:10.1525/ae.2002.29.4.797

Indonesian Constitution (1945). Article 5. Available at https://www.constitutionofindia.net/constitution_of_india/citizenship/articles/Article%205.

Kahn, M. (2011). *Tahiti beyond the Postcard: Power, Place, and Everyday Life*. Seattle: University of Washington Press.

Kirch, P. V. (2000). *On the Roads of the Wind: An Archaeological History of the Pacific Islands before European Contact*. Berkeley: University of California Press.

Knickerbocker, K. (2017). The Sumba Foundation Year End Report 2018. Available at https://sumbafoundation.org/wp-content/uploads/SF_yearend_2017.pdf.

KPHL (the Southwest Sumba Protection Forest Management Unit) (2015). Long Term Forest Management Plan for the Southwest Sumba Protection Forest Management Unit (KPHL). Available at https://fdokumen.com/document/rencana-pengelolaan-hutan-jangka-kphlsim-dan-mengembangkan-kemitraan-dengan-para.html.

Lee Peluso, N., Afiff, S., and Rachman, N. F. (2008). Claiming the Grounds for Reform: Agrarian and Environmental Movements in Indonesia. *J. Agrar. Change* 8, 377–407. doi:10.1111/j.1471-0366.2008.00174.x

Li, T. M. (2001). Masyarakat Adat, Difference, and the Limits of Recognition in Indonesia's Forest Zone. *Mod. Asian Stud.* 35 (3), 645–676. doi:10.1017/s0026749x01003067

Li, T. M. (2018). After the Land Grab: Infrastructural Violence and the "Mafia System" in Indonesia's Oil Palm Plantation Zones. *Geoforum* 96, 328–337. doi:10.1016/j.geoforum.2017.10.012

Lowe, C. (2007). *Wild Profusion: Biodiversity Conservation an Indonesian Archipelago*. Princeton, NJ: Princeton University Press.

Manek, E., Pakereng, P., Suryandari, D., Florence, K., Beribe, D. R., Anggul, S., et al. (2013). *Provincial Development Guideline for East Nusa Tenggara for Year 2013*. Kupang: Integrated Secretariat for Development Cooperation and ENT Provincial Government and PGSP-UNDP Cooperation.

McCall, C. (2015). *The Next Bali: Can Sumba in Indonesia Marry Tourism with Tradition?* Hong Kong, The Post. 26 September 2015. Available at https://www.scmp.com/magazines/post-magazine/article/1860987/next-bali-can-sumba-indonesia-marry-tourism-tradition.

Mehta, L., Veldwisch, G., and Franco, J. (2012). Water Grabbing? Focus on the (Re) appropriation of Finite Water Resources [special Issue]. *Water Altern.* 5 (2), 193–468.

Nihi Sumba (2020a). About. Available at https://nihi.com/nihi-sumba/about-our-story/.

Nihi Sumba (2020c). Cultural Experiences. Available at https://nihi.com/nihi-sumba/experiences/culture/.

Nihi Sumba (2020d). Fact Sheet. Available at https://nihi.com/wp-content/uploads/2017/10/2017_factSheet_digitalVersion_oct.pdf.

Nihi Sumba (2020b). Sumba Culture. Available at https://nihi.com/nihi-sumba/experiences/culture/.

Onvlee, L. (1980). "8 the Significance of Livestock on Sumba," in *The Flow of Life: Essays on Eastern Indonesia*. Editor J. Fox (Cambridge: Harvard University Press), 195–207. doi:10.4159/harvard.9780674331907.c9

Pardo, I., and Prato, G. B. (2018). The Ethnography of Legitimacy and its Theoretical Ramifications. *Urbanities* 8 (10), 2–8.

Prato, G. B. (2018). Dynamics of Legitimacy: Formal and Informal Contexts. *Urbanities* 8 (10), 9–15.

Ramenzoni, V. C. (2013). Endenese Fisheries: Exploratory Findings on Environmental Perceptions, Fish Effort, and Overfishing in Eastern Indonesia. *Ethnobiol. Lett.* 4, 39–51. doi:10.14237/ebl.4.2013.8

Reading, C., and Wien, F. (2009). *Health Inequalities and Social Determinants of Aboriginal People's Health*. British Columbia, Canada: Prince GeorgeNational Collaborating Center for Aboriginal Health.

Rey, C. (2019). Book into These Socially-Conscious Luxe Hotels Around the World. Harper's Bazaar Singapore. Available at https://www.harpersbazaar.com.sg/life/socially-conscious-hotels-around-the-world/.

Rodríguez-Labajos, B., and Martínez-Alier, J. (2015). Political Ecology of Water Conflicts. *WIREs Water* 2, 537–558. doi:10.1002/wat2.1092

Rulli, M. C., Saviori, A., and D'Odorico, P. (2013). Global Land and Water Grabbing. *Proc. Natl. Acad. Sci. U.S.A.* 110, 892–897. doi:10.1073/pnas.1213163110

Saraswati, M. S. (2018). Land Conflict from Tourism Development in East Nusa Tenggara, Indonesia. Available at https://ejatlas.org/conflict/land-conflict-from-tourism-development-in-east-nusa-tenggara.

Sungkar, S., Pohan, A. P. N., Ramadani, A., Albar, N., Azizah, F., Nugraha, A. R. A., et al. (2015). Heavy Burden of Intestinal Parasite Infections in Kalena Rongo Village, a Rural Area in South West Sumba, Eastern Part of Indonesia: a Cross Sectional Study. *BMC Public Health* 15, 1296. doi:10.1186/s12889-015-2619-z

Travel and Leisure (2020). Nihi Sumba Island (Formerly Nihiwatu). Available at https://www.travelandleisure.com/travel-guide/bali/hotels/nihi-sumba-island-formerly-nihiwatu.

Tsing, A. L. (2004). *Friction: An Ethnography of Global Connection*. Princeton, NJ: Princeton University Press.

UNDP Indonesia (No date). Strategic Planning and Action to Strengthen Climate Resilience of Rural Communities (SPARC). Available at https://www.id.undp.org/content/indonesia/en/home/operations/projects/environment_and_energy/strategic-planning-and-action-to-strengthen-climate-resilience–.html (Accessed on June 15, 2021).

Vel, J. (2008). *Uma Politics: An Ethnography of Democratization in West Sumba, Indonesia, 1986-2006*. Leiden: Brill.

Vel, J., and Makambombu, S. (2019). Strategic Framing of Adat in Land-Acquisition Politics in East Sumba. *Asia Pac. J. Anthropol.* 20 (5), 435–452. doi:10.1080/14442213.2019.1670239

von Benda-Beckmann, F. (2007). "Contestations over a Life-Giving Force: Water Rights and Conflicts, with Special Reference to Indonesia," in *A World of Water: Rain, Rivers, and Seas in Southeast Asian History*. Editor P. Boomgaard (Leiden, Netherlands: KItlv Press), 259–277. doi:10.1163/9789004254015_011

von Braun, J., and Meinzen-Dick, R. (2009). Land Grabbing" by Foreign Investors in Developing Countries. https://www.ifpri.org/publication/land-grabbing-foreign-investors-developing-countries#:~:text=One%20of%20the%20lingering%20effects,to%20ensure%20their%20food%20supplies.

Wonderful Indonesia (2018). Nihiwatu Sumba Resort: World's Best Private Hotel. Available at https://www.indonesia.travel/us/en/news/nihiwatu-sumba-resort-world-s-best-private-hotel.Thursday 8 March 2018.

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Consumption and Preferences for Wild and Domestic Meat in Indigenous Communities in the Brazilian Atlantic Forest

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Wild animals have traditionally been the main sources of protein available, if not the only, to numerous indigenous populations worldwide. However, greater access to markets, reduced availability or access to wildlife, and policies in support of agricultural development, have shifted food habits toward domestic and industrial sources of protein. In this study, we evaluated consumption patterns and preferences/avoidances for wild animals (wildmeat, crustaceans, and fish) in comparison to domestic sources of protein among the Potiguara living on the Brazilian coast. Using data from 843 semi-structured interviews applied to students from 28 indigenous villages, we found that domestic meats were more consumed and preferred as compared to wild animals (aquatic and game animals), despite the high abundance of fish and crustacean resources in the surveyed area. Consumption and preference for game were higher among male students while avoidance was higher among female students. The avoidance of domestic meats and fish was low for both genders. The occupation of the fathers affected students' food habits, in those nature-related occupations (farmer, fisherman/woman, sugarcane worker) conditioned greater consumption of wildmeat and fish, while non-nature related occupations lead to greater consumption of protein from domestic sources. The consumption of protein from all sources increased with the distance between villages and a protected area. Our results indicate that the younger generation of Potiguaras does not regularly consume wildmeat and fish and their preference for domestic sources of protein is shaped by the socio-environmental context, access to different types of meat, and taste preferences.

Keywords: wildlife, game, fish, domestic protein, diet, ethnozoology, nutrition, protect area

INTRODUCTION

The use of wild animals for food is a millennial practice across diverse cultures (Alves et al., 2018; Anderson, 2020; Braga-Pereira et al., 2021a) and continues to contribute to diet diversification around the world (Hanazaki et al., 2009; Powell et al., 2015; Alves and van Vliet, 2018; Donders and Barriocanal, 2020; Oliveira et al., 2022). Wild animals harvested to meet nutritional needs include numerous taxa, but vertebrates make the bulk of the animals sought after for their meat, fat, bones, and eggs (Bodmer et al., 1997). Between 230 and 833 million people rely on wild meat (the meat from wild mammals, reptiles, amphibians, and birds) as a source of protein (Nielsen et al., 2018). Insects, mollusks, crustacea, and fish are also sought after as a source of protein, particularly in coastal or riverine ecosystems (Vallega, 2013). In Brazil, for example, shellfish catching is a common extractive activity concentrated close to estuaries (Nishida et al., 2006, 2008) and land crabs (Brachyura crabs) represent one of the major groups in terms of economic relevance in mangrove ecosystems (Alves and Nishida, 2002, 2003; Alves et al., 2005; Nishida et al., 2006; Nordi et al., 2009; Capistrano and Lopes, 2012; Nascimento et al., 2012, 2016, 2017). The traditional knowledge of indigenous people across the globe has played a key role in identifying living organisms that are endowed with nutritional and medicinal values important for humans. These traditional human societies have accumulated a vast store of knowledge about animals through the centuries, and this zoological knowledge is an important part of our human cultural heritage (Kendie et al., 2018; Braga-Pereira et al., 2021b).

Nowadays, while indigenous communities continue to represent this legacy through the continuation of practices that involve the use of wild animals for food, several factors linked to globalization, such as access to markets, migration, urbanization, and changes in lifestyles, have induced the rapid replacement of wild animals (van Vliet et al., 2014; Donders and Barriocanal, 2020; Leyva-Trinidad et al., 2021) to the advantage of domestic and industrial sources of protein, often incentivized by the market and governmental programs (Sarti et al., 2015; Bellinger and Andrade, 2016). For example, in the Bolivian Amazon, the Tsimane's diet is characterized by an increase in market foods (in particular pasta, refined sugar, salt, and oil) and a decreased consumption of game (Kraft et al., 2018). Chicken and eggs are now the most frequently consumed source of protein among Ticuna, Cocama, and Yagua children in Puerto Nariño, Colombia, far beyond fish and game (van Vliet et al., 2015a). Recent studies in Brazil suggest that particularly in the North-Eastern region contemporary Indigenous diets are lacking in quality, and are characterized by a high prevalence of purchased foods (Welch et al., 2021).

While most of the recent literature looking at nutritional transitions in South America has focused on the Amazon region (Coimbra and Santos, 1991; Santos and Coimbra, 2003; Tavares et al., 2003; Lourenço et al., 2008; Welch et al., 2009; Nardoto et al., 2011; van Vliet et al., 2015a; Donders and Barriocanal, 2020) and the Andes (Walrod et al., 2018; Chee et al., 2019), less is known about the changes observed in nutritional patterns in the Atlantic forest biome. This forest represents the second-largest rainforest of the American continent. Being home to 30% of the Brazilian indigenous lands (ISA, 2021), but also coincides with the most urbanized areas of Brazil (Tabarelli et al., 2005). Even though it has been largely destroyed, the Atlantic forest biome is still home to more than 8,000 endemic species of vascular plants, amphibians, reptiles, birds, and mammals (Myers et al., 2000) and includes several key formations such as mangroves, restingas (coastal forest and scrub on sandy soils), high-elevation grassland (campo rupestre), and brejos (humid forests resulting from orographic rainfall in otherwise semidesert scrub in the northeast of Brazil) (Câmara, 2003).

In the current study, we investigated the consumption of wild animals and domesticated animals among the Potiguara living in the Atlantic Forest. The Potiguara have traditionally based their livelihoods on the use of marine wild animals (such as shellfish, crabs, and fish) and terrestrial wild vertebrates as main sources of food (Rocha et al., 2008). Based on semi-structured interviews conducted among Potiguara teenagers, we assessed the frequencies of consumption of wild and domesticated animals and preferences or aversion for different animal species. We analyzed the influence of gender, socio-economic background of the household, and access to market and natural resources as predictors for consumption and preference behaviors.

METHODS

Study Area and the Potiguara Indigenous

The research was carried out in indigenous schools of the Potiguara Indigenous Land (Potiguara IL) (33,757 ha). The Potiguara IL is in the Atlantic Forest biome and spreads over three municipalities, Baia da Traição, Marcação and Rio Tinto, in the State of Paraíba, Brazil (**Figure 1**). It was demarcated in 1983, homologated in 1991, and its population is divided among 32 villages. The Potiguara IL partially overlaps with two designated protected areas, the Area of Relevant Ecological Interest Manguezais da Foz do Rio Mamanguape and the Environmental Protection Area Barra do Rio Mamanguape (EPA BRM) (Rodrigues et al., 2008). This region includes the Mamanguape River estuary which harbors *ca.* 6,000 ha of reasonably preserved mangrove ecosystem, the largest of its kind in the State of Paraíba. The mangrove forest at Mamanguape is typically well preserved although certain sites show signs of anthropogenic disturbance. Main land use types in the Potiguara IL are sugar cane fields (*ca.* 10,000 ha), crops and pastures (*ca.* 5,100 ha), fallows and *carrasco* (*ca.* 4,800 ha), (a shrubby phytophysiognomy typical of North-eastern Brazil) gardens and small-scale farmings (about 1,300 ha), forest remnants and open arboreal savanna, named "Tabuleiro" (*ca.* 8,400 ha) (Cardoso and Guimarães, 2012).

The mangrove is an economically profitable environment for the Potiguara. It is where fish, crustaceans, and mollusks are obtained, and a space upon which many of the inhabitants of the area depend for a living (Nishida et al., 2008; Rocha et al., 2008). Fishermen and women have a very keen knowledge of the mangrove and are hence able to locate aquatic animals and develop efficient techniques for capturing them (Nishida et al.,

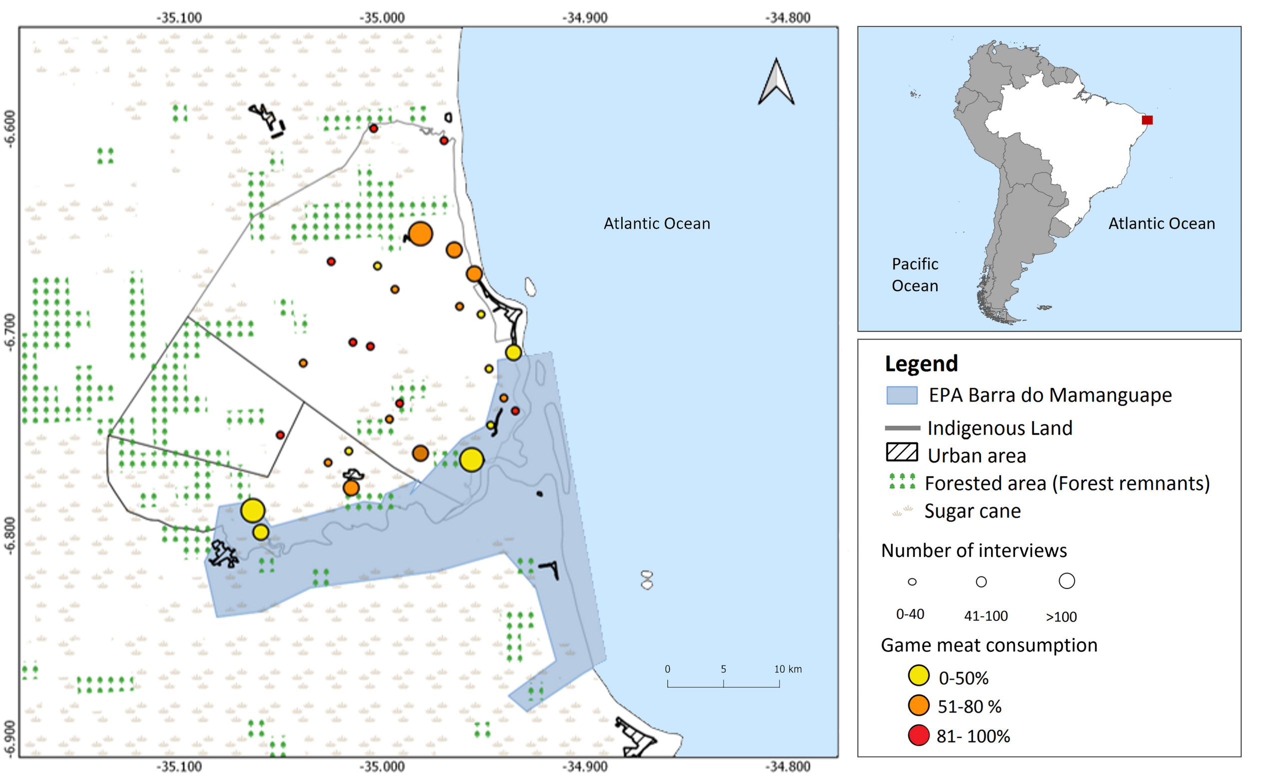

FIGURE 1 | Map of the study area portraying the 28 indigenous villages in the Potiguara territory where the study was carried out. Solid dots indicate the villages of the interviewed students. Dot sizes are proportional to the number of interviewed students from each village. Circle colors denote the number of students that have consumed game at least once in their lifetime in each village, ranging from yellow (smaller number) to red (greater number). Map generated using QGIS; Datum: SIRGAS2000. Source: IBGE, Editedin Adobe Photoshop and Elaborated in March 2022.

2006; Rocha et al., 2012). Part of the fish is consumed or given to kinspeople and neighbors with whom one is on friendly terms, and part is sold in the village or the local market when the catch is bigger (Araújo, 2019).

During the eighteenth century, deforestation for sugar cane plantations transformed the physical scenery and the social and technical relations among the Potiguaras. The expropriation of lands and the expansion of sugar cane cultivation led to widespread discontent, requiring the Potiguara to seek the demarcation of their lands as early as the 1980s. Intense deforestation did not simply result in the drastic reduction of animal and vegetal populations (both in individual numbers and in variety); the phenomenon also caused significant modifications in hydrography. With the mills, sugarcane stretched into the productive space of the Potiguara, ravaging existing areas of vegetation and restricting agricultural and fishing activities (Araújo, 2015).

As of 1993, the use of wild resources by the Potiguara was further restricted by the creation of the EPA BRM, which was created primarily to protect manatee (*Trichechus manatus*) and other aquatic species (Federal decree No. 924, 10 September 1993). Currently, fisheries (fishes, crustaceans, and mollusks), aquaculture (shrimp farming), and agriculture (crops and ranching) are regulated inside the EPA BRM (Mourão and Nordi, 2003; Araujo and Nishida, 2007; Rodrigues et al., 2008; Cardoso and Guimarães, 2012; Nascimento et al., 2016). Over time, conflicts have arisen between distinct modalities of management or access to and use of resources, and by the socially unequal display of the environmental damages and risks caused by industrial endeavors during the historical process. It is precisely against the conditions imposed by dominant policies that the Potiguara seek to impose their power, to access and control the resources present in their territory—through the household ecology, where they build domanial spaces and define mobilities (Araújo, 2019).

The villages are scattered throughout the indigenous territory, connected by unpaved roads and a paved road that connects them to the nearest urban centers of the Mamanguape, Baía da Traição, Rio Tinto, and Marcação cities in less than 30 min drive. In these neighboring towns, industrialized foods of animal and vegetable origin are readily available in the supermarkets (Cardoso and Guimarães, 2012). In the villages themselves, there are small grocery stores that also supply industrialized products, meat from domestic animals, and processed meats.

Ethics Statement

This research was authorized by the Brazilian Agency for Indigenous Affairs (FUNAI) (No. 94/AAEP/PRES/2017) and indigenous leaders in compliance with CNS Resolution No. 304 of 2000. The research project was approved by the Research

Ethics Committee and the National Research Ethics Commission (CEP/CONEP) number CAAE 7695941790008069, following Resolution No. 466/2012 of the National Health Council (CNS) of the Ministry of Health (no. 2,491,305). Authorizations to conduct the research in schools and free and informed consent forms were obtained from school principals, teachers, legal age students (18 plus), and parents or legal guardians in the case of underage students. The research process was thoroughly explained before each classroom and the interviewees were assured that their identities would not be disclosed. Still, some students refused to participate in the study, as well as 1 of the 10 Potiguara IL schools within the educational levels targeted by the study.

Data Collection

We conducted data collection between February and August 2018 in nine public schools (State and municipally managed, 8 and 1, respectively) of the Potiguara IL, located in the municipalities of Baia da Traição (three schools), Rio Tinto (two schools) and Marcação (four schools). These schools were attended by students from 28 indigenous villages, seven of which are located inside the EPA BRM. Before the study, a pilot was carried out with 83 random students from three schools to verify if students understood the proposed questions and to verify the need for adjustments in the questionnaire. Subsequently, visits were made to all public schools ($n = 10$) within the Potiguara IL to explain the research goals and to request authorization from the schools' directors to carry out the research.

Nine schools granted us the authorization requested. Out of the 84 classrooms present in those 9 schools, we used a sub-sample of 64 classrooms (about 7 classrooms per school) trying to cover different school levels. For the elementary school, we covered an average of 1.4 classrooms per scholar level ($SD = 0.11$) and for high school, we covered an average of 1.14 classrooms per scholar level ($SD = 0.13$). Authorization from the teacher was also requested before applying the questionnaire to the students.

Questionnaires were applied individually to 843 students out of 1,850 (45.6%) enrolled in Potiguara IL public schools. Interviewed students were 55% ($n = 463$) female and 45% male ($n = 380$), aged 10 to 73 years old (94.4% between 10 and 20 years, 4.1% between 21 and 30, and 1.5% between 31 and 73) and attending Middle and high school. Interviewees lived in villages located inside or outside the EPA BRM (321 and 522 students, respectively). To reduce any risks of potential bias in responses, due to the restrictions of hunting within the PA, the objectives of this study were framed around nutrition and food security, not around conservation or environmental education. The teachers in each classroom, who are trusted and respected by the students, were in charge of explaining the research goals to the class and reading out loud a consent form guaranteeing the confidentiality of the student's identity in the classroom. Moreover, the teacher explained that the children should not feel any shame or reservations to share their nutritional preferences and habits and that no judgment would be made on their choices, which would remain anonymous. In each classroom, a researcher distributed the questionnaires among the students and, after the classroom teacher read the questionnaire aloud, we asked the students to answer the questions. A researcher and a teacher in each classroom clarified possible doubts of the students about the questions. The questionnaire was divided into the following sections:

(1) Social information: The first section of the questionnaire inquired about the socioeconomic background of the respondent's household, such as the student's parents' occupation, age, and gender.
(2) Meat consumption: The students were asked to list the type of animals they consumed, the frequency of consumption, and the last time they had consumed that animal. As a follow-up, a 24-h recall was used to assess recent consumption of animal protein (from domestic or wild origin). The 24-h recall method is a low-cost and effective tool for rapid evaluations, collecting information from several respondents in a minimum amount of time (van Vliet et al., 2014).
(3) Meat taste preference and meat avoidance: Students were asked to select three types of preferred sources of protein-based on a multiple-choice list derived from all available sources of protein in the region. The question asked: "Among the sources of protein listed below, please list those that you like eating the most in terms of taste?" Students were also asked to freely mention animals protein that they would avoid eating if offered.

Data Compilation

The occupation of the students' fathers and mothers was independently categorized as (1) nature-related (fisher, farmer, or sugarcane plantation worker) and (2) not nature-related (service industry worker, public or private employee, business owner, merchant, unemployed or retired).

Spatial information was downloaded from the Brazilian Institute of Geography and Statistics (IBGE, 2010). The shortest distance from each village to the EPA BRM boundary was manually estimated using the Measure Distance tool in Google Earth. For villages located within the EPA, BRM distance was set to zero.

Meat protein classification: Wild animals were categorized as aquatic animals (mollusks, crustaceans, and fish) and game (terrestrial mammals, birds, reptiles, and amphibians). Species identification was determined through visits to local communities and by consulting recent ethnotaxonomic and ethnozoological studies conducted in the study region (Mourão and Nordi, 2003; Araujo et al., 2006; Feijó and Langguth, 2013; Nascimento et al., 2016). For non-wild meat, we considered the domestic source of protein (eggs, the meat of cow and pig, chicken, etc.) and processed meat (canned meat/fish, etc.).

Data Analysis

Consumption and Taste Preference for Domestic or Wild Animals

We performed a linear model to investigate the relationship between species consumed in the last 24 h and preferred species.

Effect of Social Variables on Consumption and Preference

We used generalized linear mixed models (GLMMs) to verify if social factors influenced on the:

(1) Consumption of domestic, fish, and game meat in the day before the interview (24-h recall);
(2) preference for these different protein sources;
(3) consumption of game in previous weeks.

Predictor variables included: (i) distance from the students' villages in relation to the environmental protection area; (ii) students' sex; (iii) students' age; (iv) mothers' occupation, and (v) fathers' occupation. We considered the student and the student village predictor variables of random effect, while other predictor variables were considered as fixed effects. We tested and found no collinearity ($p > 0.06$) between all predictor variables.

We used residual checks to verify whether our models were, in principle, suitable or otherwise. We used the Akaike information criterion to select models of interest if ΔAIC values > 6 (ΔAIC obtain from the difference between a null and complete model AIC values) (Harrison et al., 2018). To evaluate the performance of each model we used the receiver operating characteristic (ROC) curve and its area under the curve (ROC AUC). The ROC AUC scores can vary from 0.5 (predictive ability expected by chance) to 1 (perfect predictive ability), with values higher than 0.7 indicating good predictive capabilities of the models (Swets, 1988; Stringham et al., 2021). All inferential analyses were performed in R ver. 3.5.3 (R Core Team, 2019) using packages MuMin, lme4 (Oksanen et al., 2013), and pROC (Robin et al., 2021).

Factors Related to Rejection of Domestic and Wild Species

We performed Principal Component Analysis (PCA) to find out how the causes used by students to explain rejection (feelings) were related to different species and students' gender. We interpreted the results when the first two components of the PCA (PC1 and PC2) represented at least 70% of the variation in the data.

The data matrix was transformed using the Hellinger method so that the PCA could properly represent our data. We used an Anosim permutation test *a posteriori* to verify the existence of groupings of cited species and the sex of the interviewee.

RESULTS

The interviewed Potiguara students ($n = 843$) reported consuming a variety of vertebrate and invertebrate species, both domestic and wild. Among vertebrates, the most representative group were mammals ($n = 14$ species) and fish ($n = 13$ species). Among invertebrates, there were five species of crustaceans and one of mollusk (**Supplementary Material**). A total of 51% of the students consumed game meat from 22 taxa at least once in their lifetime. Of those, 46% had consumed game meat during the year of the interview (the year 2018) and 54% in past years. The game species consumed by most students were armadillos (Dasypodidae) ($n = 237$; 28%), capybara (*Hydrochoerus hydrochaeris*) ($n = 166$; 20%) and iguana (*Iguana iguana*) ($n = 128$; 15%).

The 24 h-recall survey yielded 40 species of animals consumed belonging to 32 genera distributed among aquatic animals ($n = 24$), game ($n = 9$), and domestic ($n = 5$) species. Despite the lower number of domestic species consumed, 70% of the 1,945 reported events of animal consumption were domestic meat sources ($n = 1{,}359$). From this, beef ($n = 377$; 28%) and chicken ($n = 263$; 19%) were the most consumed sources of domestic meat. Wild animals were only consumed by 40% of the respondents in the 24 h recall ($n = 586$). Of those, most had consumed aquatic animals (95%), and 5% had consumed game. Armadillos (Dasypodidae) was the game taxon consumed by most students ($n = 11$), followed by capybara ($n = 5$) (**Figure 2**).

Preference

Potiguara students cited a total of 45 taxa as preferred meat divided among aquatic wildlife (24 taxa and 12 identified species), game animals (15 taxa and 9 identified species), and six domestic species[1]. However, from a total of 2,559 citations of preferred meat, the percentage of domestic sources (1,459; 57%) was significantly higher than that of wild sources (1,110; 43%) ($p = 6.932\text{e-}16$). The preferred items among domestic sources were beef ($n = 458$ citations, 31%) and processed meats ($n = 315$ citations, 28%).

Considering only wild animals, preference for aquatic animals was significantly higher than that for game ($p < 2.2\text{e-}16$) (**Table 1**). The most cited items were crustaceans ($n = 521$ citations, 46%), fish ($n = 234$, 22%) and mollusks (16%). Across all taxa, preference and consumption on the previous day were positively correlated ($p < 2.2\text{e-}16$) (**Figure 2**).

Social Factors Affecting Consumption and Preference for Different Sources of Meat

A total of 321 students in the study's cohort lived in villages within the protected area (EPA BRM) and 116 (36%) of them had consumed game at least once. The proportion of students from outside the protected area ($n = 522$) who had consumed game meat was almost double (60%, $n = 314$) that of students living inside the protected area (**Figure 1**). Our analyses show that consumption of game in previous weeks (**Figure 3A**) and preference (**Figure 3C**) increased with the distance from the protected area. The consumption of fish and domestic meat (but not the preference) also increased with the distance from the protected area (**Figures 3D,F**). We found that male students and students whose fathers are involved in nature-related work eat game more often (24 h survey and overall) and show a higher preference for it (**Figures 3A–C**). Fish consumption was higher for students whose fathers are involved in nature-related work (**Figure 3D**), while a non-significant trend indicates that students whose parents do not develop nature-related work consume more

[1] https://www.sciencedirect.com/science/article/abs/pii/S0006320710000182

TABLE 1 | Estimates of generalized linear mixed models selected based on the Akaike Information Criterion (AIC) and the area under the curve (AUC) of the receiver operating characteristic (ROC).†

Response variable	Predictor variables	Estimate	Std. Error	*z*-value	Pr (>|z|)	AIC	AIC null model	ΔAIC	AUC
Game consumption	Fathers' occupation (Nature related ÷ Not nature related)	1.61E-01	7.63E-02	2.111	0.0351*	1485.4	1546.2	60.8	0.759
	Mothers' occupation (Nature related ÷ Not nature related)	8.34E-02	9.24E-02	0.902	0.3675				
	Male sex	2.78E-01	6.95E-02	3.998	7.03E-05***				
	Age	4.19E-03	7.76E-03	0.539	0.5899				
	Distance to the protected area	4.00E-05	8.44E-06	4.743	2.52E-06***				
Game recall	Fathers' occupation (Nature related ÷ Not nature related)	8.20E-01	4.91E-01	1.668	0.095695	241.96	245.2	3.2	0.692
	Mothers' occupation (Nature related ÷ Not nature related)	4.07E-01	4.54E-01	0.896	0.370381				
	Male sex	7.92E-01	4.03E-01	1.963	0.050068				
	Age	−4.06E-02	6.19E-02	−0.656	0.511943				
	Distance to the protected area	3.93E-05	4.59E-05	0.856	0.392201				
Game preference	Fathers' occupation (Nature related ÷ Not nature related)	4.70E-01	1.99E-01	2.369	0.01809*	661.64	719.64	58.0	0.704
	Mothers' occupation (Nature related ÷ Not nature related)	1.10E-01	2.20E-01	0.498	0.61897				
	Male sex	7.70E-01	1.79E-01	4.311	1.84E-05***				
	Age	−3.03E-02	2.71E-02	−1.117	0.26451				
	Distance to the protected area	7.31E-05	2.00E-05	3.65	0.00028***				
Fisheries Recall	Fathers' occupation (Nature related ÷ Not nature related)	2.41E-01	1.15E-01	2.092	0.0368*	1135.0	1165.0	30.0	0.715
	Mothers' occupation (Nature related ÷ Not nature related)	1.40E-01	1.35E-01	1.035	0.301				
	Male sex	1.01E-01	1.04E-01	0.969	0.3328				
	Age	9.04E-03	1.08E-02	0.841	0.4007				
	Distance to the protected area	3.06E-05	1.26E-05	2.424	0.0156*				
Fisheries preference	Fathers' occupation (Nature related ÷ Not nature related)	−1.79E-02	1.28E-01	−0.14	0.889	1020.4	1021.4	1.0	0.571
	Mothers' occupation (Nature related ÷ Not nature related)	5.92E-02	1.60E-01	0.371	0.711				
	Male sex	1.15E-01	1.18E-01	0.975	0.33				
	Age	8.24E-03	1.25E-02	0.661	0.509				
	Distance to the protected area	2.23E-05	1.45E-05	1.542	0.124				
Domestic recall	Fathers' occupation (Nature related ÷ Not nature related)	−5.67E-02	3.12E-02	−1.821	0.06902	1940.9	1948.1	7.2	0.695
	Mothers' occupation (Nature related ÷ Not nature related)	−3.59E-02	4.02E-02	−0.893	0.37235				
	Male sex	−1.61E-02	2.90E-02	−0.556	0.57813				
	Age	2.09E-03	3.23E-03	0.646	0.51818				
	Distance to the protected area	8.17E-06	3.63E-06	2.252	0.0246*				
Domestic preference	Fathers' occupation (Nature related ÷ Not nature related)	−2.10E-02	2.33E-02	−0.899	0.369	2001.5	2003.5	2.0	0.609
	Mothers' occupation (Nature related ÷ Not nature related)	1.19E-02	2.98E-02	0.399	0.69				
	Male sex	−2.53E-02	2.17E-02	−1.17	0.242				
	Age	−8.42E-04	2.44E-03	−0.345	0.73				
	Distance to the protected area	3.27E-06	2.72E-06	1.2	0.231				

†*Estimate values indicate the coefficient associated with the variables listed on the left and represent how response variables values would change as a result of a one-unit variation in the predictor variables (log x). The standard errors are the average estimates of how response variables would fluctuate if the study was executed the same way, however, with new data. The Z-values indicate the level at which the explanatory variables would have a significant effect. Pr (> |z|) are listed as two-tailed p-values that correspond to the z-values following a normal distribution pattern. Significance levels are as follow: ns $p > 0.05$; *$p \leq 0.05$; ***$p \leq 0.001$.*

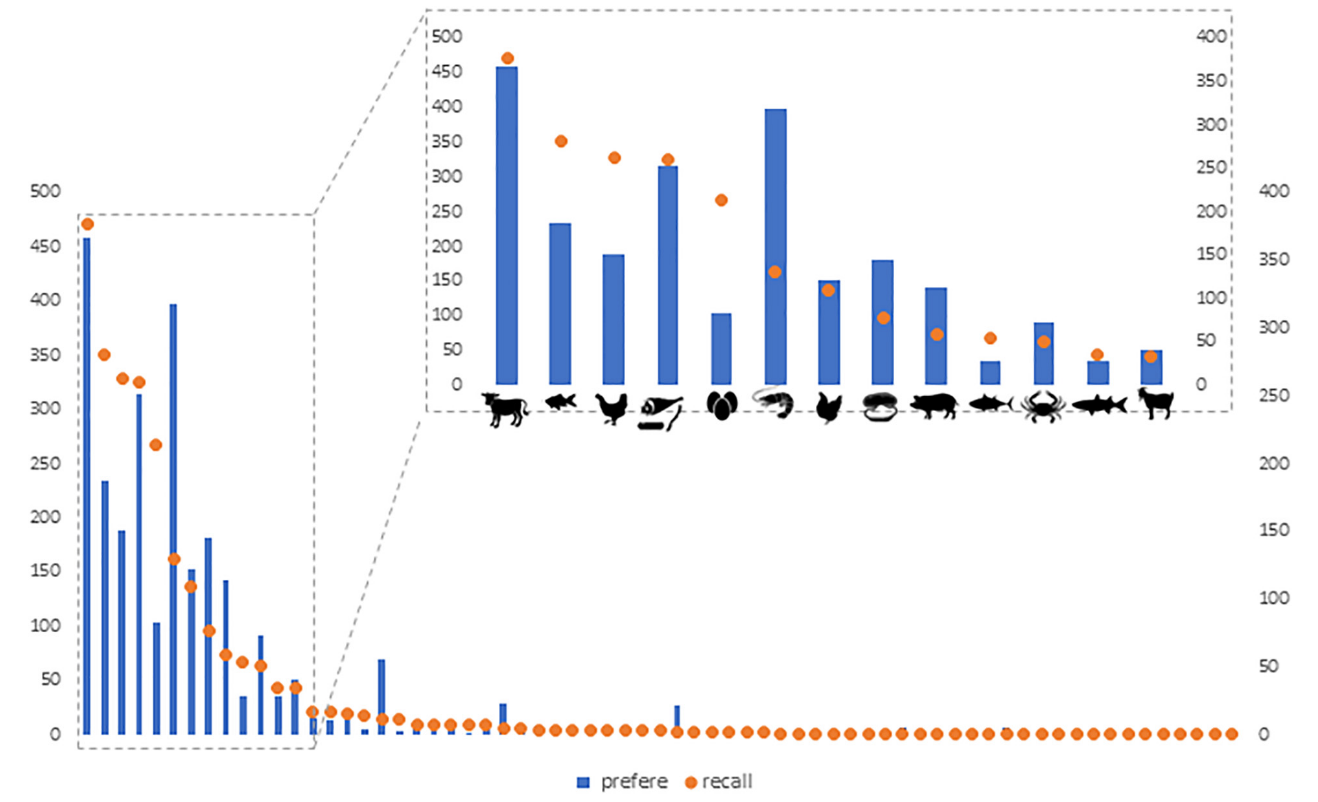

FIGURE 2 | Potiguara students' consumption (24-h recall) (orange circle) and preference (blue bars) for sources of animal protein. The left Y-axis is the number of consumption events reported per species and the right Y-axis is the number of times the species was mentioned as preferred. Zoomed area shows the 13 most consumed types of meat the day before the interview.

domestic meat (**Figure 3F**). We did not find any influence of the variables analyzed on the preference for aquatic animals and domestic resources (**Figures 3E,G**).

Avoidances

Most of the students expressed rejection to some type of meat ($n = 677$; 80.3%). Among those students, 77% cited game animals ($n = 524$ students), 20% domestic animals ($n = 133$) and 3% aquatic wildlife ($n = 20$). A total of 42 taxa were mentioned, being 34 wild and 8 domestics. Taxa rejected by more students were snakes ($n = 114$) and armadillos ($n = 61$). Disgust (14%) and pity (13%) were the most common causes for rejecting different types of meat.

The PCA analysis described a total of 77% of the data variance and shows how different causes for rejection (feelings) are related to the most rejected animal species and the gender of the students (**Figure 4**). Rejection toward the meat of some species was shown to be related to people's feelings and their perception of its visual appearance. For male and female students, the feeling of pity was associated with the sloth (*Bradypus variegatus*) and the Brazilian rabbit (*Sylvilagus brasiliensis*), while certain qualities of the meat, like smell, taste, and appearance, motivated the rejection of caiman (*Caiman latirostris*). The rejection of pork and snake meat by students of both genders was strongly related to them being considered harmful if eaten.

DISCUSSION

In this paper, we assessed the dietary patterns among the Potiguara, particularly the consumption of animal-based sources of protein. Our study confirms trends observed in other parts of South America where industrial meats bypass the consumption of wild-sourced proteins among the younger generations of indigenous peoples (Murrieta and Dufour, 2004; Nardoto et al., 2011; van Vliet et al., 2015b). This transition is particularly common as urbanization progresses, domestic and industrialized sources of animal protein become readily available, and wildlife decreases as a result of habitat fragmentation and water pollution (Nardoto et al., 2011; Prist et al., 2012; van Vliet et al., 2014, van Vliet et al., 2015b,c; Vanegas et al., 2016). In this context, our study shows that young Potiguara does not consume game animals frequently and that they prefer to eat beef or industrial meats.

The higher consumption of domestic sources of animal protein outside the protected area might be associated with the dense road network and easier access to food markets from neighboring urban centers. Connection to markets via roads has been pointed out in several places as an important determinant of household food consumption (Kramer et al., 2009). This is because the roads allow access to industrialized products, thus

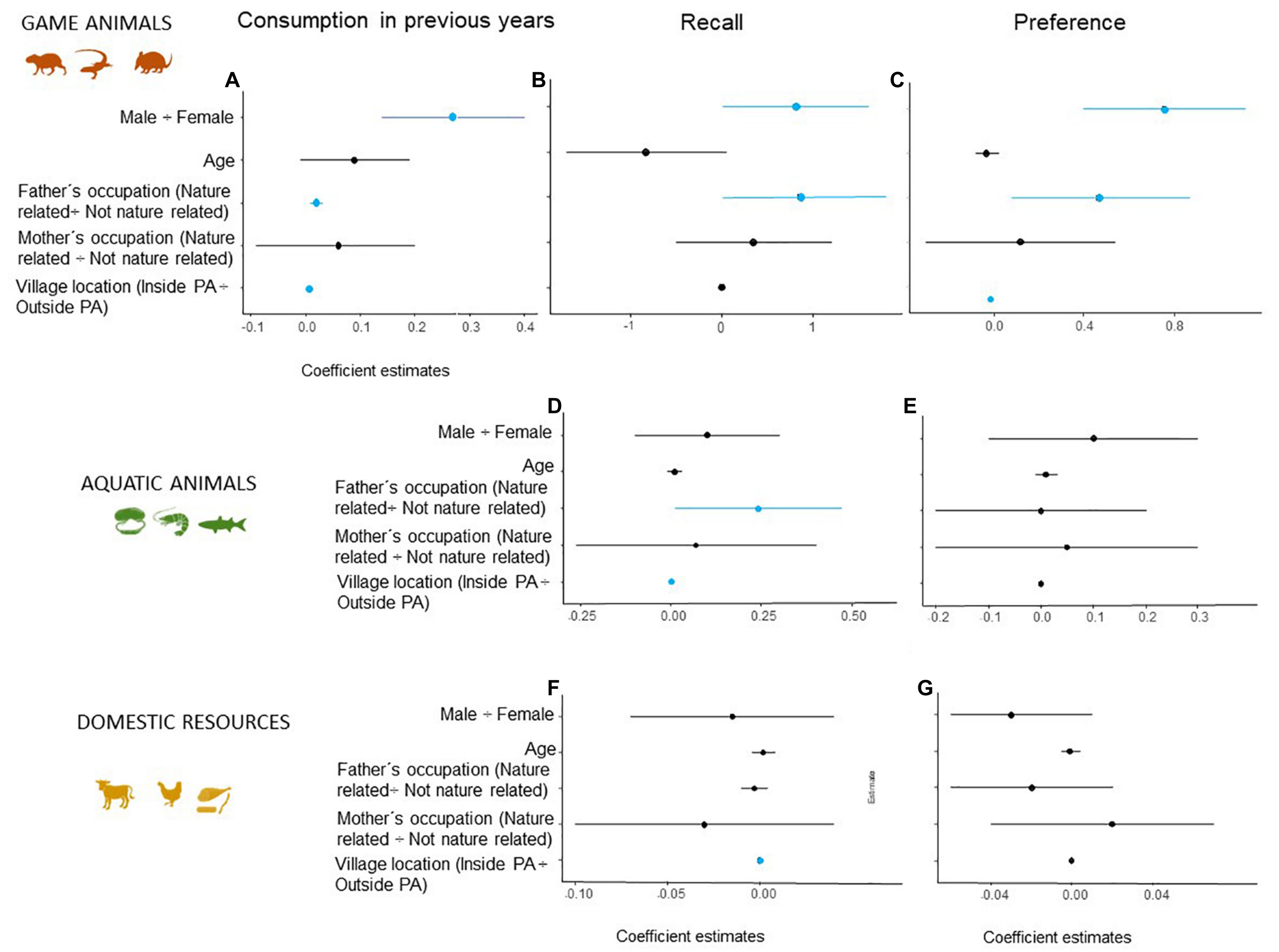

FIGURE 3 | Generalized linear mixed models (GLMMs) to evaluate consumption in previous weeks, consumption the day before the interview (24-h recall), and preference for game resources (**A–C**, respectively), aquatic wildlife **(D,E)**, and domestic sources of meat **(F,G)**. Coefficient estimates (±95% confidence interval) show how social factors modulate (direction and magnitude) consumption of game. Black and blue dots represent, respectively, the absence of significant effect and significant positive effect in the response variable.

providing a diet shift from traditional to market-based foods. Conversely, the low frequency of game consumption found can probably be explained by low wildlife abundance. In our study site, the landscape is composed of small forest remnants immersed in a matrix of agricultural fields, sugarcane plantations, and shrimp farming ponds. Most villages are connected and nearby urban centers through a network of highways and dirt roads (Cardoso and Guimarães, 2012).

Wildlife abundance in the Potiguara IL has dramatically decreased since the agricultural and real estate expansion in the 1980s, a general pattern across the Atlantic Forest of Northeastern Brazil, which has led to the highest defaunation rates of terrestrial vertebrates in the country (Bogoni et al., 2018). These changes have a marked effect on the consumption of game animals in the study area.

In contrast, aquatic wildlife represents a considerable portion of the Potiguara diet, the majority of the Potiguara population depends on aquatic wildlife harvested at the Mamanguape river estuary and mangrove, especially fish and crustaceans (Mourão and Nordi, 2003; Araujo et al., 2006; Araujo and Nishida, 2007). For instance, the third most consumed animal recorded by the 24-h recall method was crab *Ucides cordatus* which for decades has been a key source of income in the region. Other species widely available in the region are commonly consumed by the young Potiguara, such as clams, *"marisco" Anomalocardia brasiliana*, and *Mugil curema* (e.g., mullet/tainha). Rocha et al. (2008) recorded 68 species of fish, crustaceans, and mollusks used for food or income in the estuary of the Mamanguape River, many of which were also recorded in this study (e.g., mullet/tainha *Mugil curema*, snook/camurim *Centropomus* sp.). Aquatic wildlife has a prominent status as part of the Potiguara identity and is the main staple in Potiguara's traditional feasts, such as during the "shrimp festival" when fish and crustaceans are shared among villages (Cardoso and Guimarães, 2012).

The high consumption of aquatic wildlife recorded in this study could be related to the numerous rivers and abundant aquatic resources (Rocha et al., 2008;

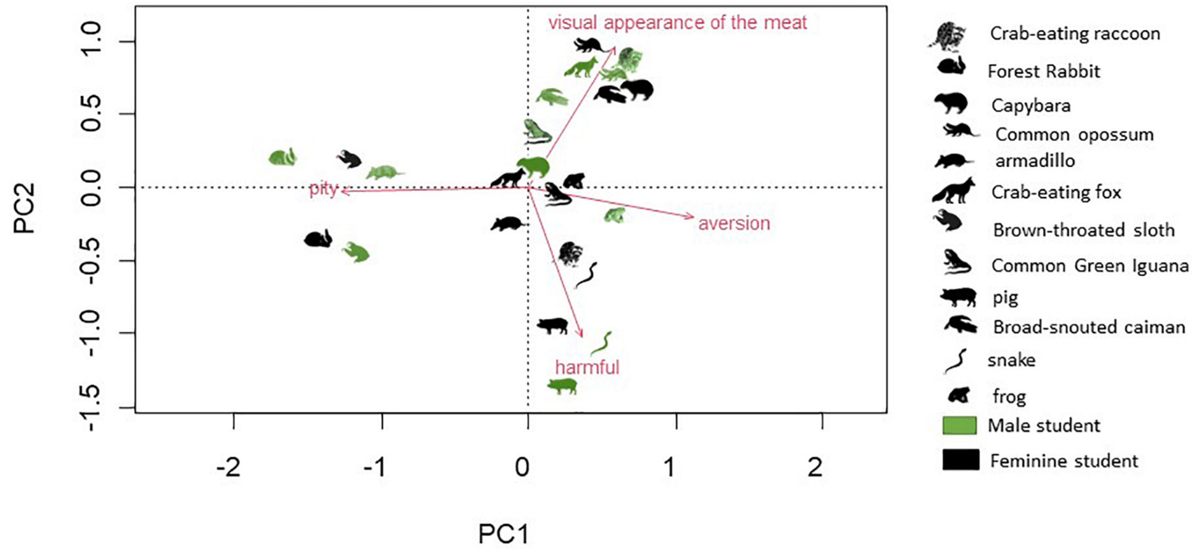

FIGURE 4 | Description of reject species in terms of motivations for rejection by female and male students obtained from a Principal Component Analysis (PCA).

Cardoso and Guimarães, 2012) which provide enough food for Potiguara households. As observed in Amazonia, greater fish availability induces lower reliance on hunting (Sarti et al., 2015; Endo et al., 2016) and this is yet another reason for the low game consumption. The healthy estuary is in stark contrast with the highly fragmented forest remnants of the region (Alves and Nishida, 2002). Villages situated in the coastal areas have access to marine environments with a variety of plant and animal species that are not available to inland communities (Turner, 1995; Mitchell and Donald, 2001; Mulrennan and Bussières, 2018), therefore, they are expected to be incorporated into the local diet. As remarked by Alves and Rosa (2006), the use of more accessible resources possibly is related to historic aspects, for example, the knowledge focusing on species familiar to the locals, reflecting the transmission of knowledge through generations.

We found that both consumptions of aquatic animals and game increased with the distance from the protected area. This might be because, inside the protected area, the use and management of aquatic resources are allowed, but hunting is forbidden (Brasil, 2000). On the other hand, indigenous peoples have rights to their land and their natural resources, game species included, warranted by the Brazilian constitution (Brasil, 1988). Since the Potiguara IL and the EPA BRM (the protected area) partially overlap, the Potiguara must constantly navigate a legal limbo of conflicting rules. Hunting is portrayed as a negative or criminal activity by the environmental agencies in charge of the EPA BRM and this contributes to further marginalizing this activity. Fears of being penalized by law enforcement jeopardize the role that hunting used to play in the protein complementation of the Potiguara living inside the protected area. Although we found a low consumption of game meat as compared to aquatic resources and domestic sources of animal protein, this consumption still occurs and deserves attention, both from the point of view of food security discussed previously, and in relation to the target species conservation. Regarding this, we emphasize that in the studied areas where hunting is allowed there is no management and monitoring program of game fauna. These programs could reduce potential impacts of hunting on game, in addition to promoting a better understanding of the current consumption and importance of game animals for the Potiguara population. Regarding on that, successful initiatives have integrated scientific and local knowledge into local hunting rules and sustainable harvest of target species, while promoting biodiversity conservation and empowering local people (Campos-Silva et al., 2018).

In our study, the consumption of wild animals (game and fisheries) was higher among children whose fathers have nature-related occupations. This pattern might result from their higher exposure to wild resources during worktime, especially among those fathers whose income comes from exploiting wild resources (e.g., fishers). Opportunistic hunting upon chance encounters during agricultural or other activities has also been reported in Madagascar (Gardner and Davies, 2014). In the studied region women play an important role in supporting families by harvesting wild species for food, such as "camurim"/snook *Centropomus* sp., and for traditional medicine use, such as seahorse *Hippocampus reidi* and tarpon *Megalops atlanticus* (Rocha et al., 2012). Nevertheless, a statistically significant relationship was not found between fisher mothers and students' consumption of fishing resources, maybe due to the low proportion of fisher mothers among the study's cohort (*ca.* 4%).

The lack of effect of age on the consumption of game meat by the Potiguara might be explained by the small age range of the cohort of students in the study (94.4% aged 10–20 years). Possibly, younger people consider consuming game meat an outdated tradition, especially in more urbanized areas.

Studies covering a wider age range have shown that game meat consumption is lower among younger people, who often regard it as not socially acceptable (Luiselli et al., 2019). We found a greater preference for game meat among male students, who also consumed it more often when compared to female students. In a study developed in Cameroon based on 1 year of weekly recall, data men reported eating game meat more often than women (149 women, 117 men, aged 16–75 years). However, this pattern was not stable across all age groups. Consumption of game meat was more frequent among younger men than among younger women (<35 years of age), whereas older women ate game meat more often than older men (aged 35–54 years) (Duda et al., 2018).

Nearly one-fourth of the students ($n = 205$) deemed wild meat of certain species as repulsive, such as snake, frog, and the lizard *S. merianae*. The main reasons for students to reject the meat of certain animals were related to feelings of pity and disgust, considering its consumption harmful, and to specific qualities of the meat, like smell, taste, and appearance. A similar pattern has been recorded in traditional communities elsewhere and is often related to food taboos (Barboza et al., 2016), animals' morphology or smell (Figueiredo and Barros, 2016), and the feeding habits of scavenger species (Souza and Alves, 2014). Prevalent rejection of sloths might result from peoples' affection since they are regularly observed in green spaces near the communities or urban areas, and the species is often subject to awareness campaigns developed by conservation projects in the area. We postulate that the greater preference for domestic meat and aquatic resources among Potiguara students is mainly due to the greater students' familiarity with those sources of protein.

The nutritional transition evidenced in our study area among the young Potiguara leads to concerns already raised in other studies that have recorded the rapid changes taking place in the diets of Indigenous peoples (Kuhnlein, 2009; Welch et al., 2009; van Vliet et al., 2015a). These transitions are sensitive indicators of the ecological and cultural costs that the changes brought about by modernity imply for indigenous people (Dounias and Froment, 2011; van Vliet et al., 2015a). The replacement of game meat or fish for industrialized meats and the change to a more sedentary lifestyle leads to increasing rates of overweight, obesity, and associated chronic diseases such as cancer, heart disease, and diabetes (Popkin, 1994; Popkin and Gordon-Larsen, 2004; Parrotta et al., 2015). The transformations of landscapes, economies, and lifestyles of these populations represent threats to their sovereignty and food security, which go beyond that since the right to healthy food is interconnected with ethnic identity, traditional knowledge systems, sustainability, and wellbeing (van Vliet et al., 2018, 2022; Jacob et al., 2021; Welch et al., 2021). In this sense, nutritional transitions and their implications for indigenous peoples must be seriously taken into consideration in public policies, especially those focused on biodiversity conservation, food, nutrition, and health.

Despite its growing dietary importance, information on animal protein consumption by indigenous groups from Brazil is scarce, emphasizing the need for further research on the topic. To our knowledge, this is the first study to address the role that wild animals and domestic and processed meat/fish play in the food security of coastal indigenous populations from Brazil.

Although we focused our interviews mainly on young people, we believe that our results can extrapolate this scope, since students' eating habits are a reflect of the daily eating behaviors of the homes where these students are inserted. This study illustrates that wild animal's consumption and preference by Potiguara students are modulated by a set of environmental and social factors, such as students' father's occupation, policies, and regulations, deforestation, and urbanization that shape the use of wildlife as a source of food and determine their role in securing food sufficiency among traditional populations.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The research project was approved by the Research Ethics Committee and the National Research Ethics Commission (CEP/CONEP), in accordance with Resolution No. 466/2012 of the National Health Council (CNS) of the Ministry of Health (No. 2,491,305). This research was authorized by the Brazilian Agency for Indian Affairs (FUNAI) (No. 94/AAEP/PRES/2017) and indigenous leaders in compliance with CNS Resolution No. 304 of 2000. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

CS, NV, and RA conceived the ideas and designed the methodology. CS collected the data. CS, FB-P, and AB compiled and analyzed the data. CS and FB-P wrote the original draft. CS, FB-P, AB, NV, and RA edited the manuscript. All authors gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.900398/full#supplementary-material

REFERENCES

Alves, R. R. N., Nishida, A. K., and Hernández, M. I. (2005). Environmental perception of gatherers of the crab 'caranguejo-uçá' (*Ucides cordatus*, Decapoda, Brachyura) affecting their collection attitudes. *J. Ethnobiol. Ethnomed.* 1:10. doi: 10.1186/1746-4269-1-10

Alves, R. R. N., and Rosa, I. L. (2006). From cnidarians to mammals: the use of animals as remedies in fishing communities in NE Brazil. *J. Ethnopharmacol.* 107, 259–276. doi: 10.1016/j.jep.2006.03.007

Alves, R. R. N., and Nishida, A. K. (2002). A ecdise do caranguejo-uçá, *Ucides cordatus* L. (Decapoda, Brachyura) na visão dos caranguejeiros. *Interciencia* 27, 110–117.

Alves, R. R. N., and Nishida, A. K. (2003). Aspectos socioeconômicos e percepção ambiental dos catadores de caranguejo-uçá *Ucides cordatus* cordatus (L. 1763) (Decapoda, Brachyura) do estuário do Rio Mamanguape, Nordeste do Brasil. *Interciencia* 28, 36–43.

Alves, R. R. N., Souto, W. M. S., Fernandes-Ferreira, H., Bezerra, D. M. M., Barboza, R. R. D., and Vieira, W. L. S. (2018). "The importance of hunting in human societies," in *Ethnozoology: Animals in Our Lives*, eds R. R. N. Alves and U. P. Albuquerque (Cambridge, MA: Academic Press), 95–118. doi: 10.1016/B978-0-12-809913-1.00007-7

Alves, R. R. N., and van Vliet, N. (2018). "Wild fauna on the menu," in *Ethnozoology: Animals in Our Lives*, eds R. R. N. Alves and U. P. Albuquerque (Cambridge, MA: Academic Press), 167–194. doi: 10.1016/B978-0-12-809913-1.00010-7

Anderson, J. K. (2020). *Hunting in the Ancient World*. Available Online at: https://ixtheo.de/Record/272807982 [accessed January 21, 2021].

Araujo, H. F. P., and Nishida, A. K. (2007). Conhecimento de pescadores artesanais sobre a composição da avifauna em estuários paraibanos: uma contribuição para a conservação. *Sitientibus* 7, 67–77. doi: 10.13102/scb8133

Araujo, H. F. P., Rodrigues, R. C., and Nishida, A. K. (2006). Composição da avifauna em complexos estuarinos no estado da Paraíba, Brasil. *Rev. Bras. Ornitol.* 14, 249–259.

Araújo, M. Q. (2015). *Entre Terreiros, Roçados e Marés: Um Estudo Sobre a Organização Doméstica Entre Os Potiguara do Litoral Norte da Paraíba*. Rio Tinto: Universidade Federal da Paraíba.

Araújo, M. Q. (2019). Household ecology, environments and technical processes among the Potiguara of Jaraguá village (Paraíba, Brazil). *Vibrant Virtual Braz. Anthropol.* 16, 1–23. doi: 10.1590/1809-43412019v16d502

Barboza, R. R. D., Lopes, S. F., Souto, W. M., Fernandes-Ferreira, H., and Alves, R. R. N. (2016). The role of game mammals as bushmeat in the Caatinga, northeast Brazil. *Ecol. Soc.* 21:2. doi: 10.5751/ES-08358-210202

Bellinger, C., and Andrade, L. (2016). *Alimentação nas Escolas Indígenas: Desafios Para Incorporar Práticas e Saberes*. Available Online at: https://cpisp.org.br/wp-content/uploads/2016/05/Alimentacao_Escolas_Indigenas.pdf [accessed January 21, 2021].

Bodmer, R. E., Eisenberg, J. F., and Redford, K. H. (1997). Hunting and the likelihood of extinction of Amazonian mammals: caza y probabilidad de extinción de mamiferos Amazónicos. *Conserv. Biol.* 11, 460–466. doi: 10.1046/j.1523-1739.1997.96022.x

Bogoni, J. A., Pires, J. S. R., Graipel, M. E., Peroni, N., and Peres, C. A. (2018). Wish you were here: how defaunated is the Atlantic Forest biome of its medium- to large-bodied mammal fauna? *PLoS One* 13:e0204515. doi: 10.1371/journal.pone.0204515

Braga-Pereira, F., Morcatty, T. Q., El Bizri, H. R., Tavares, A. S., Mere-Roncal, C., González-Crespo, C., et al. (2021b). Congruence of local ecological knowledge (LEK) based methods and line-transect surveys in estimating wildlife abundance in tropical forests. *Methods Ecol. Evol.* 13, 743–756. doi: 10.1111/2041-210X.13773

Braga-Pereira, F., Peres, C. A., Alves, R. R. N., and Van-Dúnem Santos, C. (2021a). Intrinsic and extrinsic motivations governing prey choice by hunters in a post-war African forest-savannah macromosaic. *PLoS One* 16:e0261198. doi: 10.1371/journal.pone.0261198

Brasil (1988). *Artigo 231 da Constituição Federal de 1988*. Available Online at: http://www.planalto.gov.br/ccivil_03/constituicao/constituicao.htm [accessed December 4, 2021].

Brasil (2000). *Lei n° 9.98, de 18 de Julho de 2000. Law Establishing the National System of Nature Conservation Units*. Available Online at: http://www.planalto.gov.br/ccivil_03/leis/l9985.htm [accessed December 4, 2021].

Câmara, I. G. (2003). "Brief history of conservation in the Atlantic Forest," in *The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook*, eds C. GalindoLeal and I. G. Câmara (Washington, DC: Center for Applied Biodiversity Science and Island Press), 31–42.

Campos-Silva, J. V., Hawes, J. E., Andrade, P. C., and Peres, C. (2018). Unintended multispecies co-benefits of an Amazonian community-based conservation programme. *Nat. Sustain.* 1, 650–656. doi: 10.1038/s41893-018-0170-5

Capistrano, J., and Lopes, P. (2012). Crab gatherers perceive concrete changes in the life history traits of *Ucides cordatus* (Linnaeus, 1763), but overestimate their past and current catches. *Ethnobiol. Conserv.* 1, 1–21. doi: 10.15451/ec2012-8-1.7-1-21

Cardoso, T. M., and Guimarães, G. C. (2012). *Etnomapeamento dos Potiguara da Paraíba*. Daito: FUNAI.

Chee, V. A., Teran, E., Hernandez, I., Wright, L., Izurieta, R., Reina-Ortiz, M., et al. (2019). 'Desculturización,' urbanization, and nutrition transition among urban Kichwas indigenous communities residing in the Andes highlands of Ecuador. *Public Health* 176, 21–28. doi: 10.1016/j.puhe.2019.07.015

Coimbra, C. E., and Santos, R. V. (1991). Avaliação do estado nutricional num contexto de mudança sócio-econômica: o grupo indígena Suruí do Estado de Rondônia, Brasil. *Cad. Saúde Pública* 7, 538–562. doi: 10.1590/S0102-311X1991000400006

Donders, I., and Barriocanal, C. (2020). The influence of markets on the nutrition transition of hunter-gatherers: lessons from the western Amazon. *Int. J. Environ. Res. Public Health* 17:6307. doi: 10.3390/ijerph17176307

Dounias, E., and Froment, A. (2011). From foraging to farming among present-day forest hunter-gatherers: consequences on diet and health. *Int. For. Rev.* 13, 294–304. doi: 10.1505/146554811798293818

Duda, R., Gallois, S., and Reyes-García, V. (2018). Ethnozoology of bushmeat. Importance of wildlife in diet, food avoidances and perception of health among the Baka (Cameroon). *Rev. Ethnoecol.* 14, 1–41. doi: 10.4000/ethnoecologie.3976

Endo, W., Peres, C. A., and Haugaasen, T. (2016). Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biol. Conserv.* 201, 129–136. doi: 10.1016/j.biocon.2016.07.006

Feijó, A., and Langguth, A. (2013). Mamíferos de médio e grande porte do Nordeste do Brasil: distribuição e taxonomia, com descrição de novas espécies. *Rev. Nordestina Biol.* 22, 3–225.

Figueiredo, R. A. A. D., and Barros, F. B. (2016). Hunting, preparing, and eating the 'bicho do mato': feeding practices among quilombolas in the Ipaú-Anilzinho extractive reserve (Pará State). *Bol. Mus. Para. Emílio Goeldi* 11, 691–713. doi: 10.1590/1981.81222016000300009

Gardner, C. J., and Davies, Z. G. (2014). Rural bushmeat consumption within multiple use protected areas: qualitative evidence from southwest Madagascar. *Hum. Ecol.* 42, 21–34. doi: 10.1007/s10745-013-9629-1

Hanazaki, N., Alves, R. R. N., and Begossi, A. (2009). Hunting and use of terrestrial fauna used by Caiçaras from the Atlantic Forest coast (Brazil). *J. Ethnobiol. Ethnomed.* 5:36. doi: 10.1186/1746-4269-5-36

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E., et al. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794. doi: 10.7717/peerj.4794

IBGE (2010). *Instituto Brasileiro de Geografia e Estatística*. Available Online at: https://censo2010.ibge.gov.br/ [accessed December 4, 2021].

ISA (2021). *Terras Indígenas*. Available Online at: https://terrasindigenas.org.br/pt-br/brasil [accessed December 4, 2021].

Jacob, M. C. M., Teixeira, C. D., Bautista, D. A., and Ramos, V. A. N. (2021). Ethnonutrition. *Ethnobiol. Conserv.* 10, 1–8.

Kendie, F. A., Mekuriaw, S. A., and Dagnew, M. A. (2018). Ethnozoological study of traditional medicinal appreciation of animals and their products among the indigenous people of Metema Woreda, North-Western Ethiopia. *J. Ethnobiol. Ethnomed.* 14:37. doi: 10.1186/s13002-018-0234-7

Kraft, T. S., Stieglitz, J., Trumble, B. C., Martin, M., Kaplan, H., and Gurven, M. (2018). Nutrition transition in 2 lowland Bolivian subsistence populations. *Am. J. Clin. Nutr.* 108, 1183–1195. doi: 10.1093/ajcn/nqy250

Kramer, D. B., Urquhart, G., and Schmitt, K. (2009). Globalization and the connection of remote communities: a review of household effects and their biodiversity implications. *Ecol. Econ.* 68, 2897–2909. doi: 10.1016/j.ecolecon.2009.06.026

Kuhnlein, H. V. (2009). "Introduction: why are indigenous peoples' food systems important and why do they need documentation?," in *Indigenous Peoples' Food Systems: the Many Dimensions of Culture, Diversity and Environment for Nutrition and Health*, eds H. V. Kuhnlein, B. Erasmus, and D. Spigelski (Rome: FAO), 1–4.

Leyva-Trinidad, D. A., Pérez-Vázquez, A., Newell, G. E., Albarado, J. C. G., and Jácome, A. G. (2021). Food security strategies of an indigenous community in Veracruz, Mexico. *Ethnobiol. Conserv.* 10:41. doi: 10.15451/ec2021-11-10.41-1-16

Lourenço, A. E. P., Santos, R. V., Orellan, J. D. Y., and Coimbra, C. E. A. (2008). Nutrition transition in Amazonia: obesity and socioeconomic change in the Suruí Indians from Brazil. *Am. J. Hum. Biol.* 20, 564–571. doi: 10.1002/ajhb.20781

Luiselli, L., Hema, E. M., Segniagbeto, G. H., Ouattara, V., Eniang, E. A., Di Vittorio, M., et al. (2019). Understanding the influence of non-wealth factors in determining bushmeat consumption: results from four West African countries. *Acta Oecol.* 94, 47–56. doi: 10.1016/j.actao.2017.10.002

Mitchell, D., and Donald, L. (2001). Sharing resources on the North Pacific coast of North America: the case of the eulachon fishery. *Anthropologica* 43, 19–35.

Mourão, J., and Nordi, N. (2003). Ethnoichthyology of artisanal fishermen from the estuary of Mamanguape River, Paraíba, Brazil. *Bol. Inst. Pesca* 29, 9–17.

Mulrennan, M. E., and Bussières, V. (2018). Social-ecological resilience in indigenous coastal edge contexts. *Ecol. Soc.* 23:18. doi: 10.5751/ES-10341-230318

Murrieta, R. S. S., and Dufour, D. L. (2004). Fish and Farinha: protein and energy consumption in Amazonian rural communities on Ituqui Island, Brazil. *Ecol. Food. Nutr.* 43, 231–255. doi: 10.1080/03670240490447550

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. doi: 10.1038/35002501

Nardoto, G. B., Murrieta, R. S. S., Prates, L. E. G., Adams, C., Garavello, M. E. P., Schor, T., et al. (2011). Frozen chicken for wild fish: nutritional transition in the Brazilian Amazon region determined by carbon and nitrogen stable isotope ratios in fingernails. *Am. J. Hum. Biol.* 23, 642–650. doi: 10.1002/ajhb.21192

Nascimento, D. M., Alves, Â. G. C., Alves, R. R. N., Barboza, R. R. D., Diele, K., and Mourao, J. S. (2016). An examination of the techniques used to capture mangrove crabs, *Ucides cordatus*, in the Mamanguape River estuary, Northeastern Brazil, with implications for management. *Ocean Coast. Manag.* 130, 50–57. doi: 10.1016/j.ocecoaman.2016.05.010

Nascimento, D. M., Alves, R. R. N., Barboza, R. R. D., Schmidt, A. J., Diele, K., and Mourão, J. S. (2017). Commercial relationships between intermediaries and harvesters of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) in the Mamanguape River estuary, Brazil, and their socio-ecological implications. *Ecol. Econ.* 131, 44–51. doi: 10.1016/j.ecolecon.2016.08.017

Nascimento, D. M., Ferreira, E. N., Bezerra, D. M., Rocha, P. D., Alves, R. R. N., and Mourão, J. S. (2012). Capture techniques' use of Caranguejo-uçá crabs (*Ucides cordatus*) in Paraíba state (Northeastern Brazil) and its socio-environmental implications. *Natl. Acad. Bras. Cienc.* 84, 1051–1064. doi: 10.1590/s0001-37652012005000066

Nielsen, M. R., Meilby, H., Smith-Hall, C., Pouliot, M., and Treue, T. (2018). The importance of wild meat in the global south. *Ecol. Econ.* 146, 696–705. doi: 10.1016/j.ecolecon.2017.12.018

Nishida, A. K., Nordi, N., and Alves, R. R. N. (2006). Mollusc gathering in Northeast Brazil: an ethnoecological approach. *Hum. Ecol.* 34, 133–145. doi: 10.1007/s10745-005-9005-x

Nishida, A. K., Nordi, N., and Alves, R. R. N. (2008). Aspectos socioeconômicos dos catadores de moluscos do litoral paraibano, Nordeste do Brasil. *Rev. Biol. Ciênc. Terra* 8, 207–215.

Nordi, N., Nishida, A. K., and Alves, R. R. N. (2009). Effectiveness of two gathering techniques for *Ucides cordatus* in Northeast Brazil: implications for the sustainability of mangrove ecosystems. *Hum. Ecol.* 37, 121–127. doi: 10.1007/s10745-009-9214-9

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., et al. (2013). *Community Ecology Package. R Package Version 2(0).*

Oliveira, M. A., El Bizri, H. R., Morcatty, T. Q., Messias, M. R., and Costa Doria, C. R. (2022). Freelisting as a suitable method to estimate the composition and harvest rates of hunted species in tropical forests. *Ethnobiol. Conserv.* 11, 1–9. doi: 10.15451/ec2022-03-11.08-1-9

Parrotta, J. A., Dey de Pryck, J., Darko Obiri, B., Padoch, C., Powell, B., Sandbrook, C., et al. (2015). "The historical, environmental and socio-economic context of forests and tree-based systems for food security and nutrition," in *Forests, Trees and Landscapes for Food Security and Nutrition*, eds B. Vira, C. Wildburger, and S. Mansourian (Vienna: IUFRO), 51–86. doi: 10.11647/OBP.0085.03

Popkin, B. (1994). The nutrition transition in low-income countries: an emerging crisis. *Nutr. Rev.* 52, 285–298. doi: 10.1111/j.1753-4887.1994.tb01460.x

Popkin, B. M., and Gordon-Larsen, P. (2004). The nutrition transition: worldwide obesity dynamics and their determinants. *Int. J. Obes.* 28, S2–S9. doi: 10.1038/sj.ijo.0802804

Powell, B., Thilsted, S. H., Ickowitz, A., Termote, C., Sunderland, T., and Herforth, A. (2015). Improving diets with wild and cultivated biodiversity from across the landscape. *Food Secur.* 7, 535–554.

Prist, P. R., Michalski, F., and Metzger, J. P. (2012). How deforestation pattern in the Amazon influences vertebrate richness and community composition. *Landsc. Ecol.* 27, 799–812. doi: 10.1007/s10980-012-9729-0

R Core Team (2019). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J. C., et al. (2021). *"Package 'pROC"', in R Package Version 1.17.0.1.*

Rocha, M. S., Santiago, I. M., Cortez, C. S., Trindade, P. M., and Mourão, J. S. (2012). Use of fishing resources by women in the Mamanguape River Estuary, Paraíba state, Brazil. *An. Acad. Bras. Cienc.* 84, 1189–1199. doi: 10.1590/s0001-37652012005000060

Rocha, M. S. P., Mourão, J. S., Souto, W. M. S., Barboza, R. R. D., and Alves, R. R. N. (2008). Uso dos recursos pesqueiros no Estuário do Rio Mamanguape, Estado da Paraíba, Brasil. *Interciencia* 33, 903–909.

Rodrigues, G. S., Rodrigues, I. A., Buschinelli, C. D. A., Queiroz, J. F., Frighetto, R. T. S., Antunes, L. R., et al. (2008). *Gestão Ambiental Territorial na Área de Proteção Ambiental da Barra do Rio Mamanguape (PB).* Available Online at: https://agris.fao.org/agris-search/search.do?recordID=BR2008115335 [accessed December 4, 2021].

Santos, R. V., and Coimbra, C. E. A. (2003). "Cenários e tendências da saúde e da epidemiologia dos povos indígenas no Brasil," in *Epidemiologia e Saúde dos Povos Indígenas no Brasil*, eds C. E. A. Coimbra, R. V. Santos, and A. L. Escobar (Rio de Janeiro: Editora Fiocruz), 13–48.

Sarti, F. M., Adams, C., Morsello, C., Van Vliet, N., Schor, T., Yagüe, B., et al. (2015). Beyond protein intake: bushmeat as source of micronutrients in the Amazon. *Ecol. Soc.* 20:22. doi: 10.5751/ES-07934-200422

Souza, J. B., and Alves, R. R. N. (2014). Hunting and wildlife use in an Atlantic Forest remnant of Northeastern Brazil. *Trop. Conserv. Sci.* 7, 145–160.

Stringham, O. C., García-Díaz, P., Toomes, A., Mitchell, L., Ross, J., and Cassey, P. (2021). Reptile smuggling is predicted by trends in the legal exotic pet trade. *EcoEvoRxiv [Preprint]* doi: 10.32942/osf.io/t42fd

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293.

Tabarelli, M., Pinto, L. P., Silva, J. M. C., Hirota, M. M., and Bedê, L. C. (2005). Desafios e oportunidades para a conservação da biodiversidade na Mata Atlântica brasileira. *Megadiversidade* 1, 132–138.

Tavares, E. F., Vieira-Filho, J. P. B., Andriolo, A., Sanudo, A., Gimeno, S. G. A., and Franco, L. J. (2003). Metabolic profile and cardiovascular risk patterns of an Indian tribe living in the Amazon Region of Brazil. *Hum. Biol.* 75, 31–46. doi: 10.1353/hub.2003.0028

Turner, N. J. (1995). *Food Plants of Coastal First Peoples (No. 34)*. Vancouver: UBC Press.

Vallega, A. (2013). *Fundamentals of Integrated Coastal Management*. Berlin: Springer Science & Business Media.

van Vliet, N., Gonzalez, A., Nyumu, J., Muhindo, J., Paemelaere, E., Cerutti, P., et al. (2022). Reducing wild meat sales and promoting local food security: lessons learnt from a behavior change campaign in Yangambi, democratic republic of Congo. *Ethnobiol. Conserv.* 11:9. doi: 10.15451/ec2022-04-11.09-1-14

van Vliet, N., Quiceno-Mesa, M. P., Cruz-Antia, D., and Yagüe, B. (2014). *Carne de Caça e Segurança Alimentar na Zona da Tríplice Fronteira Amazônica (Colômbia, Peru e Brasil)*. Available Online at: http://www.cifor.org/publications/pdf_files/Books/BVanVliet1401P.pdf [accessed December 4, 2021].

van Vliet, N., Quiceno-Mesa, M. P., Cruz-Antia, D., Tellez, L., Martins, C., Haiden, E., et al. (2015a). From fish and bushmeat to chicken nuggets: the nutrition transition in a continuum from rural to urban settings in the Tri frontier Amazon region. *Ethnobiol. Conserv.* 4:6. doi: 10.15451/ec2015-7-4.6-1-12

van Vliet, N., Nebesse, C., and Nasi, R. (2015b). Bushmeat consumption among rural and urban children from Province Orientale, Democratic Republic of Congo. *Oryx* 49, 165–174. doi: 10.1017/S0030605313000549

van Vliet, N., Quiceno, M. P., Cruz, D., de Aquino, L. J. N., Yagüe, B., Schor, T., et al. (2015c). Bushmeat networks link the forest to urban areas in the trifrontier region between Brazil, Colombia, and Peru. *Ecol. Soc.* 20:21. doi: 10.5751/ES-07782-200321

van Vliet, N., Schulte-Herbruggen, B., Vanegas, L., Yair-Cuesta, E., Sandrin, F., and Nasi, R. (2018). Wild animals (fish and wildmeat) contribute to dietary diversity among food insecure urban teenagers the case of Quibdó, Colombia. *Ethnobiol. Conserv.* 7:2. doi: 10.15451/ec2018-01-7.02-1-15

Vanegas, L., van Vliet, N., Cruz, D., and Sandrin, F. (2016). Contribución proteica de animales silvestres y domésticos a losmenús de los contextos rurales, periurbanos y urbanos de variasregiones de Colombia. *Biota Colomb* 17, 26–43. doi: 10.21068/C2016v17r01a03

Walrod, J., Seccareccia, E., Sarmiento, I., Pimentel, J. P., Misra, S., Morales, J., et al. (2018). Community factors associated with stunting, overweight and food insecurity: a community-based mixed-method study in four Andean indigenous communities in Ecuador. *BMJ Open* 8:e020760. doi: 10.1136/bmjopen-2017-020760

Welch, J. R., Ferreira, A. A., Santos, R., Gugelmin, S., Werneck, G., and Coimbra, C. (2009). Nutrition transition, socioeconomic differentiation, and gender among adult Xavante Indians, Brazilian Amazon. *Hum. Ecol.* 37, 13–26. doi: 10.1007/s10745-009-9216-7

Welch, J. R., Ferreira, A. A., Souza, M. C. D., and Coimbra, C. E. (2021). Food profiles of indigenous households in Brazil: results of the first national survey of indigenous peoples' health and nutrition. *Ecol. Food Nutr.* 60, 4–24. doi: 10.1080/03670244.2020.1781105

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