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Predicting the Risk of Exotic Plant Invasions in the Orinoco Region: Importance of Distribution Models, Climatic Niche and Functional Richness

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The process of biological invasions resulting from the introduction of exotic species is one of the most critical components of global environmental change. Although many hypotheses try to explain the processes underlying biological invasions, changes in land use are essential drivers mediating the colonization of exotic species at the landscape level. We used potential species distribution models developed in Maxent and a database of nine functional traits associated with invasion success for 18 exotic species with a high risk of establishment and difficulty of control in the Orinoco region from Colombia. We found that 67% of the species differed from the centroid in the climatic niche when comparing native and invaded localities. Overall, the native distribution localities showed a more restricted dispersal in their climatic niche, and for most species, native distribution was found within the broad environmental gradients of the invaded localities. Additionally, we found high climatic suitability for all exotic species across all the biomes and ecosystems; however, transformed ecosystems showed exotic plant species' higher potential functional richness. Our research allowed us to identify key geographical areas that are highly susceptible to invasions and prioritize species that need control in particular ecosystems and biomes. This work provides early warnings on the potential risks of invasion of exotic species, and it will improve the monitoring and management efforts in the Orinoco region of Colombia.

Keywords: exotic species, functional trait, transformed ecosystems, natural biomes, biological invasion

INTRODUCTION

Biological invasion, resulting from the introduction of exotic species, is one of the most critical components of global environmental change (Sala et al., 2000), causing homogenization of biota (McKinney and Lockwood, 1999; Quian and Ricklefs, 2006) and strong impacts on ecosystem functioning (Strayer et al., 2006; Vásquez-Valderrama et al., 2020). Several studies have revealed that land-use change is a critical factor driving the colonization and establishment of exotic species

(DeGasperis and Motzkin, 2007; Chytrý et al., 2008; Mosher et al., 2009). Land-use changes may promote invasions by reducing local species diversity (Simberloff et al., 2013). Diverse communities, like those present in natural ecosystems, are highly competitive and have near complete use of resources (space, light, or nutrients), resulting in greater resistance to invasions due to low resources availability for the establishment of the exotic species (Levine and D'Antonio, 1999; Kennedy et al., 2002). Another hypothesis postulates that disturbance is the main factor promoting biological invasions by eliminating strong native competitors who could not use limited resources adequately (Hobbs and Atkins, 1988; Burke and Grime, 1996). Additionally, land-use changes may also increase resource availability for exotic species, expand colonization opportunities (Davis et al., 2000), or create corridors that promote exotic species dispersion (With, 2002; Vilá and Ibañez, 2011). Despite many hypotheses explaining invasions, little is known about the potential invasion risk using distribution models and trait-based ecology following changes in land use.

Understanding the potential distribution of exotic species and the underlying biological mechanisms is essential to guiding appropriate control and management strategies of these species in non-native habitats. The ecological niche modeling (ENM) uses associations between geolocalized species records and environmental variables of the species to calculate the suitability of the habitat known to be occupied by the species or the habitat that can be potentially occupied by the species (Peterson, 2003; Phillips et al., 2006). The ENM has been widely used to predict the extent of plant invasion (e.g., Peterson, 2003; Thuiller et al., 2005; Atwater et al., 2018; Briscoe Runquist et al., 2019). It is widely accepted that the similarity in climate and environmental conditions between native and invaded habitats is essential for a successful invasion (Panetta and Mitchell, 1991; Thuiller et al., 2005). However, mixed evidence has been found regarding climatic niche shifts during an invasion. For instance, in a meta-analysis with 50 invasive species, just 15% of the species had more than 10% of their invaded distribution outside their native climatic niche (Petitpierre et al., 2012), and the transferability was close to 70% for 163 invasive plant species (Liu et al., 2020a). Conversely, several studies have reported changes in niche breadth and/or position (i.e., niche shift) between native and invaded areas (Broennimann et al., 2007; Pearman et al., 2008; Guisan et al., 2014; Atwater et al., 2018). These niche changes may result from changes in biotic and abiotic conditions in new colonized places (realized niche) or even shifts in the fundamental niche through genetic recombination, interspecific hybridization, or natural selection (Pearman et al., 2008; Guisan et al., 2014). Under this conflicting evidence, exploring climatic niche shifts is fundamental for including native and invaded localities in the ENM. Additionally, the information is essential for improving our predictions of the spatial distribution of exotic species as well as increasing our ability to forecast species responses to upcoming climate changes (Wiens et al., 2009).

It is now widely accepted that successful colonization and establishment of exotic plants depend on invaded habitat properties, and it is highly related to species' functional traits (*sensu* invasiveness; Kempel et al., 2013). However, functional strategies promoting successful biological invasions seem habitat-dependent (Daneshgar and Jose, 2009; Bernhardt-Römermann et al., 2011). For instance, C_4 grasses have an advantage in dry and open environments such as tropical savannas because their leaves fix more carbon than C_3 plants in those environments, causing higher growth rates and efficiency in water use (Bond, 2008; Schmidt et al., 2011; Mora-Fernandez and Peñuela-Recio, 2013; Silvério et al., 2013). However, C_3 woody species such as *Leucaena leucocephala* or *Ricinus communis* have been reported as successful colonizers in savannas due to their extensive ability to acclimate to contrasting shade levels (Benjamin et al., 1991; Martins et al., 2011). Additionally, they have human-assisted dispersal and soil seed banks waiting for the best conditions to germinate (USDA-NRCS, 2002; Martins et al., 2009). The facets of functional diversity summarize the complexity derived from the biotic communities under study and their functional traits (Mouchet et al., 2010). In this sense, potential functional richness maps of exotic species allow us to give early warning that go beyond the presence of the species in an ecosystem, focusing the monitoring and control on species that are particularly hazardous because of their functional traits.

Many studies exploring the relationship between land-use change and biological invasions have focused on temperate forests or grasslands (Quian and Ricklefs, 2006; DeGasperis and Motzkin, 2007; Chytrý et al., 2008; Mosher et al., 2009). Unique tropical ecosystems, such as savannas, have been poorly studied despite their high diversity and importance to local community livelihoods. The Orinoco region, located in Venezuela and Colombia, is a mosaic of different biomes and ecosystems, including savannas, forests alongside rivers, and tropical rainforest remnants, that have been exposed to high anthropogenic transformation for decades (Etter et al., 2010). For instance, in the early 1970s, exotic grass species were introduced for extensive livestock ranching, and between 1980 and 2000, forestry practices were implemented (Andrade et al., 2009; Romero-Ruiz et al., 2011). In the last two decades agro-industrial uses and forest plantations such as rice and African oil palm have been promoted by the national governments, substantially increasing their extension across the Orinoco landscape (Romero-Ruiz et al., 2011; Vargas et al., 2018). These agricultural practices have intensified the land-use transformation, creating a mosaic of natural and transformed lands that converts this region into an ideal model to understand the relationships between functional richness, land-use change, and the potential for biological invasion.

We explored the climatic niche variation between native and invaded localities for 18 exotic species in the Orinoco region in Colombia. Additionally, we identified which natural biomes and transformed ecosystems are potentially susceptible to invasion by exotic plants and how functional richness could vary under these new invasion scenarios. We chose nine plant functional traits related to the spread and establishment phases of invasion. The species were selected due to their high risk of establishment, the

TABLE 1 | Natural biomes and transformed ecosystems for the Orinoco's Region and area in km^2. Descriptions based on Etter (1998) and Etter et al. (2010), Etter et al. (2017).

Spatial categories	Abbreviation	Description	Extension (km^2)
Amazonian litobiomes	Am_lit	Amazon area with vegetation and ecosystems on soils that are mostly composed of hard rock.	618
Amazonian orobiomes	Am_oro	Area in which averages of temperature and precipitation characteristic of the Amazon region occur.	5,517
Andean orobiomes	And_oro	Pronounced mountainous sectors with typical climatic characteristics of the Andean region.	502
Amazonian peinobiomes	Am_pei	Amazon region in which vegetation and ecological processes are influenced by being in soils with very low fertility.	9,345
Plains peinobiomes	Pla_pei	Area in the eastern plains of Colombia, in which vegetation and ecological processes were carried out in soils with very low fertility.	139,419
Amazonian helobiomes	Am_hel	Areas in the Amazon in which vegetation is mainly determined by flood pulses.	24,209
Zonobiome of Tropical Humid Forests	Tro_for	High and dense forests of altitudes lower than 500 m, which present a surplus precipitation and some degree of seasonality from 1 to 3 months without generating marked water deficits.	29,043
Orinoco helobiomes	Ori_hel	Dense lowland forests in savannas in the Planar highlands. They have the same temperature and precipitation as the Zonobiome of Tropical Humid Forests.	22,194
Undifferentiated intervened rural areas (<20% of the original ecosystem)	Rur<20	Transformed areas in which less than 20% of the original ecosystem persists.	14,513
Undifferentiated intervened rural areas (20%–50% of original ecosystems)	Rur20-50	Transformed areas in which between 20% and 50% of the original ecosystem persists.	1,641
Mixed settler agroecosystems	Mix_agr	Areas with undifferentiated Agroecosystems types.	3,976
Irrigation rice business agroecosystems	Rice	Transformed areas with rice farming systems.	2,536
Semi-intensive and intensive livestock agroecosystems	Liv	Areas with a predominance of intensive and semi-intensive livestock systems.	525
African palm agroecosystem	Af_pal	Areas with a predominance of African palm crops.	190
Rainfed enterprise agroecosystems (soybeans, sorghum, cotton)	Ent_agr	Areas with mostly soybeans, sorghum and cotton crops.	332
Coffee fields	Coff	Areas with coffee cultivars	11

difficulty of control and their potential to spread at the landscape level, which may cause negative impacts on natural ecosystems (Cárdenas-López et al., 2010; Cárdenas-López et al., 2017). Specifically, we addressed the following questions: 1) How does the climatic niche of exotic species vary between native and invaded localities? 2) Which natural biomes and transformed ecosystems are most suitable for exotic plant species' establishment? And 3) using the potential distribution of exotic species, how does functional richness vary among natural biomes and transformed ecosystems?

MATERIALS AND METHODS

Study Site

The macro-basin of the Colombian Orinoco covers approximately 35,616,167 hectares and comprises a mosaic of different types of landscapes due to its topographic and geologic diversity (Prüssmann et al., 2020). The region includes several ecosystems and biomes (**Table 1**), but primarily savannas with an elevation range from 200 to 1,200 m a.s.l. (Etter et al., 2010). Vegetation is adapted to soils with low nutrient content and little productive capacity since they are usually acidic with superficial lateritic shells. However, the vegetation surrounding streams and lakes is denser because of more recent sediments and elevated moisture in the soil. Forest-type vegetation is also observed to the west of the region, in the areas that border the foothills of the Andes Mountain range (Etter et al., 2010). The economy of this region is based mainly on petroleum, livestock (cattle ranching), African oil palm, and forestry monocultures (e.g., *Pinus caribaea*), all activities that introduced extensively exotic plant species to the landscape (Lozano et al., 2007; Etter et al., 2010; Romero-Ruiz et al., 2011; Vargas et al., 2018).

Species Selection and Functional Traits

From a list of 42 potentially invasive species of Colombia (Cárdenas-López et al., 2010; Giraldo-Cañas, 2011), 18 plant species whose presence has been confirmed in the Colombian Orinoco region were selected (Cárdenas-López et al., 2017). Species selection included 13 herbs (four C_3 species and nine C_4 grasses) and five woody species distributed among nine families (**Supplementary Table S1**).

Nine functional traits related to different plant strategies were obtained for each species (**Supplementary Table S1**). Growth form is a vegetative trait determined by canopy structure and height and may be associated with light competition and responses to climatic and land-use factors (Cornelissen et al., 2003). Spinescence plays a prominent role in anti-herbivore defense (Hanley et al., 2007). It could be essential to reduce heat or drought stress, a primary environmental filter in Orinoco ecosystems. Vegetative propagation is associated with the plant's competitive vigor, ability to expand its distribution range, and capacity to persist after environmental disturbance (Klimes et al., 1997; Cornelissen et al., 2003). Dispersal syndrome and the presence of seed banks are related to dispersion and colonization success (Moravcová et al., 2015). Photosynthetic pathways and leaf shape have significant consequences for the leaf energy and water balance and CO_2 assimilation rates under contrasting environments (Ripley et al., 2007; Ghannoum, 2009). Sexual reproduction is related to dependence on a pollinator, where dioecious species may be more vulnerable than monoecious and hermaphroditic species. Finally, allelopathy is associated with the negative effect of one plant on another one through the release of chemical compounds into the environment (Hierro and Callaway, 2003). Several studies have demonstrated the importance of these traits to invasion success, particularly in the spread and establishment stages (Callaway and Aschehoug, 2000; Pyšek and Richardson, 2007; van Kleunen et al., 2010).

Functional trait information was obtained from academic databases (ISI Web of Science, SCOPUS, ScienceDirect, and Google Scholar) using the species name and the name of each functional trait. Additionally, specialized botanical and invasive species databases were reviewed, such as the IUCN Global Invasive Species Database, JSTOR Global Plants, Invasive Species Compendium CABI.org, KEW (online World Grass Flora), Missouri Botanical Garden, HEAR (Hawaiian Ecosystem at Risk Project), CONABIO's Mexican Invasive Species database (Invasive species fact-sheet), the Inter American Biodiversity Network (Invasive Species), TRY (Plant Trait Database), the flora do Brasil, the flora of North America, and some others.

Species Occurrence Data

We downloaded 111,924 occurrences (native and non-native distributions) from the Global Biodiversity Information Facility database (GBIF.org, 2020; http://www.gbif.org/) using the occ_search function of the rgbif package (Chamberlain et al., 2021) in R (R Core Team, 2019) on 27 October 2020, for the 18 invasive species with probable distribution in the Orinoco region from Colombia. We retained 15,409 records with longitude and latitude data, removing duplicates and other records with inconsistent geo-referencing (on the sea, zero- longitude and latitude; Chapman, 2005). To avoid model overfitting due to spatial autocorrelation and geographical sampling bias, occurrence data was thinned with a 50 km radius rule (Briscoe Runquist et al., 2019), using the R package spThin (Aiello-Lammens et al., 2015). Based on these criteria, the maximum number of localities used for modeling was 2,865, and the minimum number of localities was 54 (**Supplementary Table S2**).

Distribution Models for Exotic Species

We generated species distribution models using the Maxent package ver. 3.4.0 (Phillips et al., 2017) to identify suitable habitats for each exotic plant species. Maxent was run using the "dismo" (Hijmans et al., 2019) and ENMeval packages (Muscarella et al., 2014) in R version 3.5.3 (R Core Team, 2019). Explanatory variables were taken from the 19 bioclimatic layers, WorldClim ver. 2.1 (Fick and Hijmans, 2017, see https://www.worldclim.org/data/worldclim21.html, accessed 24 September 2020), at a resolution of 30 arc-seconds ($\sim$1 km^2). We included the complete set of variables due to the algorithm learning which ones are important *via* regularization (Phillips et al., 2006; Feng et al., 2019). Models were calibrated using explanatory variables and records without distinguishing between the species' native and non-native ranges. We built the final models using the settings chosen as optimal for each species and all spatially filtered occurrence records. Finally, the optimal models were transferred to the study area in the Colombian Orinoco Region. A logistic output format was used to describe the probability of a species' presence (Phillips and Dudík, 2008), which is a continuous habitat suitability range between 0 (unsuitable) and 1 (the most suitable). Details of the modeling protocol and maps of potential distribution per species can be consulted in **Supplementary Tables S2, S3, S4**.

Taxonomic and Functional Richness

We analyzed two diversity dimensions of the exotic plant community: species and functional richness. Functional diversity is usually split into three components: functional richness, functional evenness, and functional divergence. Functional richness is the most widely used approach for measuring and investigating functional diversity (Legras et al., 2018). Therefore, we selected functional richness (FD, Petchey and Gaston, 2002) to represent the functional diversity. FD based on functional richness measures the extent of trait complementarity among species through a continuous metric. Meanwhile, species richness indicates the number of species distributed in a location. Taxonomic and functional metrics were represented in maps at 1 km^2 pixel resolution (**Supplementary Tables S5, S6**). To calculate species richness predictions, we stack the binary maps of the individual Species Distribution Models (SDM) as the total sum of the number of species in each pixel. To calculate the index of functional richness (FD) that measures the total length of the branches from all species pool on a functional dendrogram of species by traits (Petchey and Gaston, 2002), we ran the function "dist" to compute a pairwise similarity matrix of the species, based on the Jaccard-type functional (dis)similarity (Anderson and Willis, 2003; Chao et al., 2019). Then, we built a dendrogram using the unweighted pair group method with the arithmetic mean (UPGMA) clustering procedure *via* a hierarchical cluster implemented in the function "hclust" of the stats package to cluster the species based on similarities of their traits. We used the "proxy" and "stats" packages to calculate the distance matrix and the UPGMA, respectively (Meyer and Buchta, 2019). We calculated the FD map using the speciesRaster package (speciesRaster: Generation of SpeciesRaster Object and Calculation of morphological and phylogenetic metrics; available at https://github.com/ptitle/speciesRaster). The dendrogram was used to calculate the branch length of the species by pixel, considering that each of them represents a biotic community of exotic plant species. The species in each pixel are characterized by the continuous habitat suitability ranges of the species. The package uses four radius cells to define the moving window and measures turnover in which branches are weighted by the inverse of the species ranges (Cardoso et al., 2014). This procedure improves the diversity comparisons among communities (Gotelli and Colwell, 2001). Finally, the FD is expressed in a map that shows values ranging from 0 to 1, indicating high FD when it takes values near 1.

Spatial Distribution of Taxonomic and Functional Richness Among Orinoco's Biomes and Ecosystems

To determine the spatial distribution of taxonomic and functional richness between transformed and natural Colombian Orinoco ecosystems and biomes, we overlapped the species richness map and FD map over the general ecosystem map of Colombia (Etter, 1998; Etter et al., 2017). Sixteen categories of ecosystems and biomes were considered, eight of which were found at the level of natural biomes. Specifically for the transformed biome, we proceeded to discriminate it at the level of eight ecosystems (**Table 1**). We used the geographical unit of the biome to identify the main natural ecological areas in the Orinoco region (Etter et al., 2017) and it has already been used in other studies (Thuiller et al., 2005). For the anthropogenically transformed biome, we choose the ecosystem category since, at this level, the effect of exotic species is better recorded in perturbed areas (With, 2002; Vilá and Ibáñez, 2011). Then, we rasterized to 1 km^2 each map unit and extracted the values for pixels of the taxonomic and functional richness maps for each of the 16 categories. Based on the distribution of 18 exotic plant species in the 242,978 pixels that comprise the Orinoco region of Colombia, we summed the presence data on each of the 16 biomes/ecosystems and calculated the distribution percentages. The analyses were performed using the raster and rgdal packages (Bivand et al., 2020; Hijmans, 2020) in R version 3.5.3 (R Core Team, 2019).

Statistical Analyses

To estimate the climatic niche shift, distance-based tests for homogeneity of multivariate dispersions (PERMDISP routine; Anderson, 2006) were conducted per species to compare the distances from native and invaded localities to their group centroid (**Supplementary Table S7**). For each biological record, values for the 19 bioclimatic variables were obtained from WorldClim ver. 2.1 at the resolution of 30 arc-seconds (~1 km^2) (Fick and Hijmans, 2017, see https://www.worldclim.org/data/worldclim21.html, accessed 24 September 2020). For each species, the values of the bioclimatic variables were standardized, and a matrix of Euclidean distances between biological records was constructed. Niche shift directionality was estimated by measuring changes in the niche centroid, which is the center of mass of the climate niche between native vs. invaded localities (Atwater et al., 2018). The PERMDISP uses the F statistic to compare the distances from biotic records among native and invaded locations to their centroid to obtain *p*-values by using 9,999 permutations of the least-squares residuals (Clarke and Gorley, 2015). Based on the Euclidean distances of climatic niche, we ran principal coordinate analyses (PCoA, Gower, 1966) to visualize the variation in species occurrences differentiating between native and invaded localities (**Supplementary Table S8**).

To determine which transformed ecosystems and natural biomes are more susceptible to invasion by exotic plant species and how functional richness varies among them, 100 pixels were randomly selected from each biome and ecosystem, and a one-way ANOVA was performed. When significant effects were found, the differences were identified using a Bonferroni test. These analyses were performed in InfoStat software (Di Rienzo et al., 2020). Additionally, a heat map was built showing exotic species' floristic composition per natural biome and transformed ecosystem. Specifically, for the floristic composition, the distribution percentage values per species for each ecosystem were previously transformed to the square root from which a Bray Curtis similarity matrix was calculated. The heat map represents the association of the exotic plant species concerning the natural biomes and transformed ecosystems based on a color gradient ranging from white (no association) to black (high association) (Somerfield and Clarke, 2013). The analyses were performed in the PRIMER 7.0.13 and PERMANOVA add-on program (Clarke and Gorley, 2015).

RESULTS

We found remarkable differences between native vs. introduced climatic niches for most species (**Supplementary Tables S7, S8**). Centroid shifts were significant for twelve of the 18 exotic species (67% of species), and exotic species tended to move towards wetter places, although this varied enormously among species (**Supplementary Tables S7, S8**). The native distribution localities showed a more restricted dispersal in their climatic niche, and for all species, native distribution was found within the broad environmental gradients of the invaded localities. For six species, breadfruit (*Artocarpus altilis*), African palm (*Elaeis guineensis*), white butterfly ginger lily (*Hedychium coronarium*), jaragua grass (*Hyparrhenia rufa*), itch grass (*Rottboellia cochinchinensis*), and Mexican sunflower (*Tithonia diversifolia*), there were no significant differences between native and invaded localities.

We did not find significant differences in potential exotic species richness between natural biomes and transformed ecosystems (F = 2.2 E-4; $p = 0.988$); however, we found high variation among them (F = 83.35; $p < 0.0001$) (**Figure 1**). Transformed ecosystems such as rice fields, livestock areas, and coffee fields are predicted to be suitable for most exotic species (**Figure 1**). Still, surprisingly, the suitability of rice fields did not vary from natural ecosystems such as Orinoco helobiomes or tropical forests (**Figure 1**). The rural areas with low to medium anthropic intervention (20–50% of the original ecosystem) showed the lowest suitability for exotic species, followed by Amazonian natural biomes such as litobiomes, orobiomes, peinobiomes, and helobiomes (**Figure 1**). Regarding functional richness, transformed ecosystems are predicted to be potentially invaded by species with more contrasting functional traits than natural biomes (F = 27.22; $p < 0.0001$), showing higher functional richness in transformed ecosystems. However, we found a high variation among transformed ecosystems and

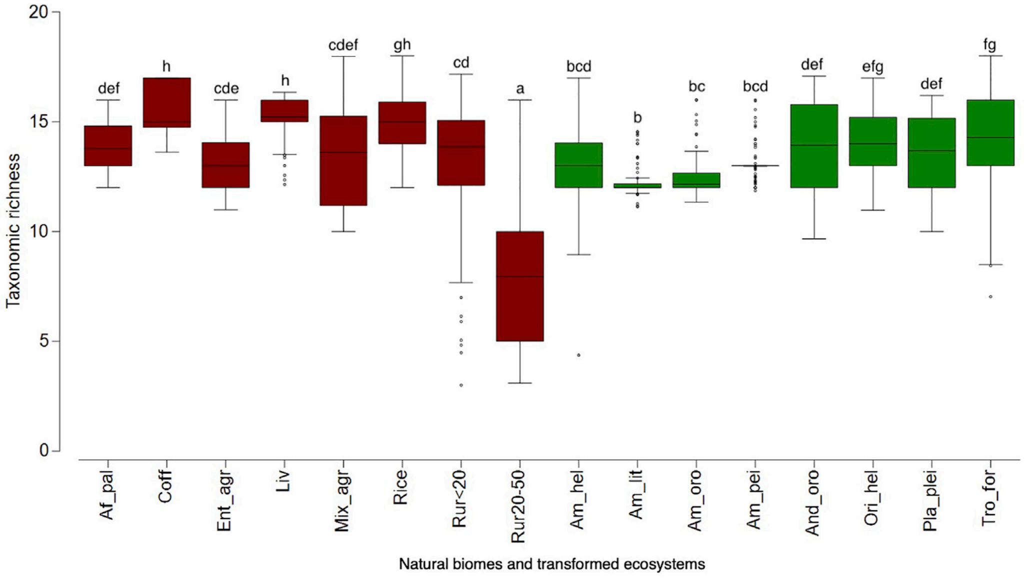

FIGURE 1 | Boxplots showing taxonomic richness among biomes/ecosystems and land-use type (natural vs. transformed) of exotic species in the Orinoco region. Different letters indicate significant differences based on the Bonferroni test. For biomes/ecosystems see **Table 1**. Red: transformed ecosystems and green: natural biomes.

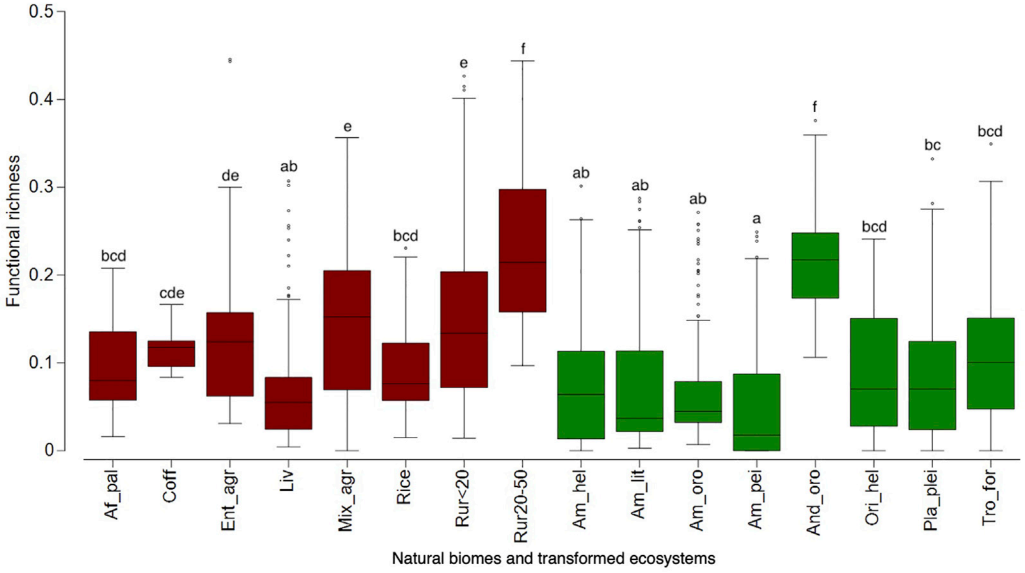

FIGURE 2 | Boxplots showing functional richness among biomes/ecosystems and land-use type (natural vs. transformed) of exotic species in the Orinoco region. Different letters indicate significant differences based on the Bonferroni test. For biomes/ecosystems see **Table 1**. Red: transformed ecosystems and green: natural biomes.

natural biomes (F = 54.98; $p < 0.0001$) (**Figure 2**). Most transformed ecosystems such as rural areas and mixed agroecosystems (Mix_agr and Ent_agr) as soybeans, sorghum and cotton are predicted to have a higher functional richness of exotic species (**Figure 2**); however, Andean orobiomes did not differ from rural areas (Rur20-50) (**Figure 2**). Amazonian peinobiomes are predicted to be colonized by exotic species functionally similar (**Figure 2**). The heat map showed that species such as *A. altilis*, bitter gourd (*Momordica charantia*), most grasses, and surprisingly, the aquatic species *H. coronarium* are expected to colonize all ecosystems and biomes (**Figure 3**). Unexpectedly, grass species

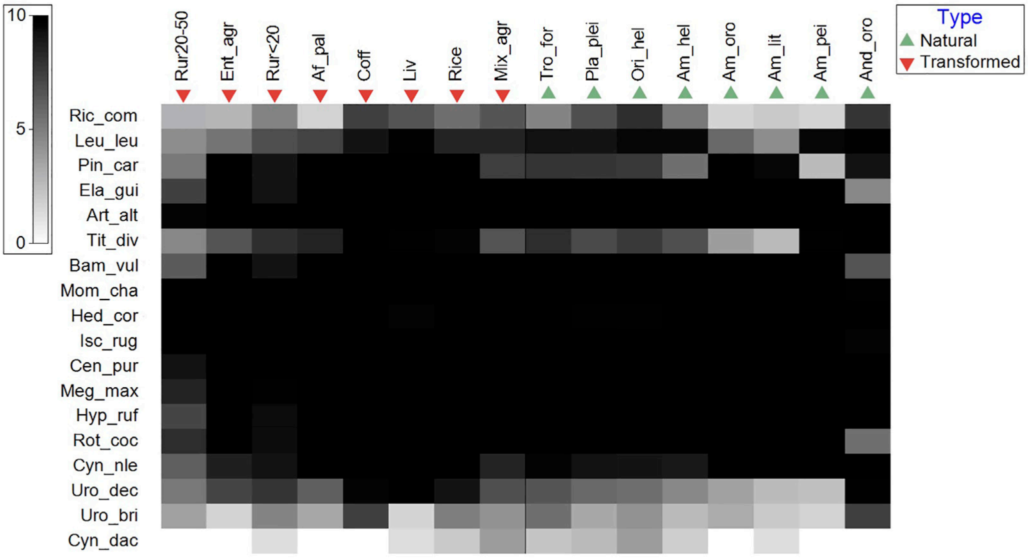

FIGURE 3 | Heat map of Whittaker (1952) association index of 18 exotic plant species concerning 16 natural biomes and transformed ecosystems in the Orinoco region.

such as bermuda grass (*Cynodon dactylon*), and signal grasses (*Urochloa brizantha* and *U. decumbens*), had a low probability of colonizing most ecosystems and biomes (**Figure 3**).

DISCUSSION

Integrating species distribution models with climatic niche shifts between native and invasive localities allowed us to identify which species have more probability of invading natural biomes and transformed ecosystems in the Colombian Orinoco region. Specifically, we found that natural biomes and transformed ecosystems had the same invasion risk of exotic species, but the latter ones had a higher functional richness of invasive species. Potential functional richness, evidenced in a spatially explicit manner (**Supplementary Table S6**; https://data.mendeley.com/datasets/s9bdytdt2f/2), allowed us to identify potential sites in which exotic species with contrasting functional traits may exclude native species through resource-intensive foraging with ecosystem functioning consequences. Our results should be seen as an early warning for the potential risk of dispersion and colonization of exotic species in other areas where they are not yet present.

Climatic niche shifts in exotic species may result primarily from unfilling (Petitpierre et al., 2012), as it takes time for introduced species to colonize all suitable niche spaces (Jiménez-Valverde et al., 2011). However, for most exotic species of our study, the invaded range was larger than the native range. This niche expansion may result from different biotic interactions in the introduced range (Shea and Chesson, 2002) or evolutionary changes in the fundamental niche through hybridization, genetic recombination, or other processes (Pearman et al., 2008; Guisan et al., 2014). The rapid evolution of invasive species has been reported as a strategy for adapting to new environmental pressures in the invaded range (Kooyers and Olsen, 2012). Nevertheless, it is essential to recognize that erroneous estimations of the native range caused by sampling bias or local extinctions can cause a "false expansion" (Atwater et al., 2018). Therefore, several authors argued that only increased occupancy of environmental space in the exotic range also available in the native range should be interpreted as a niche shift (Liu et al., 2020b). Conversely, the absence of the differences in the climatic niche between native and invaded ranges for five of our studied species may be related to climatic preadaptation to recipient environments (Petitpierre et al., 2012). For instance, this could be the case for species from tropical Africa, such as *A. altilis*, or *H. rufa*. However, as most of these species were recently introduced to the Orinoco region, some of them may evolve with time, modifying climatic niches between native and invaded ranges (Liu et al., 2020b). In our study, Caribbean pine (*P. caribaea*), elephant grass (*Cenchrus purpureus*), *H. coronarium*, castor bean (*R. communis*), and common bamboo (*Bambusa vulgaris*) showed the most remarkable differences in mean deviations from the centroid between native and invaded localities (**Supplementary Table S8**). The capacity of these species for colonizing and establishing in climatically different places from their native localities is a wake-up call to prioritize the management and control of their populations in the Orinoco region.

As our results showed that most species had climatic niche shifts between native and invaded ranges (**Supplementary Table S8**), we built species distribution models including both native and invaded range records to represent, in the potential distributions, as much of the climatic niche as is represented in the set of biological records of the species. Our results about habitat suitability are based on the assumption that under no dispersal limitations are the climatic preferences of a species the primary driver of its distribution. Therefore, the species preferences may be used to predict the early stages of an invasion (Thuiller et al., 2005). Although the Orinoco region has a high climatic homogeneity, we found differences in the invasion risk among biomes and ecosystems. For instance, livestock agroecosystems, characterized by intense dry periods and high solar radiation and evaporation rates (Knapp, 1985; Forrestel et al., 2014), were highly susceptible to the invasion of plants such as African grasses and tree species such as *E. guineensis* and *Pinus caribea* (**Figure 3**). Natural Amazonian biomes such as orobiomes and litobiomes (characterized by montane areas with a temperate climate and rocky and sand formations, respectively) showed low susceptibility to the invasion of exotic species such as *R. communis*, and *T. diversifolia*, and grasses of the *Urochloa* genus (synonyms of *Brachiaria brizantha* and *B. decumbens*) (**Figure 3**). Despite contrasting invasion risks among ecosystems/biomes, the high climatic homogeneity makes the Orinoco region particularly vulnerable to establishing any exotic species that are already invading since no environmental filters control the dispersal and establishment of the species. This high vulnerability to invasion can be reflected in the wide potential distribution of at least 12 of the 18 species throughout the Orinoco region (**Supplementary Table S5**; https://data.mendeley.com/datasets/s9bdytdt2f/2). Additionally, most of these species are native to tropical areas (Cárdenas-López et al., 2017); therefore, their requirements may be supplied by the Orinoco regional environmental conditions. Under this scenario, our maps of potential distribution per biome and ecosystem are fundamental tools for prioritizing monitoring and control efforts that can help guard against further introductions and the initiation of new invasion forces (Thuiller et al., 2005).

It is essential to highlight that the successful establishment and actual distribution of exotic species depend on other local factors such as propagule density, soils, or biotic interactions (Willis and Whittaker, 2002). Several studies have shown a higher performance of exotic species under anthropogenic management regimes in transformed ecosystems (Wang et al., 2018). It could be related to eliminating strong native competitors that could not use limited resources adequately (Hobbs and Atkins, 1988; Burke and Grime, 1996). Likewise, sites with high potential functional richness show that invasive species could occupy the entire spectrum of resource use, displacing native species and altering ecosystem processes (Mason et al., 2005). African grasses, for instance, promote and are stimulated by fire. The large standing necromass left by these grasses at the end of the dry season facilitates the combustion and increases the intensity of fires (Williams and Baruch, 2000), modifying nutrient and carbon cycling and affecting biodiversity. This disturbance increases the net resources available that, summed to anthropogenic management (e.g., direct fertilization or other sources of pollution), would facilitate invasion (Davis et al., 2000), enabling exotic species establishment in transformed ecosystems that are frequently burned as part of management practices, such as rice fields and livestock areas (Mandal et al., 2004; Armenteras et al., 2021). Additionally, anthropogenic fire may exclude native fire-intolerant species, reducing woody plant cover (Armenteras et al., 2021) and impacting long-term non-management ecosystems. The disturbance and the massive expansion of exotic species plantations such as African palm (*E. guineensis*) and *P. caribaea* make all-natural biomes of Orinoco's region potentially vulnerable to invasions of these species in the future (Lozano et al., 2007). Currently, *E. guineensis* is a commonly used crop for biodiesel production. Colombia is the primary producer of oil palm in Latin America (Erazo et al., 2020), with an annual area devoted to plantations increasing at a rate of 7,396.3 ha/year (Cordovez and Guhl, 2015). Unfortunately, anthropogenic disturbances at the landscape level or social dynamics (e.g., colonization of new areas by the development of road infrastructure and associated tourism) are rarely considered because accurate maps at an appropriate scale or field estimates are seldom available.

The establishment and actual distribution of exotic species is also related to their functional traits that determine species' success at the different stages of invasion (introduction, establishment, and spread) under different environmental conditions (Kempel et al., 2013). It would be expected that species with contrasting functional traits have different probabilities for colonizing ecosystems and biomes. For instance, species with water dispersal may be easily transported through the freshwater flooding pulses that characterize Orinoco's helobiomes promoting their spread from other ecosystems. Examples of these species are grasses such as *Urochloa decumbens*, *Ischaemum rugosum*, *C. dactylon*, and *R. cochinchinensis*. Additionally, the superior water and nutrient use efficiency, and the higher photosynthetic rates of C_4 grasses in environments characterized by high solar radiation and soil temperatures and low soil fertility (Knapp, 1985; Forrestel et al., 2014; Atkinson et al., 2016) increase their establishment probability in Amazonian peinobiomes dominated by savannas, but also in transformed ecosystems. High dispersal abilities like producing and storing seeds or having animal and assisted dispersal syndromes are important traits to guarantee successful dispersion to new areas. Species such as *E. guineensis*, *L. leucocephala*, and *P. caribeae* do not depend on other individuals for reproduction (monoecious reproduction) and have animal and assisted dispersion, allowing them to expand their distribution ranges beyond plantations (Kuo, 2003). Native forests surrounded by African palm plantations show high palm regeneration and recruitment in Colombia (Lozano et al., 2007). Individuals of *L. leucocephala* frequently invade riverbanks, roadsides, and forest margins as well as cultivated lands and wastelands in Thailand (Marod et al., 2012). Additionally, *L. leucocephala* has fast growth rates and high drought stress tolerance (Luo et al., 2020), increasing its probability of establishment under any ecosystem/biome in the Orinoco region. Species such as *L. leucocephala*, *H. coronarium*, *M. charantia*, *R. communis*, and several grass species have allelopathic compounds inhibiting the growth of native species (**Supplementary Table S1**). For instance, *L. leucocephala* releases an amino acid (mimosine) that is poisonous to other plants (Matthews and Brand, 2004), inhibiting the growth and reproduction of native species (Wolfe and Van Bloem, 2012).

U. decumbens allelopathic potential is reported in different organs and may remain throughout its lifetime including senescence (Barbosa et al., 2008), reducing the germination of native species (Barbosa et al., 2008). As exotic species have contrasting functional strategies, knowing the species' life history and functional traits is another fundamental tool to prioritize the species that must be monitored and controlled. Therefore, building potential functional richness maps (**Supplementary Table S6**; https://data.mendeley.com/datasets/s9bdytdt2f/2) will allow field studies to focus on current processes of biological invasion and their relationship with the disturbances caused by the transformation of the landscape (*sensu* Huston, 2004; Gross et al., 2005).

Species potential distribution models are a powerful management and monitoring tool for exotic species (Jiménez-Valverde et al., 2011; Srivastava et al., 2019). Although several studies have shown their importance as unbiased first-step screening for early warning systems (Thuiller et al., 2005), it is essential to recognize that the species richness based on overlapping distribution maps is commonly higher than those inferred from species survey data that do not occur everywhere within their climatic range due to other local processes that are not considered in the correlative species' niche modeling (Hurlbert and White, 2005; Jímenez-Valverde et al., 2011). It is crucial to control type 1 and 2 errors in predicting species distributions before proposing management and monitoring actions (Uden et al., 2015). Therefore, our species distribution models and richness maps should be considered early warning maps delineating probable occupancy of areas based on climatic suitability for a single species or groups of them (Thuiller et al., 2005; Jímenez-Valverde et al., 2011; Srivastava et al., 2019). In our study, this spatial overprediction in species' distribution maps is a desirable property that reflects the nature of invasive species (Jímenez-Valverde et al., 2011) that can colonize both natural biomes and transformed ecosystems. Given that it is usually easier and more economical to prevent an introduction or spreading than to control an invasion (Pejchar and Mooney, 2009), distribution maps based on ecological niche models will be fundamental for guiding early detections and promoting rapid responses to invasion risks in the Orinoco region. As suggested by Thuiller et al. (2005), those areas identified as having a high probability of invasion due to their high climatic suitability for some exotic species should be monitored since eradication is costly and inefficient once the populations are established (Rejmánek and Pitcairn, 2002).

Management Implications

Since a national economic frontier is emerging throughout the Orinoco region (Andrade et al., 2009), it is crucial to understand how exotic plant species are distributed among different natural biomes and transformed ecosystems and which functional traits may promote their invasion processes. The main strength of our study is the identification of key geographical areas that are highly susceptible to invasions and the prioritization of species that need control in particular ecosystems and biomes. Our study may be helpful as an early warning to improve monitoring and management efforts for biological invasions in one of the most transformed regions in Colombia. The dilemma emerges regarding the economic benefits and negative impacts of intentionally introduced exotic species and their management (Pejchar and Mooney, 2009; Dickie et al., 2014). Considering our study, almost 50% of exotic species are of economic value as forage, agroforestry products, and biofuels, among other uses (Andrade et al., 2009; DNP, 2018). Currently, the big environmental challenge in the Orinoco region is to pursue cost-effective management within economic and ecological functional limits as a critical basis for stakeholders and decision-makers (Andrade et al., 2009). Therefore, the implementation of an integrative land-use and management planning should incorporate ecological regimes as well as natural and anthropogenic spatiotemporal dynamics that are of the utmost urgency and should be given priority (e.g., Lourival et al., 2011). In this sense, the exotic plants reported in this study should be monitored based on rigorous fieldwork to demonstrate by measuring hard functional traits (e.g., ecophysiological), the effects on communities of native species, and ecosystem processes and services. Future studies should consider the plasticity of functional traits measured in the field for exotic plant species in order to build mechanistic niche models (e.g., Chapman et al., 2017) and project them under global change scenarios (e.g., future changes in climate and land use). Finally, monitoring plans sharing information between sectors should consider the inclusion of exotic plant species lists as a potential risk in agricultural production databases as preliminary initiatives discussed by the UPRA (Unidad de Planificación Agropecuaria) of the Agricultural Ministry, as well as its articulation in the government's interministerial agendas.

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 authors. Raster maps of taxonomic and functional diversity, as well as species distribution models can be freely downloaded from the Mendeley Data repository at the link: https://data.mendeley.com/datasets/s9bdytdt2f/2.

AUTHOR CONTRIBUTIONS

BS-N, NU-C and MB conceived and designed the research. EN-U and CC-R performed species distribution models and taxonomic richness and functional diversity maps. NU-C performed the statistical analysis. BS-N wrote the first version of the manuscript and all authors contributed to 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/fenvs.2022.687723/full#supplementary-material

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