

# Human impacts on bats in tropical ecosystems: Sustainable actions and alternatives

## Edited by

Paulo Estefano Bobrowiec, William Douglas Carvalho, Ana Rainho, Paul W. Webala and Ludmilla M. S. Aguiar

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# Human impacts on bats in tropical ecosystems: Sustainable actions and alternatives

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# Editorial: Human impacts on bats in tropical ecosystems: sustainable actions and alternatives

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agricultural systems, Chiroptera, ecosystem services, landscape change, mining, replacing native vegetation, rubber plantation, selective logging

## Editorial on the Research Topic

Human impacts on bats in tropical ecosystems: sustainable actions and alternatives

## Background

Globally, the most extraordinary biodiversity is in the tropics, spread in a great diversity of vegetation types and habitats. Among the myriad mammalian groups, bats stand out for their remarkable taxonomic, functional, and phylogenetic diversity (Wilson and Mittermeier, 2019). Within the tropics, bats can be found in different vegetation types varying in a gradient of structural complexity from dense ancient forests to more open landscapes and woodlands in the savannas and fields (Meyer et al., 2004; Carvalho et al., 2021). Bats provide essential ecosystem services such as seed dispersal and pollination of the many plants that have a role in the income of the most impoverished human populations and the formal economy (Lacher et al., 2019). Moreover, as voracious insect predators, bats play a vital role in suppressing agricultural pests, an invaluable service in this part of the world, and disease vectors for humans (Aguiar et al., 2021; Tuneu-Corral et al., 2023).

It is widely recognized that the main threat to bats globally is the extensive conversion of natural ecosystems, especially in tropical developing countries (Meyer et al., 2016). This shift in land use results in habitat loss and environmental degradation, with consequent loss of species, ecosystem services, and lineages (Frick et al., 2020; Atagana et al., 2021; Colombo et al., 2023). There is thus an urgent need to disseminate correct information about bats and

explore best practices for mitigating the adverse effects stemming from human activities such as vegetation clearing for cattle ranching, agriculture, human settlements, and urbanization. Therefore, in this Research Topic, we aimed to bring together current research that assesses the influence of multiple environmental transformation drivers on the diversity of tropical bats. Nine papers were published in this Research Topic, and they present novel insights into how bats react to human-driven environmental changes and address significant gaps in bat conservation. These studies were conducted by 36 authors in six countries across the American, African and Asian continents (Figure 1). While the sampling was local in seven studies, [Brasileiro et al.](#) used data spanning Brazilian biomes, and [Xavier et al.](#) carried out a global systematic review. Three key themes emerge from the papers presented in this Research Topic, and we discuss the findings and knowledge gaps related to each theme in the following sections.

## Critical role of forest cover in bat conservation

Most studies underscore the critical role of forest cover in bat conservation within human-made landscapes. These papers assessed various environmental perturbations, including mining, selective logging, rubber plantations, agricultural systems, and vegetation modified by pasture and farming activities. [Cory-Toussaint and Taylor](#) found that insectivorous bat activity of open-air and clutter-edge foragers was negatively impacted over areas close to diamond opencast mining devoid of vegetation cover in South Africa. According to [Deshpande et al.](#), the areas in India with the greatest levels of forest cover and the fewest rubber plantations also had the highest levels of bat activity across all insectivorous bat guilds. This suggests that maintaining undergrowth can help lessen the negative impacts of rubber plantations. [BakwoFils et al.](#) showed a difference in species composition between disturbed and undisturbed habitats of the Afromontane biome of Cameroon. This difference is primarily caused by the high presence of closed-spaced insectivorous bats in the undisturbed habitat and the high proportion of frugivorous bats in the altered habitats, which are drawn in by fruit trees. [Costa and Ramos Pereira](#) found that the structural connectivity of the landscape in the Brazilian-Uruguayan savanna played a pivotal role in the occupancy of edge-space foraging bats, suggesting that landscapes with natural elements favor aerial insectivores. On the other hand, [Peña-Cuéllar and Benítez-Malvido](#) found that species capture rates in southern Mexico were skewed towards females in riverine corridors surrounded by pastures. Together, these articles show that human-modified landscapes reduce the richness and abundance/activity of species of different neotropical bats. Considering the alarming rates of loss and fragmentation of tropical forests, the preservation of large areas of undisturbed forest, as well as the use of forestry systems that keep, for example, the understory standing, is necessary to maintain bat species diversity and its related ecosystem services.

## Interactions between bats and other organisms

Maintaining interactions in biological communities is a key factor in maintaining biodiversity and ecosystem services. In this regard, two studies delved into the interactions between bats and other organisms. [Hemprich-Bennett et al.](#) found minimal variation in prey richness consumed by the fawn leaf-nosed bat *Hipposideros cervinus* in both selectively logged and preserved forests in Borneo. This suggests that this bat species may be resilient to habitat degradation. [Ramalho et al.](#) showed that ecological networks between parasitic flies and host bats were more nested in disturbed sites, with a decrease in the specialization of the bat-fly interaction in the Brazilian Cerrado. In this case, reduced roost density in altered habitats can lead to higher species aggregation within a single roost, potentially promoting parasite transmission amongst bat species. Therefore, these studies show that the level of landscape modification can influence interactions between bats and prey and ectoparasites. On one side, planned timber harvesting in selectively logged forests has little influence on the diet of an insectivorous bat. On the other hand, the loss and modification of forests in the Brazilian Cerrado alter the bat-parasite relationship with increased transfer of parasites between species. For the Cerrado biome, we still do not have a solution to block the effects of forest degradation, as there are few studies on bats in this Brazilian biome.

## Impacts of environmental transformation on ecosystem service provision by bats

Habitat loss and fragmentation are the main drivers of species losses globally, resulting in significant impacts on ecological services and ecosystem functioning through species extinction and replacement. At a large scale, the findings of [Brasileiro et al.](#) reveal a substantial decline in the ecosystem services provided by bats in the central and eastern Brazil, with species loss being an important factor in the Atlantic Forest and Cerrado and reduced species occurrence in the Amazon, Caatinga, and Pantanal regions. In their global review of research on bats in agricultural systems, [Xavier et al.](#) highlighted aspects requiring empirical investigation, such as biogeographic regions, sampling methods and scale, and biodiversity descriptors, to understand the factors influencing bat survival in cultivated landscapes. Also, these authors address that these knowledge gaps could foster cooperation with rural producers, facilitating bat protection and the development of relevant public policies. Therefore, we see that locally or globally, the effects of man-made changes in different landscapes have a major impact on bat fauna. However, there are solutions to reduce these impacts and many of these solutions involve improving the sustainability of the production system, with direct action from agricultural producers.



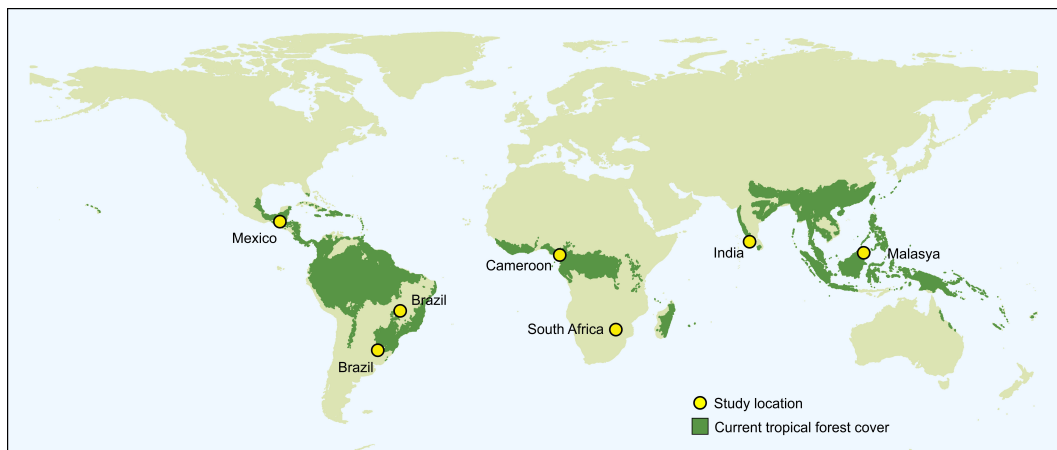


FIGURE 1

Global map with the distribution of sampling sites of the nine papers published in this Research Topic. Only seven sampling sites are represented, as two papers used data from multiple locations and countries.

## Practical actions for a sustainable future

We learned in this Research Topic that the preservation of intact forests, the restoration of secondary forests, and initiatives with local populations and producers were the primary mitigating strategies for the conservation of tropical bats in the face of anthropogenic landscape changes. As suggested by studies here, this can be accomplished by designating new protected areas and enhancing the management of existing ones near major developments, and provide enough space to support both the original diversity of bat species and the potential or actual ecosystem services that bats provide. Additionally, restoring secondary forests has also been suggested as a way to lessen edge effects by increasing the size of the forest and improving connectivity between forest patches. It is our hope that this Research Topic will stimulate further research that offers insights and fill knowledge gaps into management actions, public policies and sustainable alternatives that effectively alleviate human impacts on bat biodiversity.

## Author contributions

PB: Conceptualization, Data curation, Investigation, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. WC: Conceptualization, Data curation, Investigation, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. AR: Conceptualization, Data curation, Investigation, Project

administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. PW: Writing – review & editing. LA: Conceptualization, Data curation, Investigation, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing.

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# Anthropization Affects the Assembly of Bat-Bat Fly Interaction Networks

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Increasing anthropization is detrimental to the natural environment and the quality of life, affecting populations, communities, and the relationships between organisms. One of the most unique relationships in the animal world is parasitism, which often involves tightly specialized interactions between pairs of species. Bat flies, for example, are obligate ectoparasites represented by two highly adapted dipteran families that usually parasite a single bat species or genus. Recent studies have shown that bat flies could carry pathogens such as bacteria and viruses, transmitting them among bat individuals in a colony. Because host roost characteristics can influence bat-fly parasitism, we aimed to assess whether the ecological networks between parasites and their host bats are influenced by the degree of habitat anthropization. Our hypothesis was that bat-fly interaction networks would be less specialized and more nested in highly anthropized sites. We collected bat fly individuals from bats captured at 21 sampling sites located in the Federal District of Brazil and quantified the amount of natural and anthropized area within a 3-km buffer from the sampling site. Areas consisting of agriculture, construction, mining, roads, or any man-made structure were considered anthropized. Sites presented different degrees of anthropization, with areas ranging from 100% anthropized to areas retaining full natural cover. We built bat-bat fly networks for each of the sites and excluded those with sampling completeness values smaller than 0.7. We calculated key weighted structural metrics for each network, such as nestedness, specialization, and modularity. The effect of the reduction in natural cover on structural metrics was assessed through GLMMs, controlling for network size and ectoparasite diversity. Nestedness increased with the amount of anthropization, while specialization and modularity did not change and were overall high in all networks. This result suggests that anthropization may influence the assembly of bat-bat fly networks, leading to the emergence of a hierarchical assembly of interactions as parasites become less specialized and interact with a wider variety of hosts. Less specialized relationships could influence parasite fitness or even increase the likelihood of transmitting pathogens between populations of different bat species.

**Keywords:** Brazil, Cerrado (Brazilian savanna), Chiroptera, habitat degradation, Hippoboscoidea, Streblidae

## INTRODUCTION

Increasing anthropization is one of the most ecologically threatening human activities worldwide as it occurs to the detriment of the natural environment and the quality of life of many species (Fahrig 2003; Haddad et al., 2015). Anthropization brings consequences such as habitat loss, increased pollution, and habitat degradation (Haddad et al., 2015; Russo and Ancillotto 2015), leading to different effects on biodiversity, such as abrupt changes in community composition (Caughley 1994; Willig et al., 2007; Mbora and McPeck 2009; Russo and Ancillotto 2015). Bats, for example, usually display shifts in species abundances, with increases in the abundance of species resistant to anthropized habitats while those with more ecologically specialized requirements are severely hampered (Willig et al., 2007; Bobrowiec and Gribel 2010; Russo and Ancillotto 2015). This shift in species abundances, coupled with environmental alterations derived from anthropization, may also affect relationships between bats and other organisms, such as prey, predators, and parasites (Russo and Ancillotto 2015). In urban areas, insect availability is lower, limiting the amount of prey for insectivorous bat species (Threlfall et al., 2011; Russo and Ancillotto 2015). Conversely, a higher abundance and diversity of predators can be found in urban areas, posing great danger to bats in those habitats (Threlfall et al., 2013; Russo and Ancillotto 2015). Moreover, recent studies have reported that bats inhabiting anthropized areas present a greater diversity of zoonotic parasites, including fungi, bacteria, and viruses (Mühldorfer et al., 2011; Nunes et al., 2017).

Parasitism is a unique relationship in the animal world as it often involves tightly specialized interactions between pairs of species (Combes, 2001). Bat flies, for example, are obligate bat ectoparasites represented by two highly adapted dipteran families: Streblidae and Nycteribiidae (Marshall, 1982). Bat flies' morphology reflects their role as ectoparasites, with many species having absent or reduced wings, with long limbs that facilitate locomotion on the host body, claws on the distal region of the limbs or ctenia on the ventral lower end of the head to help individuals to hold onto the fur, and specialized buccal structures for piercing the skin (Peterson and Wenzel 1987; Whitaker Jr. 1988). Both bat fly families are usually highly specific parasites, with each species of bat fly parasitizing a single bat species or genus (Wenzel et al., 1966; Marshall 1982). Although there is no evidence that bat flies could affect the health condition of the host, recent studies showed that those flies harbor potentially pathogenic microorganisms such as bacteria, viruses, and fungi (Morse et al., 2012; Dick and Dittmar 2013; Gay et al., 2014; Abundes-Gallegos et al., 2018; Martínez et al., 2021).

Bat-fly parasitism can be influenced by different characteristics of the host, such as age, sex, body size, reproductive status, activity, and abundance (Muñoz et al., 2003; Bertola et al., 2005; Patterson et al., 2008a,b; Presley and Willig 2008; Esbérard et al., 2012; Fagundes et al., 2017). This interaction can also be shaped by the type and characteristics of the roost used by the host, with larger and more enclosed colonies exhibiting higher parasitic rates, including higher prevalence, mean intensity of infestation, and parasite richness (Patterson

et al., 2007). Habitat degradation can also influence parasitism dynamics by affecting ectoparasitic survival and reproduction rates or by causing stress in the host population (Patterson et al., 2007; Mbora and McPeck 2009; Pilosof et al., 2012; Ramalho et al., 2018). Moreover, in degraded areas, decreased roost availability could force bats to roost in colonies with different species, again affecting parasitism as well as facilitating horizontal transmission (Urbietta et al., 2020), even between different bat species. Because of the high degree of specialization of bat flies to bats (Wenzel et al., 1966; Marshall 1982), the relationship between them is considered an excellent model for studies of host-parasite association.

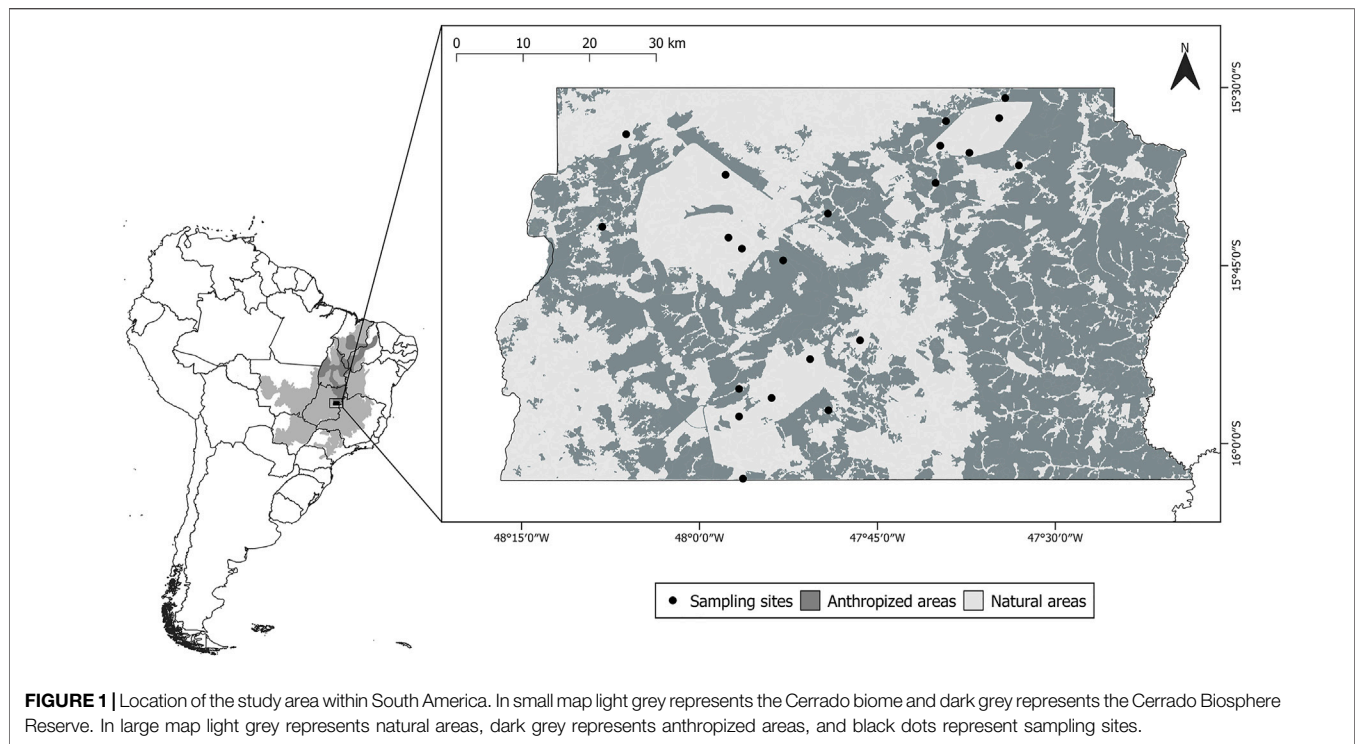
Network science is a valuable framework for investigating interspecific and community-wide assemblies of interactions, as it can yield quantitative information on species specialization and shared dependence on interacting partners (Dormann et al., 2009; Ings et al., 2009). This tool has become increasingly popular for describing several types of interaction at community-wide levels, including host-parasite networks (Vázquez et al., 2005; Löwenberg-Neto 2008; Canard et al., 2014). Bat-bat fly interaction networks have recently gained much attention, and research has shown that interactions in these systems tend to be highly specialized, with networks often being compartmentalized (Zarazúa-Carbajal et al., 2016; Saldaña-Vázquez et al., 2019; Hiller et al., 2021), pointing to tight coevolution of certain parasites with their host bats. However, the effect of land-use change on the assembly of such networks has been poorly explored. Hernández-Martínez et al. (2018) observed that bat-bat fly networks were more specialized in less fragmented areas, while Urbietta et al. (2020) have shown that bat-ectoparasite networks preserve their structural characteristics even in areas with differences in land use. However, no study to date has performed a formal analysis to assess how the assembly of bat-ectoparasite networks changes along an anthropization continuum. We aimed to reconstruct several interaction networks between ectoparasites and their host bats at sites within and outside protected areas in central Brazil, encompassing a wide range of anthropized land cover, to assess the effect of the reduction of natural habitats on network structure and assembly rules. We tested the hypothesis that bat-fly interaction networks are affected by the degree of anthropization surrounding the studied sites, leading to less specialized and more nested networks in highly anthropized areas.

## MATERIALS AND METHODS

### Study Area

We conducted this study in the Federal District of Brazil, located in the core area of the Cerrado Biosphere Reserve (Figure 1). The area comprises a mosaic of different vegetation types, with the dominant types consisting of savanna habitats and forested riparian areas. The climate in the study area is classified as Tropical Savanna (Aw) and consists of two well defined seasons, a rainy season from September to April and a dry season from May to August (Ratter et al., 1997).





In order to assess information from different communities of bats and their ectoparasites, we conducted captures in areas within and in the proximity of the three main protected areas in the Federal District: Brasília National Park (PNB) (42,389 ha, 15°41'42"S, 48°08'10"W), Gama-Cabeça de Veado Environmental Protection Area (AGCV) (25,000 ha, 15°52'29"S, 47°50'48"W), and Águas Emendadas Ecological Station (ESECAE) (10,547 ha, 15°36'32"S, 47°33'03"W) (**Figure 1**). We defined 21 sampling sites with different degrees of anthropization in the study area to characterize the effects of habitat loss on bat-bat fly assemblies. The minimum and maximum distances between sampling sites were 2.6 and 64.8 km, respectively.

### Quantification of Anthropization

For each sampling site, we defined a 3-km buffer and quantified the percentage of natural and anthropized area within that radius. The distance was defined based on previous studies that registered a flight distance between 1 and 3 km for bats in Neotropical savanna areas (Bernard and Fenton 2003; Aguiar et al., 2014). We used Mapbiomas Collections classification maps (Souza et al., 2020, <https://mapbiomas.org/>) to identify land use within each buffer in QGIS 3.6 Noosa (QGIS Development Team 2021). Areas consisting of agriculture, construction, mining, roads, or any man-made structure were considered anthropized, while areas with natural vegetation of any type (e.g., savanna, grasslands, and gallery forests) were considered natural. Each site received an anthropization value corresponding to the ratio of anthropized cover in relation to natural vegetation within the 3-km buffer.

### Capture of Bats and Bat Flies

We captured bats during 89 capturing sessions, with each of the 21 sites being sampled 4 or 5 times between April 2012 and August 2013. Bats were captured with six to ten mist nets (12 × 3 m) installed along natural paths through the vegetation or near trees located in the sampling sites. Nets were opened at sunset and remained open for 6 h per night. Bats were identified upon capture under the criteria of Díaz et al. (2016). Shortly after removing the bats from the nets, we inspected each individual for the presence of ectoparasites with brushes and tweezers, placing collected flies inside Eppendorf® microtubes containing 70% ethanol. Bat flies were identified under a stereomicroscope (Motic K-series) at the Bat Biology and Conservation Lab at the University of Brasília using specialized identification keys (Guerrero, 1993, 1994a,b, 1995a,b, 1996). Species identification was confirmed by Prof. Dr. Gustavo Gracioli from the Federal University of Mato Grosso do Sul. After manipulation, all bats were tagged with numbered rings and released at the location of capture.

### Network Analysis and Effect of Anthropization

We used interactions between bats and ectoparasites at each of the sampling sites to build weighted adjacency matrices. Pairwise interactions (cell values) corresponded to the number of individuals of a bat species carrying a parasite species. With each matrix, we built a weighted bipartite interaction network. We assessed the sampling completeness of each network through individual-based rarefaction curves (Colwell et al., 2012) of ectoparasites found on bats, using the nonparametric Chao1 estimator of asymptotic species

richness (Chao et al., 2009). We calculated the completeness of each network as the ratio between observed ectoparasite richness and the estimated asymptotic richness (Chacoff et al., 2012). We set a cutoff of 0.7 of sampling completeness, below which networks were discarded from further analysis.

From each network, we calculated three structural metrics that describe different aspects of network assembly and distribution of interactions: nestedness, through the weighted NODF (wNODF) metric (Almeida-Neto and Ulrich 2011); weighted modularity (Qw) (Schleuning et al., 2014); and complementary specialization ( $H_2'$  metric) (Blüthgen, 2010). Nestedness refers to whether the interactions of specialist species form a subset of the interactions of generalists (Bascompte et al., 2003). The wNODF index varies from zero to 100, and a fully nested network is a highly asymmetric network, where specialists always interact with generalists that have a larger pool of partners. Modularity assesses the existence of subgroups of species within the network that interact more among themselves than with the rest of the species and reveals patterns of affinity between the two levels of the network (Olesen et al., 2007). The index Qw varies from zero to one, and networks with high modularity have conspicuous and tightly knit subgroups of species. Finally, specialization is calculated as the average niche breadth of species within the network. The index  $H_2'$  corrects for network size and varies from zero to one, and species in a highly specialized network have narrower niches and interact strongly with one or few partners and thus leading to high niche complementarity (Blüthgen, 2010). Analyses were conducted in R Studio 3.6.0 (R Core Team, 2015). Network and sampling completeness analyses were performed using the bipartite (Dormann et al., 2008) and vegan (Oksanen et al., 2020) packages, respectively.

We ran three distinct mixed-effect generalized linear models (GLMMs) to assess the effect of anthropization on network structural metrics. The proportion of anthropized area within each site's buffer was set as an explanatory variable, and each of the three metrics was each set as a response variable. We ran all models with a logit link function and quasibinomial error distribution to account for the proportion values of response variables. Network size and ectoparasite diversity were set as random variables. The metric wNODF was standardized to range from zero to one to be consistent with the other metrics (values were divided by 100). All models were checked *a posteriori* for overdispersion.

Moreover, we constructed three meta-networks grouping individual networks according to their degree of anthropization to synthesize interactions: fully preserved (100% natural cover within buffer), moderately anthropized (99.9–50% natural cover) and highly anthropized (49.9–0% natural cover). The three aforementioned structural metrics were calculated for each of the meta-networks. Meta-networks were constructed with Gephi 0.9.2 (Bastian et al., 2009).

## RESULTS

We captured 2,243 bats of 36 species in the 21 sampling sites, of which 899 bats of 23 species were carrying bat flies, which

comprised 1,721 individuals of 38 species (**Supplementary Table S1**). After excluding sites with low sampling completeness ( $<0.7$ ), 18 sites remained, leaving 21 bat species, 33 ectoparasite species and 711 pairwise interactions between 611 bats and 1,389 flies (**Supplementary Table S1**). Sites showed a broad variation in the percentage of natural cover within the buffer, from fully preserved sites within protected areas (100% natural cover) to fully anthropized sites outside of the national parks (0% natural cover) (**Supplementary Table S2**).

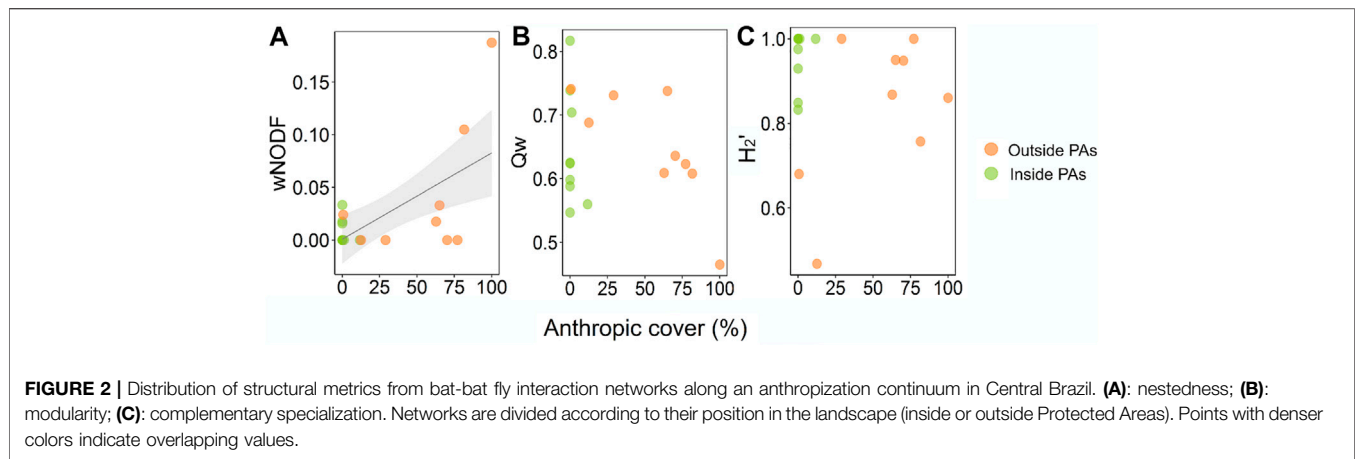
Networks were overall highly specialized ( $H_2' = 0.90 \pm 0.14$ ), modular (Qw =  $0.65 \pm 0.08$ ), and showed a remarkable lack of nestedness (wNODF =  $2.41 \pm 4.68$ ). Anthropization did not affect network specialization ( $\beta = -0.001$ ,  $t = -0.105$ ;  $p = 0.917$ ) nor modularity ( $\beta = -0.004$ ;  $t = -1.452$ ;  $p = 0.166$ ), but nestedness showed a positive response to an increase in anthropic cover ( $\beta = 0.034$ ;  $t = 3.45$ ;  $p < 0.005$ ) (**Figure 2**). The most anthropized sites (81.6 and 100% of anthropic cover) showed the most nested networks among the pool (10.50 and 18.75 wNODF, respectively) (**Figure 2**).

Regarding the meta-networks, the highly anthropized one exhibited the highest nestedness value, followed by the fully preserved and moderately anthropized meta-networks. The highly anthropized meta-network was also the least modular and the least specialized among the three meta-networks, and consisted of only two separated compartments, contrasting with three and eight compartments in the fully preserved and moderately anthropized networks, respectively (**Figure 3**).

## DISCUSSION

We evaluated how anthropization affects network assembly between bats and their ectoparasitic bat flies. Network's specialization and modularity remained similar across all the sampling sites in the study, while anthropization positively affected nestedness across sites. Therefore, we rejected our hypothesis that specialization would be lower in highly anthropized sites and accepted the hypothesis that networks were more nested in those sites. Previous studies considering anthropic effects on bat-fly interactions have considered only specialization (Hernández-Martínez et al., 2018) or specialization and modularity (Urbíeta et al., 2020) in their analysis, with different responses for specialization. Similar to our results, Urbíeta et al. (2020) observed that modularity and specialization remained consistent among three sites with different degrees of urbanization in an area of Cerrado in central Brazil. On the other hand, Hernández-Martínez et al. (2018) recorded more specialized networks in areas with lower degrees of fragmentation in a dry forest habitat in western Mexico.

The decreased specialization of bat-fly interaction networks in degraded areas could result from the smaller number of roosts in those areas, which would lead to increased aggregation of different species in the same roost, thus facilitating intraspecific transmission and leading to accidental infestations (Urbíeta et al., 2018,



2020). However, in our study area, roost availability can be considered high, as the Brazilian Federal District is a largely green city, with over 140 recorded tree species, most of them exotic (Vale et al., 2005; Alencar 2008; Guimarães 2020). Moreover, the presence of expansion joints on many of the buildings in the city also facilitates the presence of house-dwelling species, especially insectivores. The high availability of roosts allows each species to roost separately, thus avoiding the type of accidental infestations observed in previous studies (Urbieta et al., 2020) and resulting in the highly specialized networks observed throughout our study area, regardless of the degree of anthropization. It's important to note that even in natural areas where species share roosts the specificity of Streblidae infestation is usually high, probably as a result of co-evolutionary processes between flies and hosts (Marshall, 1982; Patterson et al., 2007; Fagundes et al., 2017).

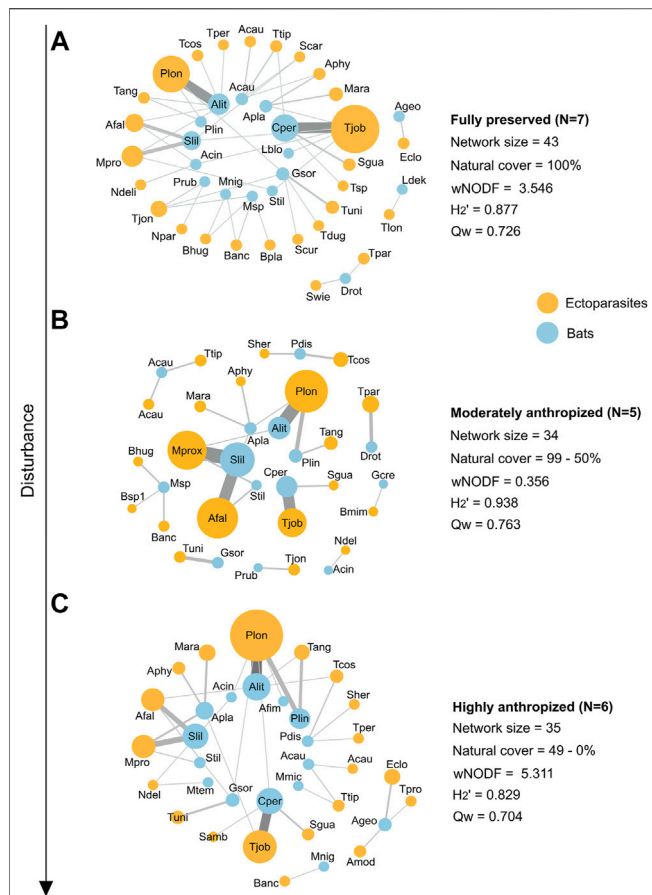
Even though we recorded no effect of anthropization on network specialization, we observed a higher level of nestedness and a reduced number of network compartments in sites located in highly anthropized areas. Increasingly nested networks indicate that, although parasites retain their host specificity, some bats tend to be more frequently parasitized by a richer ectoparasite assemblage, becoming hub species and approaching the role of keystone species often present in mutualistic networks (Mello et al., 2015). Thus, the most anthropized networks exhibit the emergence of a hierarchical assembly of interactions, as interaction asymmetries start to become apparent, that is, more generalist bats harboring specialized ectoparasites.

The increased level of nestedness and reduction of network compartments observed along the anthropization continuum in our study area suggest that specialization is not the best metric for evaluating how bat-fly networks respond to habitat degradation. Our results suggest that, even in anthropized areas, bat flies still retain their specialized host selection, possibly because of adaptations and evolutionary constraints that prevent them from parasitizing other bat species (Petersen et al., 2007; Dick and Dittmar 2013; Dittmar et al., 2015). For bats, on the other

hand, anthropization may lead to a higher diversity of ectoparasites per host, possibly due to increased stress or worsened health conditions (Pilosof et al., 2012; Russo and Ancillotto 2015).

Regarding the meta-networks, we observed that the fully preserved meta-network behaved similarly to the highly anthropized one in terms of nestedness, probably because the fully preserved meta-network is larger, which may influence nestedness (Freitas Júnior et al., 2020). Such an outcome was expected, as more preserved areas tend to have richer species assemblages (Russo and Ancillotto 2015) potentially sharing roosts more often. A more informative comparison can be made between the moderately anthropized and the highly anthropized networks, which have similar sizes but behave very differently in terms of specialization and nestedness. The less anthropized meta-network is much more fragmented into compartments and is highly specialized, with fewer bats connected by common ectoparasites. Meanwhile, species previously occurring in compartments were incorporated into the network core in highly anthropized areas. Due to a lower availability of natural roosts in anthropized sites, different bat species may share man-made roosts more often or share the same natural roosts encroached upon by rural or urban environments (Kunz, 1982). This scenario may lead to the exchange of ectoparasites between bat species that were not previously in contact (Urbieta et al., 2018, 2020), which leads to a more structured network. Such exchanges may have important epidemiological implications.

Recent studies indicate that ectoparasitic bat flies can carry disease agents, such as bacteria of the genus *Bartonella* (Morse et al., 2012) and viruses from families Flaviviridae, Rhabdoviridae, Reoviridae, and Peribunyaviridae (Abundes-Gallegos et al., 2018; Martínez et al., 2021). Moreover, Gay et al. (2014) observed a positive correlation between ectoparasite and virus richness in Southeast Asia, which is especially concerning considering that both the prevalence of infectious diseases and the diversity of zoonotic parasites in bats are higher in urban areas (Mühldorfer et al., 2011; Nunes et al., 2017). Therefore, an increased number of



**FIGURE 3 |** Bat-bat fly interaction meta-networks and their structural metrics from natural and disturbed areas in Central Brazil. The 18 individual interaction networks were grouped according to the degree of anthropization of their areas of origin: **(A):** fully preserved (100% natural cover within buffer), **(B):** moderately anthropized (99.9–50% natural cover), and **(C):** highly anthropized (49–0% natural cover). Node size is associated with species abundance and link width pairwise interaction frequency. Bat labels: Acau: *Anoura caudifer*; Ageo: *Anoura geoffroyi*; Acin: *Artibeus cinereus*; Afim: *Artibeus fimbriatus*; Alit: *Artibeus lituratus*; Apla: *Artibeus planirostris*; Cper: *Carollia perspicillata*; Drot: *Desmodus rotundus*; Gcre: *Gardneriactes crenulatus*; Gsor: *Glossophaga soricina*; Lblo: *Lasiurus blossevillii*; Ldek: *Lonchophylla dekeyseri*; Mmic: *Micronycteris microtis*; Mtem: *Molossops temminckii*; Mnig: *Myotis nigricans*; Msp: *Myotis* sp.; Pdis: *Phyllostomus discolor*; Plin: *Platyrrhinus lineatus*; Prub: *Pteronotus rubiginosus*; Sill: *Sturnira lilium*; Stil: *S. tildae*. Parasite labels: Acau: *Anastreba caudiferae*; Amod: *A. modestini*; Afal: *Aspidoptera falcata*; Aphy: *A. phyllostomatis*; Banc: *Basilia anceps*; Bhug: *B. hughscotti*; Bmim: *B. mimoni*; Bsp1: *Basilia* sp. 1; Bsp1: *Basilia* sp. 2; Eclo: *Exastininon clovisi*; Mara: *Megistopoda aranea*; Mpro: *M. proxima*; Ndel: *Neotrichobius delicatus*; Npar: *Nycterophylla parnellii*; Plon: *Paratrachobius longicrus*; Samb: *Speiseria ambigua*; Scar: *Strebla carvalhoi*; Scur: *S. curvata*; Sgua: *S. guajiro*; Sher: *S. hertigi*; Swie: *S. wiedermanni*; Tper: *Trichobioides perspicillatus*; Tang: *Trichobius angulatus*; Tcos: *T. costalimai*; Tdug: *T. dugesii*; Tjob: *T. joblingi*; Tjon: *T. johnsonae*; Tlon: *T. lonchophyllae*; Tlon: *T. longipes*; Tpar: *T. parasiticus*; Tpro: *T. propinquus*; Tsp: *Trichobius* sp.; Ttip: *T. tiptoni*; Tuni: *T. uniformis*.

accidental infestations of ectoparasites in different bat species could facilitate the spread of such disease agents in anthropized areas, leading to public health issues.

Many studies have indicated that environmental degradation, including anthropization and habitat suppression, could be responsible for the increased occurrence of emerging diseases (Daszak et al., 2001; Nabi et al., 2020). Nevertheless, the role of bat flies in microorganism transmission and the extent to which environmental degradation affects bats and their ectoparasites still requires better elucidation.

## 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 animals were reviewed and approved by Ethics Commission on Animal Use from University of Brasília (CEUA/UnB) (process #116319/2011). Capture in Protected Areas was permitted by Chico Mendes Institute for Biodiversity Conservation from Brazilian Ministry of the Environment (ICMBio/MMA) (license #39296-1).

## AUTHOR CONTRIBUTIONS

DR captured and identified individuals, conducted statistical analysis, and contributed to the writing of the paper; UD conducted network and statistical analysis and contributed to the writing of the paper and experimental design of the study.

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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.2021.752412/full#supplementary-material>



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# Selective Logging Shows No Impact on the Dietary Breadth of a Generalist Bat Species: The Fawn Leaf-Nosed Bat (*Hipposideros cervinus*)

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Logging activities degrade forest habitats across large areas of the tropics, but the impacts on trophic interactions that underpin forest ecosystems are poorly understood. DNA metabarcoding provides an invaluable tool to investigate such interactions, allowing analysis at a far greater scale and resolution than has previously been possible. We analysed the diet of the insectivorous fawn leaf-nosed bat *Hipposideros cervinus* across a forest disturbance gradient in Borneo, using a dataset of ecological interactions from an unprecedented number of bat-derived faecal samples. Bats predominantly consumed insects from the orders Lepidoptera, Diptera, Blattodea, and Coleoptera, and the taxonomic composition of their diet remained relatively consistent across sites regardless of logging disturbance. There was little difference in the richness of prey consumed per-bat in each logging treatment, indicating potential resilience of this species to habitat degradation. In fact, bats consumed a high richness of prey items, and intensive sampling is needed to reliably compare feeding ecology over multiple sites. Multiple bioinformatic parameters were used, to assess how they altered our perception of sampling completeness. While parameter choice altered estimates of completeness, a very high sampling effort was always required to detect the entire prey community.

**Keywords:** molecular ecology, logging, tropical ecology, bats (Chiroptera), metabarcoding

## INTRODUCTION

Logging is a common form of anthropogenic disturbance in forests, with over 90% of those in the tropics logged to some degree and selective logging taking place at a greater rate than clear-felling (Asner et al., 2009). Selective logging tends to favour removal of the largest, and highest-quality trees, and while this disturbance can have lasting effects on forest structure (Milodowski et al., 2021), it tends to be much less destructive than clear-felling.

Forest modification through logging is especially pronounced on the island of Borneo, which has lost half of its forest area since 1940 (Gaveau et al., 2014) and 62% of the remaining forest

is classified as “degraded” or “seriously degraded” (Gaveau et al., 2016). Most studies of the impact this has on biodiversity have focussed on species composition (e.g., Edwards et al., 2011; Slade et al., 2011; Kitching et al., 2013; Struebig et al., 2013; Deere et al., 2018; Hayward et al., 2021). These often subtle changes to ecological communities can result in changes to ecosystem functioning (Ewers et al., 2015) and the structure of trophic networks (Hemprich-Bennett et al., 2020), indicating that selective logging may alter resilience to future perturbations. Understanding the ecological shifts that take place in degraded forest is of great importance for conservation, especially given the vast scale at which forest is managed for timber extraction globally.

Animal diet can differ between individuals of a species depending on numerous intrinsic and environmental factors. In insectivorous bats, for example, inter-individual variation in diet appears to correlate with multiple factors, including wing morphology (de Oliveira et al., 2020), sex (Burgar et al., 2014), reproductive condition (Czenze et al., 2018), season (Andriollo et al., 2019; Kolkert et al., 2020), geographic location (Czenze et al., 2018; Vallejo et al., 2019), and habitat (Aizpurua et al., 2018; Hemprich-Bennett et al., 2020; Tournayre et al., 2021). Such variation is of interest because intraspecific differences in the feeding behaviour of consumers can alter the abundance, community composition, and ecological functioning of their prey (Des Roches et al., 2018).

Intraspecific variation in diet is also an important consideration for research design. The analysis of diet in a highly generalist species requires many observations to obtain a representative sample. This can be especially true when studying the dietary ecology of insectivorous bats through metabarcoding, as the technique gives an unprecedented level of taxonomic resolution (Clare et al., 2009), highlighting variation which would not have been apparent with morphological study. Inter-individual variation in bat diet is however often obscured by the use of samples collected from underneath roosts, where numerous bats are defecating (hereafter “roost-sourced” samples) (Clare et al., 2014; Andriollo et al., 2019) and samples cannot be linked to an individual. Obtaining faecal samples from individually identifiable animals (hereafter “individual-sourced” samples) is labour-intensive due to the large trapping effort required, and so while many studies have used individual-sourced samples (e.g., Czenze et al., 2018; de Oliveira et al., 2020), their sample sizes tend to be small. Mata et al. (2018) used a dataset of individual-sourced samples to analyse the importance of technical and biological replication on the dietary completeness of *Tadarida teniotis* and reiterated the common rule of thumb that 20–50 such samples per species is preferable, but stressed that higher sample sizes may be required for bat species with greater dietary richness or intraspecific variation. The issue of sample size is further complicated in networks generated from metabarcoding data because of methodological considerations such as PCR primer bias and stochasticity (Alberdi et al., 2018), and the influence of bioinformatic choices on the final data analysed (Hemprich-Bennett et al., 2021).

Here we use an unprecedented number of individually sourced insectivorous bat faecal samples to test the hypothesis that

selective logging alters the taxonomic composition and the richness of Molecular Operational Taxonomic Units (MOTUs) in bats’ diets. We also assess how sample size and bioinformatic parameters affect our inferences of insectivorous diet when using data derived from metabarcoding. Our evaluation focuses on the fawn leaf-nosed bat, *Hipposideros cervinus* – a cave-roosting insectivorous bat found throughout much of maritime Southeast Asia to northeastern Australia. Using high-duty cycle (HDC) echolocation, it is thought to use Doppler-shift compensation to detect the wingbeats of fluttering of prey such as moths (Bell and Fenton, 1984) against a cluttered backdrop (Schnitzler and Kalko, 2001; Lazure and Fenton, 2011). Although some bat species are negatively affected by logging, *H. cervinus* remains a dominant species in both old growth and logged forest in Borneo (Struebig et al., 2013; Hemprich-Bennett et al., 2020). It is not known whether bats such as *H. cervinus* respond to forest degradation by modifying their diets, or are able to maintain stable diets through prey selection or behavioural changes in foraging. We address three main predictions:

- 1) Taxonomic composition of the diet of *H. cervinus* is altered by rainforest degradation.
- 2) Bats are more specialised in logged forest sites than in primary forest, due to reduced available prey taxa richness.
- 3) Estimates of sampling completeness are heavily influenced by MOTU clustering threshold, quality-control methods used and the number of samples.

## MATERIALS AND METHODS

We sampled bats using six harp traps per night at four lowland tropical rainforest sites in Sabah, Malaysia, each <500 m above sea level and limited seasonality. Two sites comprise mostly old growth rainforest (Danum Valley and Maliau Basin), and two sites have been subject to substantial logging disturbance (the Sabah Biodiversity Experiment and the Stability of Altered Forest Ecosystems Project) (**Supplementary Table 1**).

- Old growth rainforest:
  - The Danum Valley Conservation Area (hereafter “Danum”) is a 438 km<sup>2</sup> region protected area of old growth rainforest in Sabah (Reynolds et al., 2011). Traps were erected in 2016 for ten nights in a 21-night period and 2017 for ten nights in a 12-night period.
  - The Maliau Basin Conservation Area (hereafter “Maliau”) is a 588 km<sup>2</sup> protected forest made up of lowland and hill forest, most of which has neither been logged nor inhabited in historical times. Traps were erected in 2016 and 2017 for ten nights in a 16-night period.
- Logged forest:
  - The Stability of Altered Forest Ecosystems Project (hereafter “SAFE”) is a large area of degraded forest being converted to oil palm plantation, with fragments of forest retained for scientific study (Ewers et al., 2011).



We sampled in the blocks “LFE,” “B,” and “C,” within the Ulu Segama Forest Reserve and Kalabakan area, during 2015, 2016, and 2017. Each block was sampled for a five-night period, and then resampled at least 5 weeks later. Our schedule in 2015 allowed an additional six nights of sampling at “LFE.”

- o The Sabah Biodiversity Experiment (Hector et al., 2011) (hereafter “SBE”) is an area of forest which was logged once in the 1950s and once in the 2000s, and during the sampling period was in the early stages of enrichment replanting (Hector et al., 2011). Sampling took place over a total of 10 nights in a 20-night period in 2016.

Fieldwork, laboratory work and bioinformatics took place as previously described (Hemprich-Bennett et al., 2020). Briefly, bats were captured using harp traps erected along linear features such as streams and trails to target bat flyways. Sampling effort is summarised in **Table 1**. Faecal samples were processed by DNA extraction, PCR amplification of the CO1 gene using the primers described by Zeale et al. (2011), and sequenced on an Illumina MiSeq. For complete methods see Hemprich-Bennett et al. (2020).

## Bioinformatics Pipeline

Sequences were assembled into contigs using mothur (Schloss et al., 2009), and forward and reverse primers were removed using the galaxy web platform on the public server at usegalaxy.org (Afgan et al., 2016) sequence falling outside of a length of 155–159 bp (2 bp outside of the expected amplicon length) were excluded from analysis.

When processing the sequence data it is common to cluster sequences into MOTUs (Floyd et al., 2002), on the basis of a given threshold of similarity, but the appropriate MOTU clustering thresholds required to best-represent the taxonomic diversity within metabarcoding samples are currently poorly understood (Hemprich-Bennett et al., 2021). At high clustering thresholds routine sequencing errors may be falsely designated as distinct MOTU, artificially inflating the measured diversity and richness within a sample (Clare et al., 2016). Algorithms implemented using software such as LULU (Frøslev et al., 2017) have been proposed as a method of mitigating this, by combining probable duplicate MOTUs based on patterns of sequence similarity and co-occurrence.

To assess the impact of clustering threshold on the datasets analysed (Hemprich-Bennett et al., 2021) we generated datasets

using MOTU clustering thresholds at ranges 91–98% similarity, using the Uclust algorithm (Edgar, 2010) as implemented in the QIIME platform (Caporaso et al., 2010). Representative sequences for each MOTU per clustering level were then compared to one another using BLAST+ (Camacho et al., 2009), with the resulting data being reduced in LULU (Frøslev et al., 2017) for quality control. All resulting bat-MOTU adjacency lists were then transformed into adjacency matrices using a custom perl script. These matrices were then split into multiple binary adjacency matrices by site. Networks were created by pooling samples from multiple years. To test prediction 2, separate analyses took place on networks both generated as composites of multiple years, and as separate networks for each site and year (see **Table 1**). All bioinformatic and statistical steps are recorded at <https://github.com/hemprichbennett/hice>.

## Prediction 1: Taxonomic Composition of the Diet of *Hipposideros cervinus* Is Altered by Rainforest Degradation

To analyse the prey taxa consumed by each bat, we used BLAST+ (Camacho et al., 2009) to compare all MOTUs to a library of all arthropod CO1 sequences identified to species level as available in the Barcode of Life Database (BOLD) on March 28, 2018 (Ratnasingham and Hebert, 2007) (3,319,062 sequences), and assigned them taxonomy in MEGAN 6 (Huson et al., 2016) using the parameters in Salinas-Ramos et al. (2015). We then assigned MOTUs to order and family level where possible, importing the resulting data into R for analysis, and calculating the proportion of *H. cervinus* individuals per site consuming each taxonomic order. To test the hypothesis that habitat type alters the order-level taxonomic composition of the species’ diet, we analysed the resulting values with a Chi-squared test. The hypothesis was further tested using a permutational multivariate analysis of variance test using distance matrices, and a non-metric multidimensional scaling ordination with 200 permutations using Bray–Curtis dissimilarity, both using the vegan package (Oksanen et al., 2017) on datasets of the order-level diets of each individual bat. We also used a similarity percentages analysis to identify the contribution of each taxonomic order to the observed dissimilarity between sites and years, using Bray–Curtis dissimilarity.

We calculated correlations between the presence/absence of prey orders in faecal samples, using the r package “corrplot”

**TABLE 1** | Trapping effort per site, in harp trap nights.

Sample site	Harp trap nights			<i>Hipposideros cervinus</i> captured			Number of faecal samples sequenced		
	2015	2016	2017	2015	2016	2017	2015	2016	2017
Danum	0	60	60	0	311	328	0	70	118
Maliau	0	60	60	0	124	104	0	42	55
SAFE	216	180	180	75	95	146	44	36	52
SBE	0	60	60	0	245	0	0	57	0

One harp trap night is a harp trap erected for a single night. Six harp traps were used per night, so a single night’s trapping was equal to six harp trap nights.

(Wei and Simko, 2017), to identify both potential significant correlations of prey consumption (e.g., bats that feed on Coleoptera may be more likely to feed on Blattodea), and any potential taxonomic bias in PCR.

### Prediction 2: Individual Bats Are More Specialised in Logged Forest Sites Than in Old Growth Forest

We created binary bipartite networks for each sampling site and year at 95% similarity clustering and quality control using LULU. In the networks each individual bat and MOTU was classed as a distinct node. A criterion of 95% similarity was chosen for this and all following analyses because it provided a balance between over and under-splitting MOTUs (Hemprich-Bennett et al., 2021). Using the R package “bipartite” (Dormann, 2011) in R 3.4.4 (R Core Team, 2017) we then calculated the number of prey MOTUs each bat consumed. Differences between the number of MOTUs consumed per bat were compared among sites using an ANOVA with Tukey's HSD test.

### Prediction 3: Estimates of Sampling Completeness Are Heavily Influenced by Molecular Operational Taxonomic Unit Clustering Threshold and Quality-Control Used

Using networks generated at each clustering threshold between 91 and 98% similarity, both with and without quality-control using LULU (Frøslev et al., 2017), we estimated total MOTU richness and sampling completeness of the diet of *H. cervinus* at each site and year using iNEXT (Hsieh et al., 2016), an R package for the interpolation and extrapolation of species diversity using Hill numbers (Chao et al., 2014).

To assess how sample size affects assessments of bat diet, we generated multiple datasets of  $n$  bats from each site, where  $n$  was a value of 10–100, increasing in increments of 10 (10, 20, 30, etc.), with  $n$  bats taken at random from each site and the number of MOTUs consumed in that sub-dataset calculated. This was repeated 100,000 times per site and value of  $n$ , with the resulting data plotted in a violin plot.

## RESULTS

For the full sequencing run of multiple bat species (see Hemprich-Bennett et al., 2020) 18,737,930 contiguous reads were output when assembling the paired-end files. After removing adapters and primers this was reduced to 10,064,815 sequences, which was then further reduced to 932,459 haplotypes after collapsing to haplotype, removing singletons and discarding sequences outside of 2 bp of the expected read-length. For full counts of MOTUs before and after clustering with LULU, see **Supplementary Information 2**. Of these, 2,957,444 reads and 187,800 haplotypes were derived from *H. cervinus* samples and included in this study.

### Prediction 1: Taxonomic Composition of the Diet of *Hipposideros cervinus* Is Altered by Rainforest Degradation

The diet of the bat communities was dominated by insects from the orders Lepidoptera, Diptera, Blattodea, and Coleoptera (**Figure 1** and **Table 2**). The Chi-squared test showed a non-significant effect of site on the order-level composition of a bat populations' diet ( $\chi^2 = 0.36$ ,  $df = 66$ ,  $p > 0.05$ ). The NMDS showed almost total overlap between the sites (**Figure 2**) with a stress of 0.21, showing poor convergence. The permutational multivariate analysis of variance test gave an  $R^2$  of 0.014 for the explanatory power of site on bat diet. A total of 23 arthropod orders were eaten based on the combined diets of all bats, with Lepidoptera, Diptera (especially family Cecidomyiidae), Blattodea (especially family Ectobiidae), and Coleoptera collectively making up at least 79% of all MOTUs identified at each site (**Figure 1**, **Table 2**, and **Supplementary Information 2**). Araneae were consumed in each site and year. Positive correlations were observed between the occurrences of several taxa, with only Araneae and Hymenoptera being negatively correlated with the presence of one another (**Supplementary Information 3**). Blattodea was the only taxon consistently observed to contribute significantly to inter-site dissimilarity scores (SAFE-Maliau  $p < 0.01$ , SAFE-SBE  $p = 0.014$ , Maliau-SBE  $p = 0.014$ , and SBE-Danum  $p < 0.01$ , see **Supplementary Information 4**). There was almost complete overlap between the different years sampled at each site (**Figure 2**) and each site in 2016 (**Figure 3**).

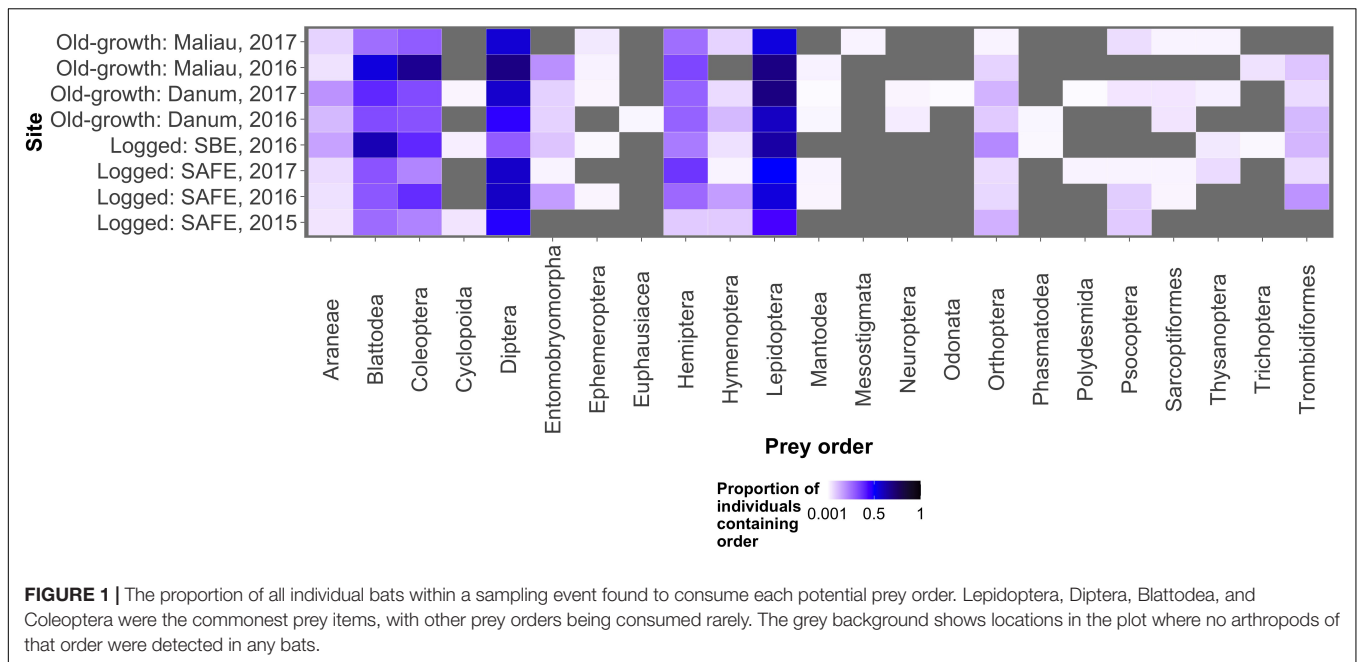
### Prediction 2: Individual Bats Will Be More Specialised in Logged Forest Sites Than in Old Growth Forest

When comparing the number of MOTUs consumed per bat at each site, significant differences ( $p < 0.05$ ) were only observed between Danum (old-growth) and SAFE (logged), and between SAFE (logged) and SBE (logged).

### Prediction 3: Estimates of Sampling Completeness Will Be Heavily Influenced by Molecular Operational Taxonomic Unit Clustering Threshold and Quality-Control Used

None of the networks were estimated as near to fully sampled, with all estimates placing completeness at under 54% (**Figure 4**), with completeness estimates varying between both sites and years. The number of MOTUs expected increased markedly with clustering threshold when not using LULU for quality control, but this effect was dramatically reduced when using LULU. This algorithm increased estimated sampling completeness by reducing observed and estimated MOTU richness, and lowered the estimated number of samples required to sample the community. Full counts can be found in **Supplementary Information 2**.

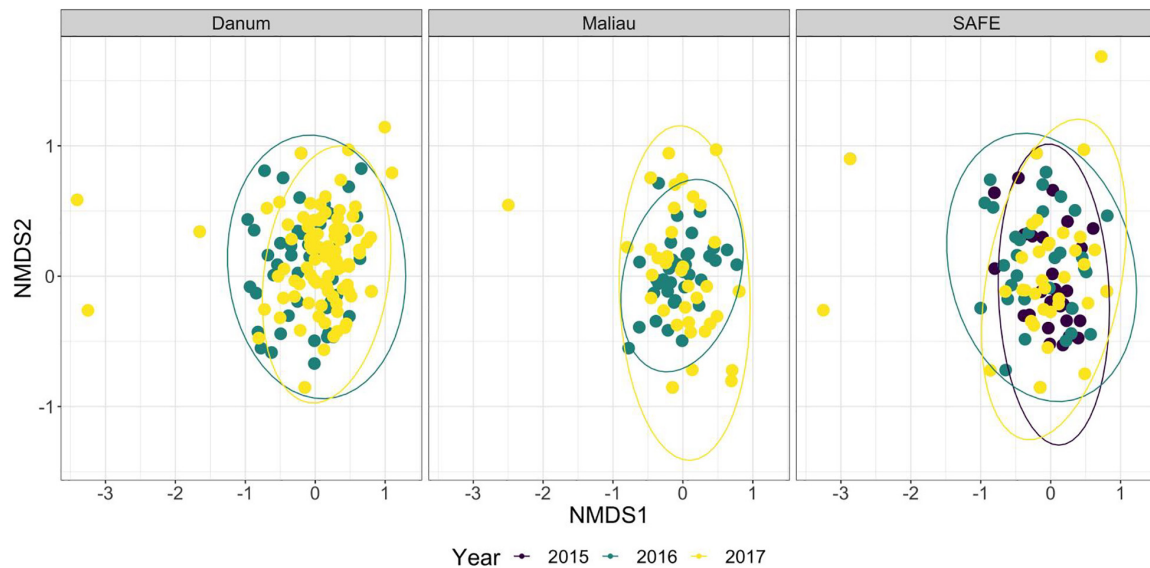
There was a positive correlation between the number of bats included in a dataset and the number of MOTUs detected



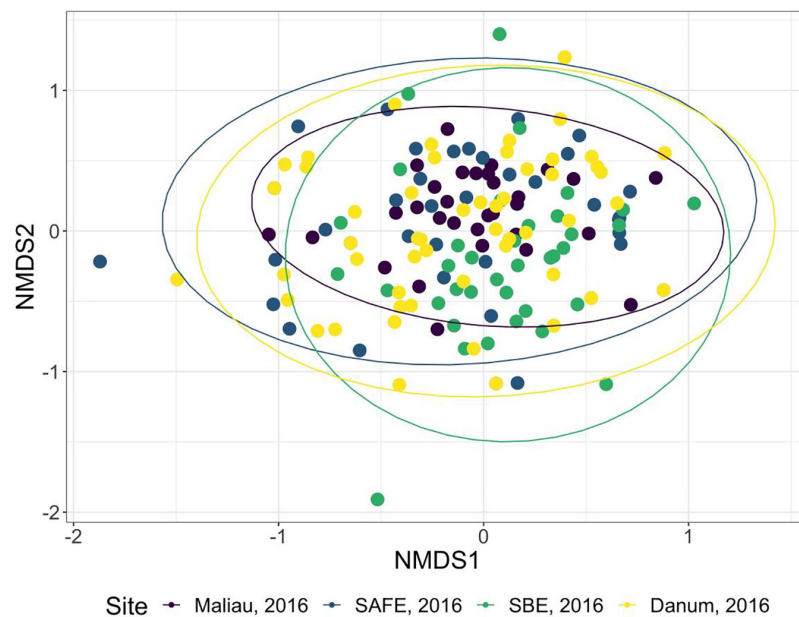
**TABLE 2 |** The proportion of all individual bats within a sampling event found to consume each potential prey order, rounded to three decimal places.

Order	Old-growth rainforest				Logged rainforest			
	Danum		Maliau		SAFE			SBE
	2016	2017	2016	2017	2015	2016	2017	2016
Araneae	0.020	0.028	0.006	0.023	0.008	0.011	0.014	0.021
Blattodea	0.183	0.218	0.206	0.159	0.171	0.096	0.135	0.338
Coleoptera	0.107	0.076	0.168	0.095	0.076	0.150	0.082	0.090
Cyclopoida	0	0.002	0	0	0.004	0	0	0.005
Diptera	0.165	0.135	0.200	0.250	0.266	0.193	0.260	0.074
Entomobryomorpha	0.013	0.011	0.023	0	0	0.027	0.010	0.013
Ephemeroptera	0	0.002	0.003	0.008	0	0.005	0	0.003
Euphausiacea	0.003	0	0	0	0	0	0	0
Hemiptera	0.063	0.045	0.049	0.076	0.046	0.075	0.106	0.032
Hymenoptera	0.023	0.007	0	0.015	0.008	0.032	0.005	0.005
Lepidoptera	0	0	0	0	0	0	0	0
Mantodea	0.365	0.421	0.316	0.348	0.365	0.310	0.308	0.354
Mesostigmata	0.003	0.001	0.003	0	0	0.005	0.005	0
Neuroptera	0	0	0	0.004	0	0	0	0
Odonata	0.005	0.002	0	0	0.004	0	0	0
Orthoptera	0	0.001	0	0	0	0	0	0
Phasmatodea	0.015	0.027	0.009	0.004	0.034	0.037	0.034	0.040
Polydesmida	0.003	0	0	0	0	0	0	0.003
Psocoptera	0	0	0	0	0	0	0	0
Sarcoptiformes	0	0.001	0	0	0	0	0.005	0
Thysanoptera	0	0.005	0	0.011	0.015	0.016	0.005	0
Trichoptera	0.013	0.005	0	0.004	0	0.005	0.005	0
Trombidiformes	0	0.003	0	0.004	0	0	0.014	0.005

*Lepidoptera, Diptera, Blattodea, and Coleoptera were the commonest prey items, with other prey orders being consumed rarely.*



**FIGURE 2 |** Non-metric multidimensional scaling ordination of the order-level consumption of individual bats across multiple years. The ellipses of each site show almost complete overlap. Stress was 0.21, indicating poor convergence. Danum and Maliau are old-growth sites, SAFE is a logged forest site.



**FIGURE 3 |** Non-metric multidimensional scaling ordination of the order-level consumption of individual bats in 2016. The ellipses of each site show almost complete overlap. Stress was 0.22, indicating poor convergence. Danum and Maliau are old-growth sites, SAFE and SBE are logged forest sites.

(Figure 5), with the highest total number of MOTUs being detected at the old-growth site Danum (Supplementary Table 1).

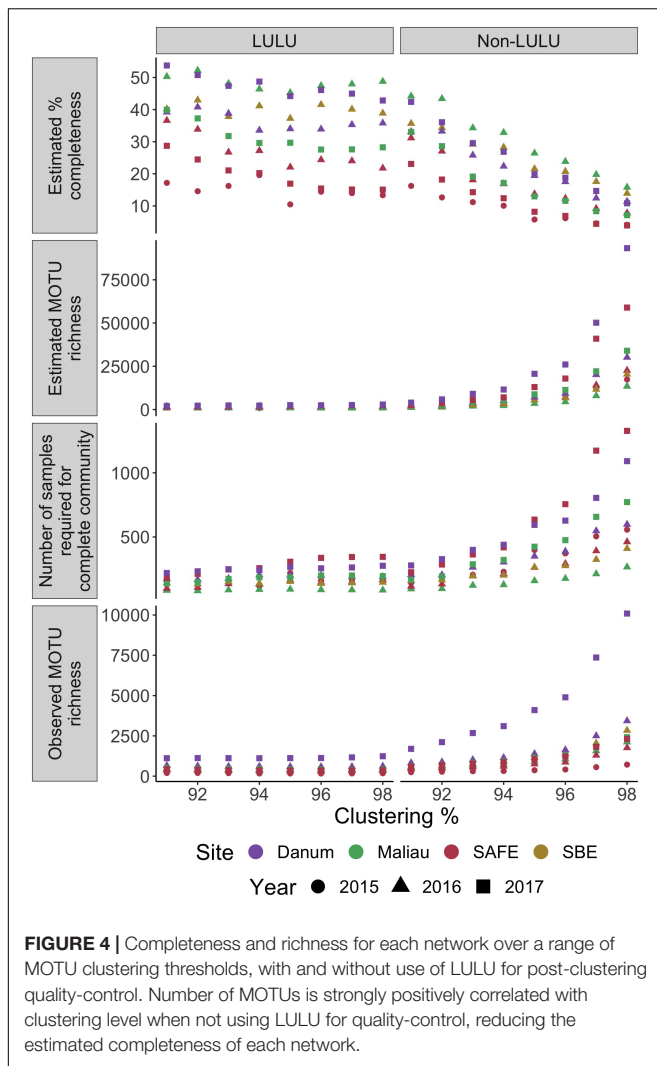
## DISCUSSION

We set out to assess how the diet of a generalist insectivorous bat differs between old-growth and degraded forest habitats. We

observed broadly similar feeding habits in fawn leaf-nosed bats across forest type with bats consuming many arthropod orders, particularly Lepidoptera, Diptera, Blattodea, and Coleoptera. Fawn leaf-nosed bats have extremely high dietary richness, with many hundreds of samples being required to fully capture their diet.

We observed very little alteration in the taxonomic composition of the diet of *H. cervinus* at the order-level





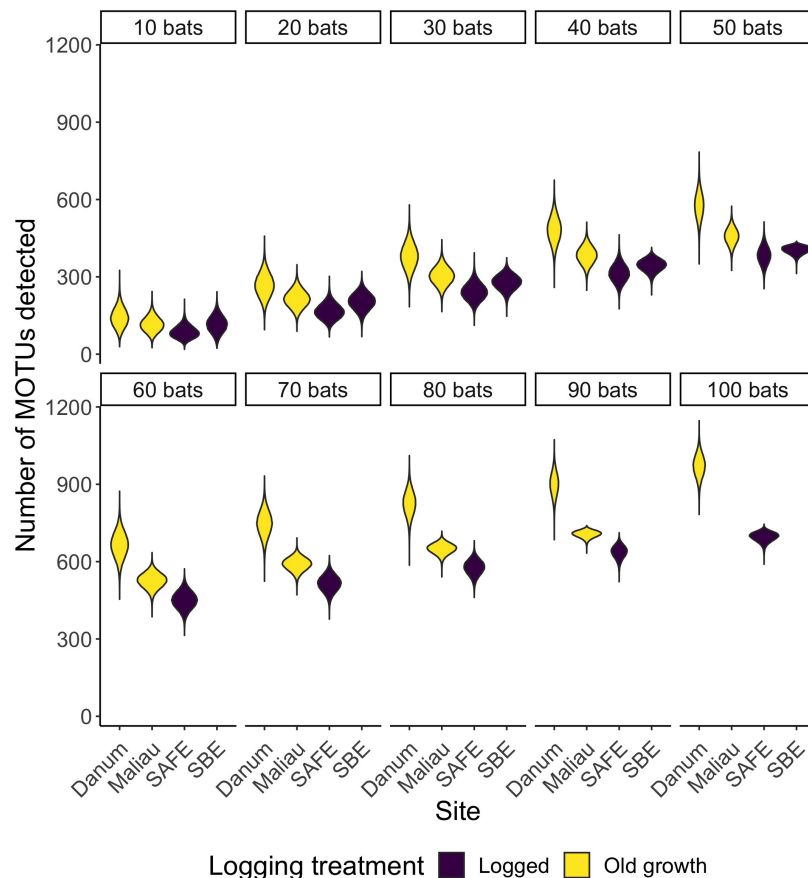
between sites or years. This suggests that while northeast Borneo may possess high beta-diversity of some insect species (Kitching et al., 2013), at coarse taxonomic levels there is little spatial difference in the prey consumed by *H. cervinus*. Previous findings suggested that, as HDC echolocators, *H. cervinus* primarily consumed flying insects (Bell and Fenton, 1984; Link et al., 1986; Schnitzler and Kalko, 2001; Lazure and Fenton, 2011), in particular Lepidoptera, Blattodea, Diptera, and Coleoptera. The regular presence of diverse families of spiders indicates a dietary contribution of these taxa previously unknown in the Hipposideridae family of bats. Hipposiderids have been observed gleaning stationary targets with fluttering wings (Bell and Fenton, 1984), but the consumption of spiders would either suggest they are gleaning non-fluttering animals, or taking them when ballooning as juveniles. Alternatively, the consumption of spiders could be due to secondary predation: where the bat consumes a primary prey item which has ingested a spider. This seems an unlikely explanation for our dataset, since predatory arthropods other than Araneae are poorly represented in the MOTU dataset.

In this study we used one of the most reliable primer sets for amplification of a wide range of digested arthropods (Zeale et al., 2011; Alberdi et al., 2018), but they are also reported to have taxonomic biases toward Diptera and Lepidoptera. However, we found no significant negative correlations between detecting Dipteran or Lepidopteran DNA in a sample, and the detection of any other prey order. This indicates that amplification of dipteran or lepidopteran DNA did not consistently inhibit the amplification of another taxonomic order during PCR, and that sequencing depth is sufficient.

We did not observe any clear pattern of the number of MOTUs consumed per bat differing between logged and old growth habitats, mirroring our finding that the taxonomic composition of prey did not differ between sites. This contrasts with our previous findings in these study sites (Hemprich-Bennett et al., 2020), that the overall assemblage of bat species in these sites consistently consumed fewer MOTUs per bat in logged forest than old growth. This contrasting pattern may reflect species level differences in their response to disturbance and resource variation. The diversity of the overall bats' diet is likely due to the high diversity of prey available to them, and the lack of observed differences in diet between sites may indicate highly flexible foraging, with low impact of land-use change on their diets. Being able to forage adaptively, or fly long distances to viable feeding sites (Struebig et al., 2009) may enable them to remain abundant despite selective logging, while conspecific species experience population declines (Struebig et al., 2013). This species may, as a result, provide ecological redundancy and continue to contribute insectivory when more sensitive bat species have become locally extinct.

A crucial concern in network ecology is the minimum number of samples or observations required to characterise reliably the structure and identity of the interactions within a network (Nielsen and Bascompte, 2007; Rivera-Hutinel et al., 2012). This requirement is complicated in studies utilising DNA metabarcoding as the number of nodes generated is dependent on the bioinformatic choices used to generate them. While MOTU approaches frequently apply a standard resolution to all nodes which helps control for variation in identification, altering MOTU clustering threshold will change the number of nodes and estimates of completeness, analogous to lumping taxonomy-based identifications to higher levels, but without a biological equivalent. We tested MOTU clustering and the use of LULU for quality-control and demonstrated that it was possible to alter estimates of sampling completeness greatly (Figure 4). However, when generating networks with a range of bioinformatics combinations, we observed that none exceeded an estimate of 50% completeness and thus regardless of parameters used, obtaining the full estimate of *H. cervinus* diet would require several hundred samples per site, with the same likely true of many ecologically similar species. Altering MOTU clustering parameters has previously been shown to cause great variation in MOTU counts (Clare et al., 2016) and changes in numerous measures of network-level architecture (Hemprich-Bennett et al., 2021). The reduction in number of estimated MOTUs provided by LULU (Frøslev et al., 2017) is expected to be of great





**FIGURE 5 |** Violin plots showing the distribution of the number of MOTUs consumed when reducing a dataset to  $n$  bats. With small datasets, sites appear to be rather similar in MOTU richness, but differences emerge as sample sizes increase.

use in future metabarcoding-based studies to reduce spurious MOTU generation.

The dietary richness found here echoes previous studies (Clare et al., 2009; McCracken et al., 2012) and highlight the substantial challenge of characterising the diets of this and other insectivorous bat species, especially in hyperdiverse ecosystems such as tropical rainforests. Their large dietary breadth is further highlighted by the fact that DNA extractions performed here were for pooled faecal samples from each individual bat, a technique which Mata et al. (2018) found underestimated the total richness of the diet per bat. Previous intensive studies of arthropod diversity in lowland tropical rainforest have failed to reach an asymptote (Novotný and Basset, 2000; Basset et al., 2012), and if bats are foraging opportunistically it is perhaps unsurprising that the taxonomic breadth of their diet is extremely large and nearly impossible to sample completely.

We demonstrate the vast richness of prey consumed by an insectivorous bat species in tropical rainforest and show that although quality-control steps in metabarcoding can reduce our estimates of the number of distinct prey items in a site, many hundreds of samples are required to collect a representative description of the diet of such species. Although we focussed our sampling on a single species of insectivorous bat, some inferences

likely also apply to similar species, and to other studies that use metabarcoding. The number of sites analysed in this study was low, but it has been shown here that this *Hipposiderid* species has a highly diverse diet; relying on cockroaches more than previously thought and potentially having a strategy of gleaning non-fluttering prey previously unknown in the family. This bat species is thus thought to exhibit low levels of dietary response to habitat degradation, potentially indicating reasons for their known versatility in the face of landscape modification.

## 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://zenodo.org/record/3247465#.YP7P3C1Q30o>.

## ETHICS STATEMENT

Bats were captured and handled using standard methods in line with recommendations set out by the American Society of

Mammalogists. Ethical review was also undertaken by the Sabah Biodiversity Council and Yayasan Sabah as part of the research approval process.

## AUTHOR CONTRIBUTIONS

SR, EC, DH-B, MS, HB, PK, and OL conceived the project. DH-B, VK, and JB undertook the field collections and laboratory work. DH-B analysed the data with input from EC. DH-B wrote the manuscript with input from all authors.

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JKM/MBS.1000-2/2 (374), JKM/MBS.1000-2/2 JLD.4 (23), JKM/MBS.1000-2/2 JLD.4 (45), JKM/MBS.1000-2/2 JLD.4 (41), JKM/MBS.1000-2/2 JLD.4 (46), JKM/MBS.1000-2/2 JLD.5 (123), and JKM/MBS.1000-2/2 JLD.5 (153); Export licenses: JKM/MBS.1000-2/3 JLD.2 (55), JKM/MBS.1000-2/3 JLD.2 (95), and JKM/MBS.1000-2/3 JLD.3 (31)]. We thank Eleanor Slade and members of the LOMBOK consortium for facilitating research in Sabah, and we are grateful to the Sabah Biodiversity Council (Danum Valley access permits: YS/DVMC/2015/221, YS/DVMC/2016/11, YS/DVMC/2015/222, YS/DVMC/2016/13, YS/DVMC/2017/42, and YS/DVMC/2017/41; Maliau Basin access permits: YS/MBMC/2015/186, YS/MBMC/2016/23, YS/MBMC/2015/187, YS/MBMC/2016/25, YS/MBMC/2017/67, and YS/MBMC/2017/66). We also thank Steven Le Comber, Hernani Oliveira, Joshua Potter, Sandra Álvarez Carretero, and Kim Warren for their analytical assistance, and Mark Brown and Darren Evans, for helpful comments on earlier versions of this manuscript. A previous version of this manuscript was published as a preprint on bioRxiv on August 1st, 2021 at <https://www.biorxiv.org/content/10.1101/2021.07.30.453964v1>, doi: 10.1101/2021.07.30.453964.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.750269/full#supplementary-material>

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# Patterns of Bat Diversity in an Undisturbed Forest and Forest Mosaic Habitats of the Afromontane Forest Biome of Western Cameroon

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Anthropogenic activities continue to degrade natural montane ecosystems globally. Bats communities are altered by these changes. We analyzed how bats are affected by human-induced habitat changes by comparing the bat species diversity and functional diversity in undisturbed forest habitats and disturbed forest habitats of the Afromontane biome of Cameroon. We recorded 244 individuals from 13 species in the undisturbed forest, while 233 individuals from 16 species were recorded in the disturbed forest. Bat diversity was higher in disturbed habitats ( $D = 0.84$ ) than undisturbed habitats ( $D = 0.67$ ). Jackknife 1 species richness estimator suggests 21.53 species for the disturbed forest and 19.30 in the undisturbed forest. Closed-space forager insectivorous bats made up nearly half of the species in the undisturbed forest, but this dropped to 25% in the disturbed forest, meanwhile, edge-space foragers increased in the disturbed forest. Bat community analyses by ordination revealed a distinct bat community composition between the two forest types, demonstrated as a significant difference in diversity between the two forest types. The distribution of *Rousettus aegyptiacus*, *Myonycteris angolensis*, *Hipposideros cf. ruber*, and *Micropteropus pusillus* contribute the most to the difference in bat community composition between the two forest types. Edge and open-space species were likely to benefit from additional resources provided by the disturbed area, by expanding their range and distribution. However, this may not compensate for the decline in the population of forest species caused by the loss of pristine forests, thus measures to conserve montane forest remnants should be of utmost significance.

**Keywords:** edge species, bats, human activities, undisturbed forest, disturbed forest

## INTRODUCTION

The biota of the tropical montane forest is very diverse and varied in endemic species (Gentry, 1995; Kessler and Kluge, 2008). These ecosystems are also amongst the most threatened globally (Hamilton et al., 1994; Doumenge et al., 1995), with the estimated rate of deforestation nearly double the rate of average global deforestation rates in the past few decades (Hamilton et al., 2012).



Threats emanate from human activities such as the uphill expansion of shifting cultivation and the exploitation of natural resources. In Africa, the situation is further exacerbated by extreme poverty that drives the immigration of subsistence farmers into the montane forest from adjacent lowland areas (Körner and Ohsawa, 2006; Mugagga et al., 2012). Indeed, tropical moist forests are estimated to have reduced by half of their original distribution in the last two decades due to agricultural activities (Myers, 1991; Gibbs et al., 2010). Given the accentuating nature of these threats, tropical forests are a conservation priority globally (Edwards et al., 2019).

The Afrotropical Highlands biome of Cameroon that encompasses the highlands of western Cameroon contain large forested areas that harbor unique ecological and biological diversity across many taxa (Myers et al., 2000; Olson et al., 2001; Oates et al., 2004). The biome covers the western highlands of southwestern Cameroon and extends northeast to the Obudu and Mambilla Plateaus in Eastern Nigeria. The unique diversity and endemism in this biome are thought to be a result of the area being a major refugium during the Quaternary glaciation (Stuart, 1986; Lawson, 1993; Stattersfield et al., 1998; Myers et al., 2000). This rich diversity has also been attributed to the region's wide variety of habitats resulting from its extensive highlands (Cronin et al., 2014). Indeed the montane forests of the Cameroon Highlands are considered a priority area for conservation globally (Myers et al., 2000), this results from the area's high biodiversity and endemism (Maisels et al., 2001; Oates et al., 2004; Linder and Oates, 2011; Abernathy et al., 2013; Cronin et al., 2014). However, despite such important features, very few parts of the highland's habitats are currently under formal protection status in Cameroon, which poses a challenge to its conservation (Bergl et al., 2007). Moreover, except for Mount Cameroon, these montane forests have been significantly degraded by human activities (Collar and Stuart, 1988; Gartlan, 1989; Alpert, 1993; Megevan et al., 2013), and most often comprise only forest fragments within montane grasslands grazed by cattle of the Fulani herdsman (Ineich et al., 2015).

One way to mitigate the adverse effects of human activities in an ecosystem is the establishment of protected areas (Geldmann et al., 2013). Protected areas harbor higher species diversity than unprotected areas (Laurance et al., 2012; Geldmann et al., 2013; Gray et al., 2016), resulting from the reduction in human-induced land-use changes such as poaching, wildfires, and deforestation (Geldmann et al., 2013; Barber et al., 2014; Gray et al., 2016). Indeed, Razgour et al. (2020) pointed out that anthropogenic land-use changes are associated with a severe decline in the population of some Afrotropical bat species. Unfortunately, most of the biodiversity hotspot of the Afrotropical biome of Cameroon is devoid of any legal protection. Consequently, decades of intensive anthropization have reduced formerly continuous montane forests to isolated fragments, cultivated landscapes, grassland, human settlements, and industrial plantations.

Bats play an important role in tropical forest succession after disturbance. Frugivorous and nectarivorous bat species can explore a wide range of resources, providing several ecological services such as pollination, seed dispersal, and

forest regeneration (Stevens et al., 2004; Willig et al., 2007). Additionally, insectivorous bats are important suppressors of agricultural pest insects (Kalka et al., 2008; Jones et al., 2009). In addition, because of their high species richness, abundance, and variety of functional guilds bats are considered as a good bioindicator taxon used to study various human-induced alterations of ecosystems, such as forest fragmentation and degradation (Jones et al., 2009; Meyer et al., 2010). Furthermore, sensitivity to habitat fragmentation can be attributed mainly to species-specific mobility-related traits (Law et al., 1999; Farneda et al., 2015; Moir et al., 2021).

Previous records of bats in the Cameroon Highlands were mostly in the form of pioneer faunistic expeditions and collection of specimens (Eisentraut, 1942, 1956, 1963, 1964, 1968, 1973; Hill, 1968; Fedden and MacLeod, 1986). Recently, surveys by Mongombe et al. (2019, 2020), Manfothang et al. (2020, 2021) added some recent information about bats of the Cameroon Highlands. However, none of these studies evaluated the effect of anthropogenic activities on bat diversity in the biome.

Several studies in a variety of biomes and taxa have revealed that the number of species that inhabit remnant patches of forest decreases significantly as habitat patch size decreases (Debinski and Holt, 2000; Devictor et al., 2008). Habitat fragmentation, because of agricultural activities is known to alter bat assemblages (Walsh and Harris, 1996; Cleary et al., 2016). However, the response of bat communities to fragmentation can be positive or negative depending on whether the bat species is a specialist or a generalist. Some generalists can better persist in anthropogenically altered environments due to the ability to exploit additional resources such as man-made habitats (secondary vegetation and cultivated farms) and food resources (Coleman and Barclay, 2012). On the other hand, habitat fragmentation can reduce bat species richness and abundance by reducing roosts and the availability of resources (Schulze et al., 2000). Even though the montane forest of the Cameroon Highlands continues to diminish because of significant human pressure, our knowledge on changes in bat communities induced by anthropogenic activities and how human activities affect bat diversity in the area is still limited. This data is imperative to predict the long-term consequences of fragmentation on the montane forest biodiversity and to mitigate any effects. Therefore, there is a need to collect such scientific information in the area before the opportunities diminish completely due to the ever-accelerating deforestation in the region. Determining the species that either become extinct or can persist in disturbed areas is crucial to developing conservation management strategies.

Herein, our main goal was to analyze bat communities in two areas of the Afrotropical forest biome of Cameroon (undisturbed area and disturbed areas) to assess bat response to habitat degradation. Our objective was to compare species richness and abundance between these two habitat types. Studies that compare bat communities in pristine forests and human-disturbed forests in similar life zones can provide insight into the original bat communities of an area and the effect that deforestation and fragmentation have on bat communities. Such studies are important to determine the extent of human influence in the spatial and temporal variations of biodiversity in an

ecosystem. This information can also throw more light on the habitat preferences of some bat species and hence understand the potential risk of local extinction and community homogenization (Henle et al., 2004; Myers et al., 2015). Furthermore, comparing bat communities across different habitats can enable researchers to assess the health of an ecosystem given that bats are suitable indicator species that show sensitivity to human induced disturbances (Medellín et al., 2002; Jones et al., 2009; Meyer et al., 2016). We expect species richness, relative abundance, and the number of forest specialist species to be higher in undisturbed areas than in disturbed areas.

## MATERIALS AND METHODS

### Study Sites

We carried out this study on Mount Cameroon, Mount Manengouba, and Mount Bamboutos (Figure 1). These mountains are part of the Afromontane forest biome of Cameroon that encompasses other mountains of the Cameroon Highlands.

Undisturbed habitats were located within the Mount Cameroon National Park (4°9'36.5" N, 9°16'44.9" E). Mount Cameroon National Park (MCNP) covers an area of 58,178 ha. The climate is maritime and equatorial, characterized by two seasons: a short dry season between December and February and a longer rainy season between March and November (Payton, 1993). The annual temperature fluctuates between 4°C at the summit and 32°C at the coast and decreases by 0.45°C with every 100 m rise in elevation (Payton, 1993). The annual rainfall averages 7,000 mm, with most of the rain occurring in July and October (Forbeseh et al., 2011). Rainfall decreases with elevation from approximately 4,000 mm at 1,000 m to less than 3,000 mm above 2,000 m (Payton, 1993). The area is characterized by a pristine forest of large and tall trees forming a continuous close canopy except in areas where the vegetation is disturbed by forest elephants. The flora composition in all 10 undisturbed habitat sites is similar. The tree species frequently encountered include African cherry (*Prunus africana*), brittle-wood (*Nuxia congesta*), African nutmeg (*Pycnanthus angolensis*), African teak (*Milicia excelsa*), umbrella tree (*Musanga cecropioides*), the monkey fruit (*Myrianthus arboreus*), with associated spiny tree ferns (*Cyathea manniana* and *Cyathea camerooniana*), and tall herbaceous plants such as *Aframomum* spp. (Letouzey, 1985).

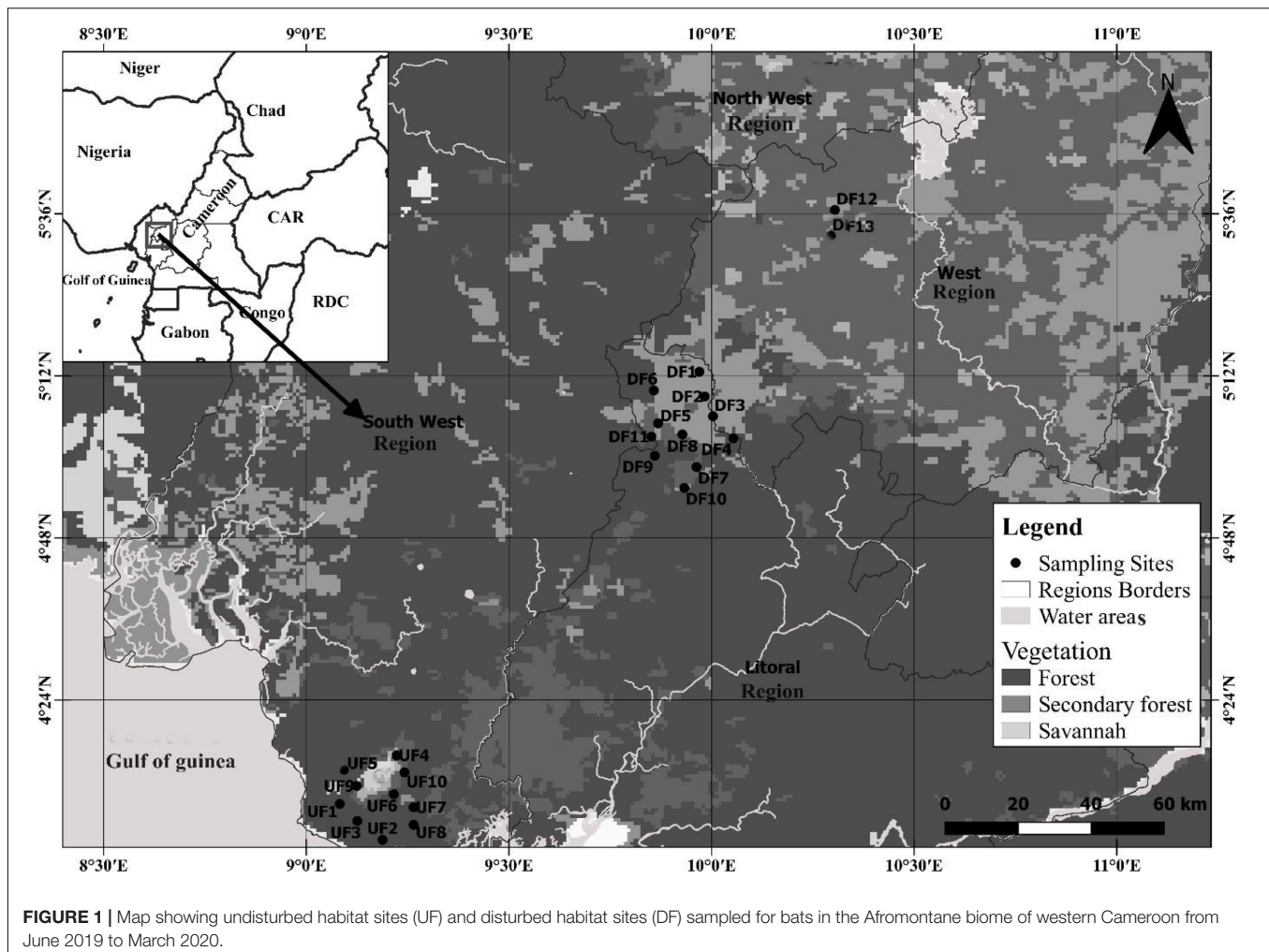
Disturbed habitat sites surveyed were located at the southeast slope of Mount Manengouba at the littoral side of the mountain and the foothill of Mount Bamboutos. The Manengouba Mountain (5°1'48" N, 9°49'48" E) is an extinct volcano that peaks at 2,411 m. The caldera harbors two volcanic lakes with the largest being 600 m across. Mount Manengouba has an equatorial climate, with an annual rainfall and temperature means of 2,316 mm and 20.3°C, respectively. The relative humidity is 84% (Enang et al., 2019). The Montane forest of Mount Manengouba is described as dry, stunted and patchy, and disturbed from farming, tree-cutting, burning, and grazing (Collar and Stuart, 1988). The peak and southern and southeastern slopes are forested.

The survey sites at lower elevations (<1,200 m) are characterized by human settlements and agricultural areas composed of small farmlands on which crops such as corn (*Zea mays*), beans (*Phaseolus vulgaris*), cocoyam (*Colocasia esculenta*), yams (*Dioscorea cayenensis*), and plantains (*Musa paradisiaca*) were cultivated. There were also backyard orchards near houses with fruiting trees such as mango (*Mangifera indica*), avocado (*Persea americana*), guava (*Psidium guajava*), plums (*Dacryodes edulis*), and oil palm (*Elaeis guineensis*) plantations. At higher elevation sites (>1,200 m) the forest was still intact with riparian forest vegetation surrounding small rivers which remain largely undisturbed. The herbaceous vegetation at these higher elevation sites is reduced because of intense grazing by cattle and sheep of Fulani communities living near the summit of the mountain.

Mount Bamboutos (5°40'0.1" N, 10°3'0" E) is the third tallest mountain of the Cameroon Volcanic Line after Mount Cameroon and Oku (Gountié Dedzo et al., 2011). A dry season that extends from November to March and a wet one from April to October characterize the climate of Mount Bamboutos. The average annual rainfall is 1,918 mm and the average temperature is 18.9°C at an elevation of 2,700 m (Kengni et al., 2009). Crop fields and eucalyptus plantations characterized the two sites sampled on the Bamboutos Mountain.

### Bat Sampling Protocol

Bat surveys employing standard mist-netting techniques were conducted in the disturbed habitats of Manengouba and Bamboutos mountains during non-consecutive nights between 13 June to 27 August 2019 in the rainy season and 28 October to 9 December 2019 in the dry season. Surveys in the undisturbed habitats between 11 January 2019 and 24 March 2020 in the dry season. Within each habitat type (undisturbed and disturbed forest). Sampling sites were chosen based mainly on the accessibility, and quality of sites for capturing bats with high-quality sites such as across or along the banks of slow-flowing streams, orchards, forest understory, and gaps between trees chosen for placement of mist nets. The coordinates of each sampling station were recorded using a GPS (Garmin eTrex 10). In total sampling was conducted for 68 nights, comprising of 34 nights in each habitat type. Six mist nets of various lengths (four 12 m × 2.5 m and two 6 m × 2.5 m Ecotone, Poland), all with four shelves, and a mesh diameter of 30 mm were deployed at each site per sampling night. The nets were kept open from about 6:00 pm to midnight in each sampling night until bat activity had reduced drastically. Mist-nets were closed earlier whenever weather conditions worsened. Sampling was only conducted during windless, rainless, and moonless nights to maximize the chances of capturing many individuals (Morrison, 1978). When capture was carried out on consecutive nights, the placement and configuration of mist nets were changed in an attempt to prevent the recapture of bats. We checked the nets every 15 min. Manipulation of all bats captured followed the guidelines of the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists, 2016). Each bat captured was identified to species, sexed, weighed using a calibrated digital scale (500 g × 0.1 g, Ohaus), and morphometric measurements were taken using a dial caliper



(Ecotone-Poland 150/0.1 mm). Age was determined by the degree of ossification of the carpal joints of the wing, conditions of the pelage, and the development of nipples and testes (Baagøe, 1977; Anthony, 1988). Each captured bat was then released near the point of capture except for a male and female representative of each species that were euthanized and kept as vouchers deposited at the Laboratory of Zoology of the University of Maroua. Field identification of bats was based on the keys provided by Patterson and Webala (2012) and species accounts provided by Monadjem et al. (2010) and Happold and Happold (2013). Taxonomic nomenclature for pipistrelle-like bats follows Monadjem et al. (2021). Species that could not be identified in the field and rare species were euthanized and stored in 70% ethyl alcohol for later identification using craniodental characteristics (Bates et al., 2005). Bat species were also grouped into different foraging guilds according to Schnitzler and Kalko (2001) and Denzinger and Schnitzler (2013).

## Statistical Analyses

Expected species richness was computed for both the undisturbed and disturbed forests using an individual-based non-parametric species estimator because our main goal was to estimate the

total number of species of a particular habitat type rather than species density (number of species per unit area). The species richness estimator Jackknife 1 was employed to estimate species richness because of its low-bias estimation and high precision even at a small sample size (Colwell and Coddington, 1994). Jackknife 1 also considers the movement heterogeneity of highly mobile animals such as bats (Brose and Martinez, 2004). All analyses were performed in EstimateS 9.1.0 software (Colwell, 2013) involving 1,000 randomizations. We assessed the completeness of the bat surveys in the two habitat types by calculating the percentage of estimated species richness that was effectively covered by our sampling. The percentage of inventory completeness was calculated as  $S_{obs}/S_{est}$  multiplied by 100 where  $S_{obs}$  is the number of species observed, and  $S_{est}$  is the number of species estimated (Estrada-Villegas et al., 2010).

Sampling effort (net hours) was obtained by multiplying the area of a mist net by the number of nets each night and the total number of hours (Straube and Bianconi, 2002). We calculated the capture success by dividing the number of bats captured at each sampling site by the sampling effort. Species accumulation curves were used to estimate species richness based on the accumulated number of species observed, compare species richness among



habitats, and measure sampling completeness (Magurran, 2004). Effects of human disturbance were measured as differences in species richness, species composition, and abundance between undisturbed and disturbed habitats.

Bat diversity in both habitat types was described based on two ecological indices of Simpson's index (Simpson, 1949) and the Evenness or Equitability index (Pielou, 1969). We computed the Simpson's index ( $D$ ), which gives the probability of any two individuals randomly drawn from a community belonging to different species. The Simpson's index provides a good estimate of diversity even for small sample sizes (Magurran, 2004). It was computed using the formula ( $D$ ) =  $1 - [\sum n(n-1)/N(N-1)]$ , where  $n$  = the total number of bats of a particular species,  $N$  = the total number of bats of all species. The value of  $D$  ranges between 0 and 1, where 0 represents complete uniformity 1 represents complete diversity (Simpson, 1949). We derived the Evenness index ( $J'$ ), which indicates how abundances are distributed among species in the community, from the Shannon index of diversity ( $H'$ ). Evenness or Equitability index was computed using the formula ( $J'$ ) =  $H'/\ln S$ , where  $\ln S$  = natural logarithm of the number of species or species richness. The Evenness index ranges from 0 (one dominant species) to 1 (all species equally abundant in the community). When the evenness index is high, it indicates that species are equally abundant while lower evenness index values indicate that species are not equally abundant (Magurran, 1988).

We performed the independent samples  $t$ -tests to investigate if there was a variation in observed bat species richness, relative abundance, bat diversity (for the Simpson index), and evenness between the undisturbed and disturbed forest habitats. The data were tested for normality using Kolmogorov-Smirnov's test, and for homogeneity of variance using Levene's test before performing the  $t$ -test. We performed the Mann-Whitney  $U$  test when the condition of normality and homogeneity of variance was not met. Box plots were used to show the relationship between species richness, abundance, evenness, and diversity between undisturbed and disturbed forest habitats.

We used non-metric multidimensional scaling (NMDS) as a non-linear ordination technique based on Bray-Curtis similarity to ordinate all 23 sampled sites to assess and visualize intersite similarity in species composition. The NMDS uses rank orders to evaluate dissimilarities between different communities instead of absolute distances, with "stress" being a measure of the distortion (final lack of agreement) (McCune and Grace, 2002). Data were square-root transformed before analysis to down-weight most abundant species relative to rare ones (i.e., the transformation reduces the magnitude of the larger number relative to the smaller ones without changing the relationship). One-way analysis of similarity (ANOSIM) with a Jaccard distance matrix was used to assess differences in bat species composition between forest habitat types (Clarke, 1993). The  $R$ -value was used to determine the similarity between the two forest habitat types. The values range from 0 to 1, with values closer to 1 indicating higher dissimilarity between a pair of sampling sites being compared, and values closer to 0 indicating greater similarity (Clarke, 1993). Finally, we carried out a similarity percentage analysis (SIMPER) to determine the contribution of each species to the overall

similarity of bat communities between undisturbed and disturbed habitat-type. All multivariate analyses were conducted using PAST software (Hammer et al., 2001). Mantel test was employed to test the prediction that greater homogeneity of undisturbed sites was based on spatial proximity rather than the lack of disturbance. Mantel test analysis was performed using the vegan package in R software version 4.1.1 (Oksanen et al., 2018).

## RESULTS

### Effects of Anthropic Disturbances on Bat Communities

A total of 477 bats representing 21 species, 15 genera, and five families were recorded in both forest habitat types surveyed (Table 1). The overall species richness we recorded was greater in the disturbed habitats (16 species) than in the undisturbed habitats (13 species; Figure 2). However, the difference was not statistically significant [ $t$ -test;  $t(21) = -1.052$ ,  $P = 0.305$ ]. The estimated Jackknife 1 species richness amounted to 27.69 for the entire area sampled (Figure 3). Therefore, our surveys sampled 75.84% of all richness estimated for the study area. The estimated species richness for the disturbed habitats was 21.53 and that for the undisturbed habitat was 19.30 species (Figure 3). In addition, more individuals were recorded in the undisturbed habitats 51.15% ( $n = 244$ ), than in the disturbed habitats 48.85% ( $n = 233$ ). The difference in population size between the two forest types sampled was not statistically significant [ $t$ -test;  $t(21) = 0.595$ ,  $P = 0.356$ ].

Among species recorded, five (23.81%) were recorded exclusively in the undisturbed habitat. These species were *Scotonycteris zenkeri*, *Doryrhina cyclops*, *Hipposideros cf. ruber*, *Glauconycteris egeria*, and *Glauconycteris* sp. On the other hand, seven species (33.33%) captured in the disturbed habitat were absent in the undisturbed habitat. These species were *Eidolon helvum*, *Epomops franqueti*, *Micropteropus pusillus*, *Rhinolophus fumigatus*, *Hipposideros cf. caffer*, *Glauconycteris argentata*, and *Laephotis inexpectatus*. Eight species (38.09%) were common to both habitat types. These species were *Megaloglossus woermanni*, *Myonycteris angolensis*, *Rousettus aegyptiacus*, *Rhinolophus landeri*, *Macronycteris gigas*, *Miniopterus* sp., *Afronycteris nana*, and *Pipistrellus nanulus*. *Myonycteris angolensis*, *Rhinolophus landeri*, and *Afronycteris nana* were the only species captured in equal proportion in both forest types.

Five families were recorded during our surveys. Pteropodidae was the most abundant, with 78.69% of all captures, followed by Hipposideridae with 7.76%, Vespertilionidae with 6.29%, and Miniopteridae with 6.08%. When taking into account the whole area sampled, the most abundant species were *Rousettus aegyptiacus* 27.85%, followed by *Myonycteris angolensis*, 23.21%. The most abundant species in the undisturbed forest was *Rousettus aegyptiacus* 25.3%, followed by *Myonycteris angolensis* with 11.5%, while in the disturbed forest habitats *Micropteropus pusillus* was the most abundant with 10.9%, followed by *Myonycteris angolensis* 10.7% (Figure 4). Few individuals of *Rousettus aegyptiacus* were recorded in the disturbed forest than in the undisturbed forest (Table 1).

**TABLE 1 |** Number of individuals, species richness, functional guild, sampling effort, capture success and relative abundances in parentheses of bats captured in undisturbed and disturbed habitat sites of the Afromontane forest biome of western Cameroon from June 2019 to March 2020.

Taxon	Undisturbed habitat	Disturbed habitat	Functional guild	Total
<b>Family Pteropodidae</b>				
<i>Eidolon helvum</i> (Kerr, 1792)	–	22 (4.6)	frugivore	22 (4.6)
<i>Epomops franqueti</i> (Tomes, 1860)	–	19 (4.0)	frugivore	19 (4.0)
<i>Megaloglossus woermanni</i> (Pagenstecher, 1885)	12 (2.5)	1 (0.2)	nectarivore	13 (2.7)
<i>Micropteropus pusillus</i> (Peters, 1868)	–	52 (10.9)	frugivore	52 (10.9)
<i>Myonycteris angolensis</i> (Bocage, 1898)	55 (11.6)	51 (10.7)	frugivore	106 (22.3)
<i>Myonycteris torquata</i> (Dobson, 1878)	–	25 (5.3)	frugivore	25 (5.3)
<i>Rousettus aegyptiacus</i> (E. Geoffroy, 1810)	120 (25.2)	12 (2.5)	frugivore	132 (27.7)
<i>Scotonycteris zenkeri</i> (Matschie, 1894)	4 (0.8)	–	frugivore	4 (0.8)
<b>Family Rhinolophidae</b>				
<i>Rhinolophus fumigatus</i> (Ruppell, 1842)	–	4 (0.8)	closed space	4 (0.8)
<i>Rhinolophus landeri</i> (Martin, 1838)	2 (0.4)	2 (0.4)	closed space	4 (0.8)
<b>Family Hipposideridae</b>				
<i>Doryrhina cyclops</i> (Temminck, 1853)	1 (0.2)	–	closed space	1 (0.2)
<i>Hipposideros cf. caffer</i> (Sundevall, 1846)	–	1 (0.2)	closed space	1 (0.2)
<i>Hipposideros cf. ruber</i> (Noack, 1893)	32 (6.7)	–	closed space	32 (6.7)
<i>Macronycteris gigas</i> (Wagner, 1845)	1 (0.2)	2 (0.4)	closed space	3 (0.6)
<b>Family Miniopteridae</b>				
<i>Miniopterus</i> sp.	4 (0.8)	25 (5.3)	edge space	29 (6.1)
<b>Family Vespertilionidae</b>				
<i>Afronycteris nana</i> (Peters, 1852)	1 (0.2)	1 (0.2)	edge space	2 (0.4)
<i>Glauconycteris argentata</i> (Dobson, 1875)	–	13 (2.7)	edge space	13 (2.7)
<i>Glauconycteris egeria</i> (Thomas, 1913)	1 (0.2)	–	closed space	1 (0.2)
<i>Glauconycteris</i> sp.	1 (0.2)	–	closed space	1 (0.2)
<i>Laephotis inexpectatus</i> (Aellen, 1959)	–	1 (0.2)	edge space	1 (0.2)
<i>Pipistrellus nanulus</i> (Thomas, 1904)	10 (2.1)	2 (0.4)	edge space	12 (2.5)
Total	244 (51.2)	233 (48.8)		477 (100)
Species richness	13	16		
Sampling effort (m <sup>2</sup> /h)	29520	28543		
Capture success (Individuals/m <sup>2</sup> h)	0.007	0.006		
Shannon index (H')	1.52	2.1		
Simpson's index (D)	0.67	0.85		
Equitability index (J)	0.59	0.77		

There was a higher diversity  $D$  (Simpson's index) of bats in disturbed forest ( $D = 0.85$ ) than undisturbed forest [ $D = 0.67$ ;  $t(21) = 3.460$ ,  $P = 0.002$ ], but no statistically significant difference in equitability for the bats captured in the disturbed habitat ( $J' = 0.77$ ) and undisturbed forests ( $J' = 0.59$ ; Mann–Whitney  $U$  test;  $U = 38$ ,  $P = 0.181$ ).

The NMDS ordination analysis showed that most of the undisturbed forest sites are more closely grouped therefore are more similar in terms of bat composition compared to disturbed forest sites (Figure 5). Analysis of Similarity (ANOSIM) indicated that there was a statistically significant difference in the overall bat community of the two forest types ( $R = 0.321$ ,  $P = 0.0001$ ). The stress value (0.23) indicated that this ordination is a good representation of the bat community structure. Similarity Percentages Analysis (SIMPER) identified four species that contributed the most to the difference in the composition of bat species between undisturbed forest habitats and disturbed forest habitats: *Rousettus aegyptiacus*, *Myonycteris angolensis*,

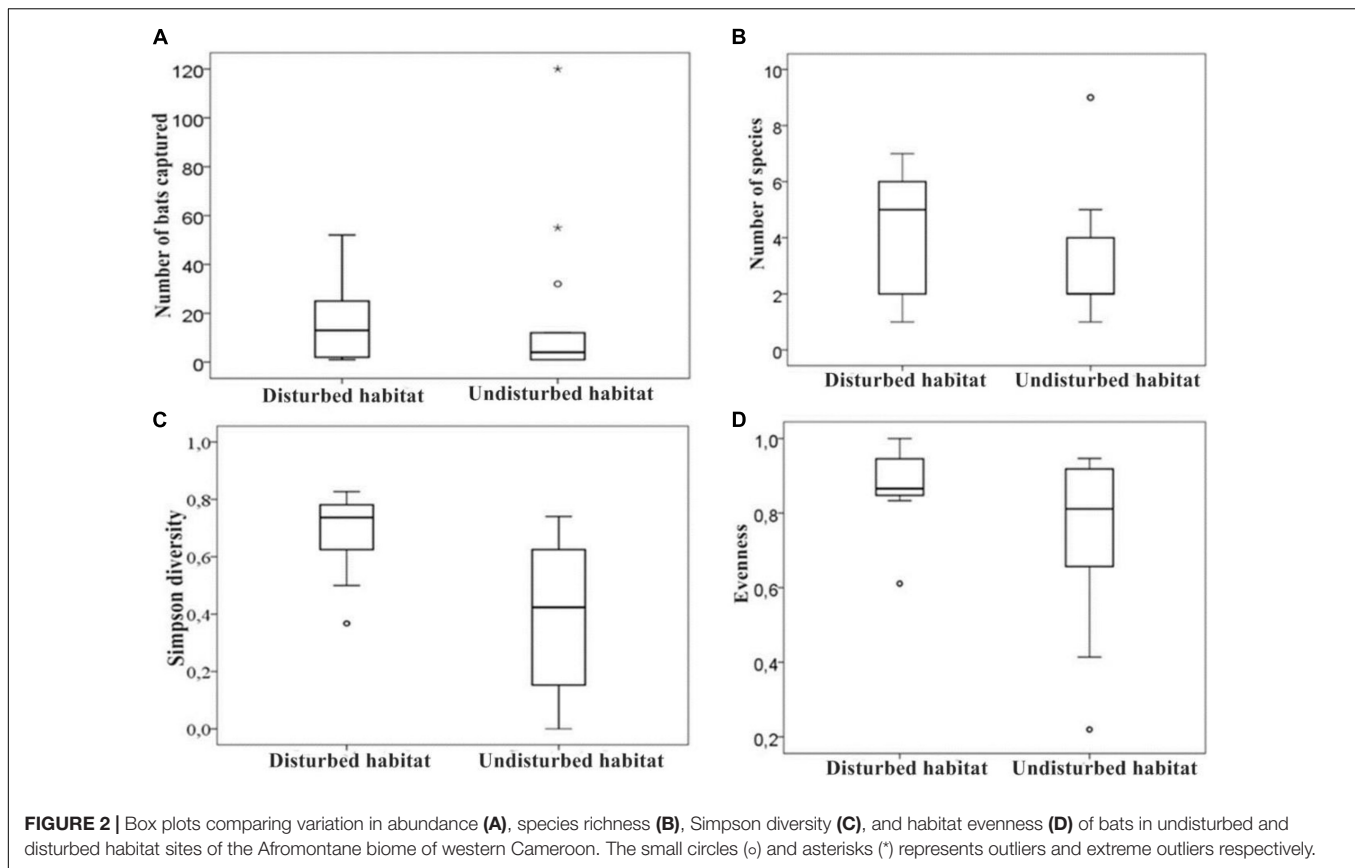
*Hipposideros cf. ruber*, and *Micropteropus pusillus* (Figure 6). Using the Bray–Curtis index, the dissimilarity of bat communities in undisturbed forest sites significantly increased with geographic distance (Mantel  $r = 0.99$ ,  $p = 0.001$ ) suggesting that sites with closer spatial proximity have more similar bat compositions.

## Composition of Bat Guilds in Undisturbed and Disturbed Forest Habitats

We recorded three different functional guilds during our surveys, namely frugivorous bats, closed-space forager insectivorous bats, and edge-space forager insectivorous bats (Figure 7).

In terms of the number of species, closed-space forager insectivorous bats were the largest guild in the undisturbed habitat with six species, while frugivorous bats were the largest guild in the disturbed habitat with seven species (Figure 7A). A comparison between both habitat types showed that there was



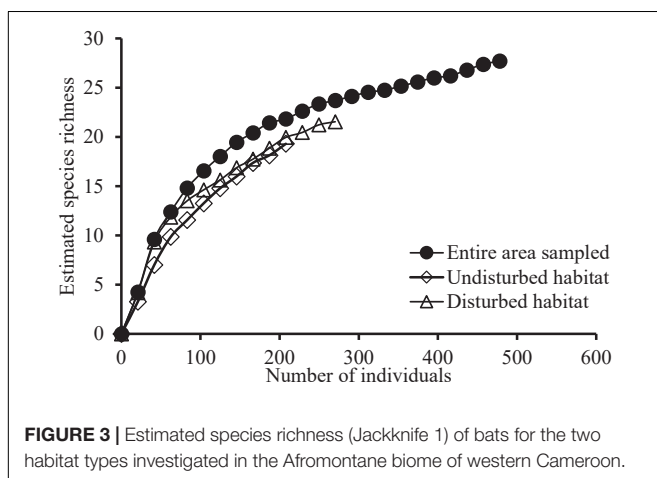


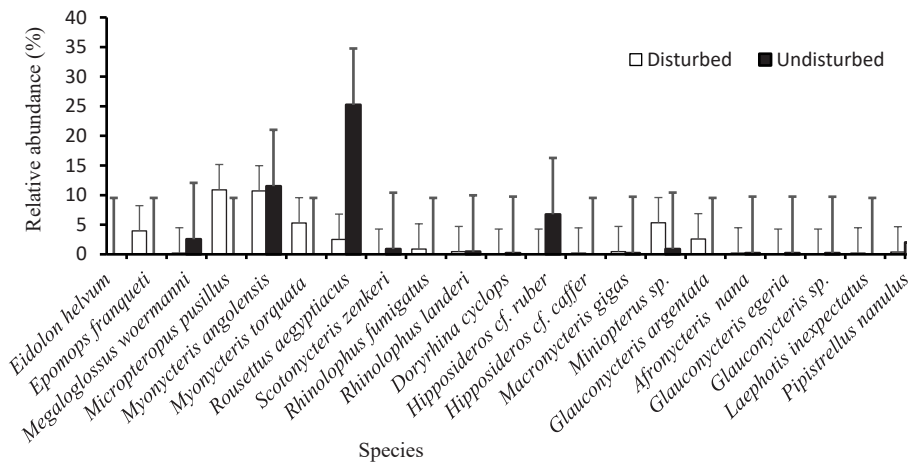
a statistically significant difference in the number of species of frugivorous bats [ $t$ -test;  $t(21) = -2.785$ ,  $P = 0.011$ ; **Figure 7A**]. However, the relative abundance of frugivorous bat species among forest types did not differ significantly [ $t(14) = -4.92$ ,  $P = 0.628$ ; **Figure 7B**]. Additionally, there was no evidence of a significant difference in the number of forest specialist insectivorous bats between disturbed and undisturbed forests (Mann–Whitney  $U$  test;  $U = 44.5$ ,  $P = 0.208$ ). Similarly, there was no significant difference in the relative abundance of

closed-space insectivorous bats between the two forest types (Mann–Whitney  $U$  test;  $U = 49.5$ ,  $P = 0.343$ ). Edge-space insectivorous bats were not considered because of few captures to enable accurate comparison.

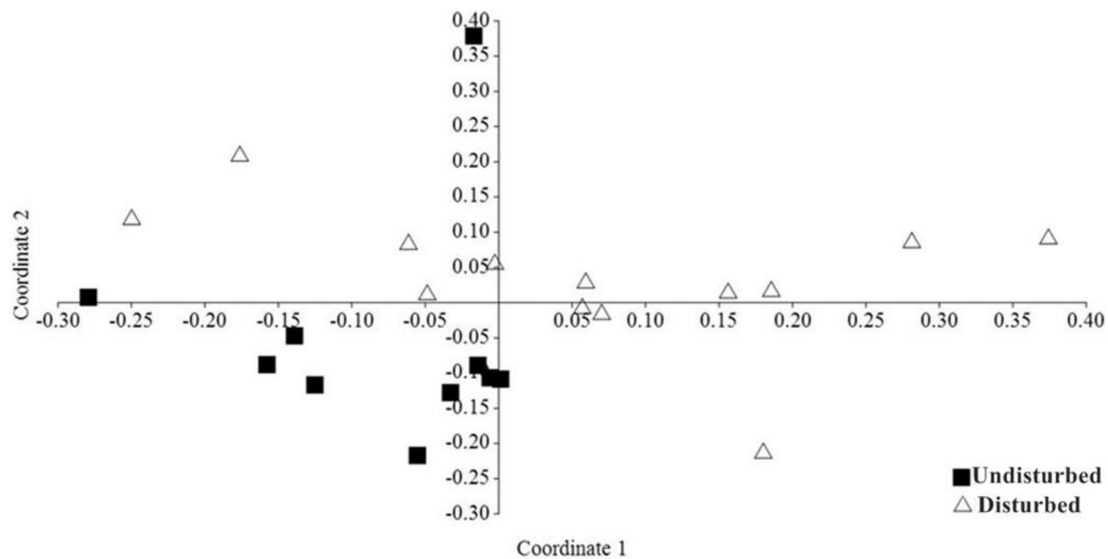
## DISCUSSION

In this study, we surveyed bats in pristine and disturbed vegetations of the Afromontane biome of western Cameroon. Our study revealed that the disturbed forest supported larger populations and more species than the undisturbed forest sites, although the species richness did not differ significantly between the two forest types. There was a significant change in bat composition from mostly widespread generalists in the disturbed forest, to forest species in the undisturbed forest. This difference in species richness and abundance could likely be explained by greater habitat heterogeneity of the disturbed forests (Estrada and Coates-Estrada, 2002; Ramos Pereira et al., 2009). Indeed, the disturbed forests were more heterogeneous comprising of areas with secondary forest patches, gallery forests, coffee plantations, palm plantations, orchards, and cultivated farmlands. On the other hand, the undisturbed forest was characterized by primary growth with large trees, continuous canopy, dense understory, and a patchier understory cover at the ecotone montane forest/montane grassland. Both forest types were located in a volcanic landscape with numerous extinct





**FIGURE 4 |** Relative abundance of 21 bat species captured in undisturbed and disturbed habitat sites of the Afromontane forest biome of western Cameroon. Bars indicate standard error.



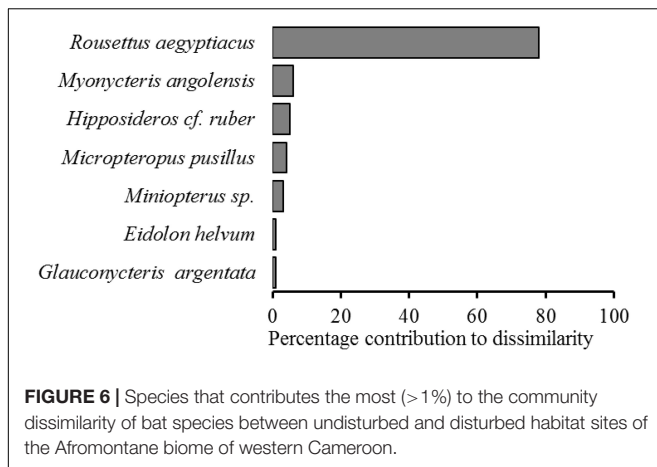
**FIGURE 5 |** NMDS ordination, showing the difference between undisturbed and disturbed habitat sites of the Afromontane biome of western, Cameroon based on the composition and abundance of bat species using the Bray-Curtis index as a measure of similarity (Stress = 0.23).

volcanic vents that probably provided day roosts for obligate cave roosters (Glover and Altringham, 2008).

Habitat structural heterogeneity is associated with an increase in bat species activity and species occurrence (Jung et al., 2012). The heterogeneous landscape offered more resource opportunities for open-adapted species in these modified habitats, due to their ability to access extra resources such as artificial shelters and food resources (Loeb et al., 2009; Coleman and Barclay, 2012). Indeed, bats are specially adapted to access a wide diversity of habitats, occupying many ecosystems (Schnitzler and Kalko, 2001). An alternative explanation is the presence of more open water bodies in the disturbed areas which provided drinking and foraging sites for bats (Grindal et al., 1999; Campbell, 2009), leading to increased bat activity and

their subsequent capture in mist-nets. The species accumulation curves did not show a tendency toward plateauing, suggesting that our surveys did not capture all species present in the study area. However, 75.84% of the estimated species richness was sampled, indicating that more species will be recorded with a greater sampling effort.

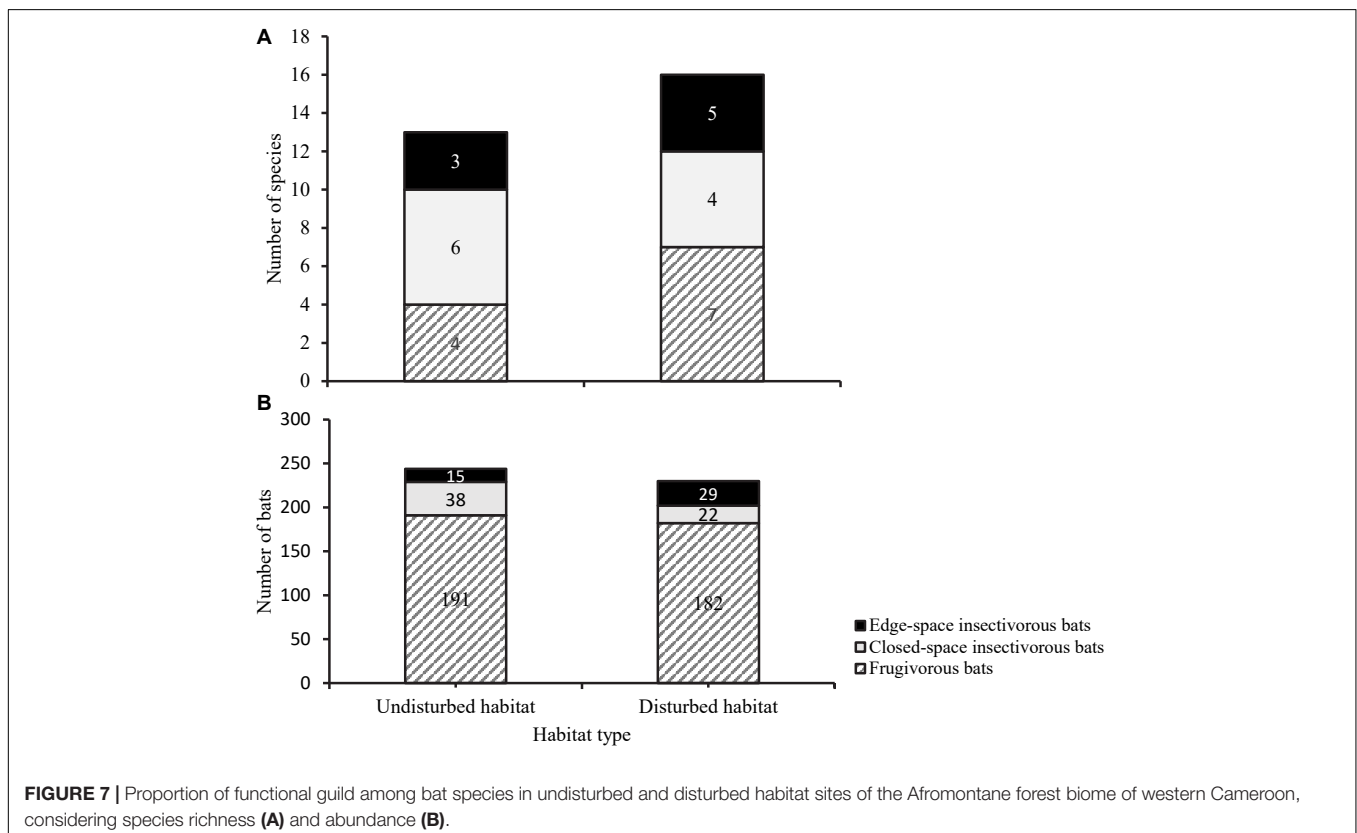
Our findings concur with other studies that demonstrated the positive effects of human disturbances on species richness and abundance of species adapted to forage in open areas, but that fragmentation negatively affects bat species that depend on pristine habitats (Klingbeil and Willig, 2009; Estrada-Villegas et al., 2010). Greater species richness and abundance in the disturbed forest can also be attributed to the greater amount of forest edge in the disturbed habitats.



According to Fried et al. (2005), edge habitats contain more flying insects, hence attracting more foraging insectivorous bats, and subsequently allowing some to be captured in mist-nets. Hence a possible consequence of the continuous deforestation and fragmentation will be the replacement of forest-interior species by more adaptable and opportunistic forest edge frugivorous bats such as *Eidolon helvum*, *Micropteropus pusillus*, *Myonycteris angolensis*, and edge tolerant insectivorous bats such as *Glauconycteris argentata* (Webala et al., 2019). Understory frugivorous bats such as *Scotonycteris zenkeri* and *Megaloglossus woermanni* are also sensitive to fragmentation, and thus will be

negatively impacted by deforestation than larger canopy foragers (Cosson et al., 1999). On the other hand, our findings contrast, some studies in the Neotropics by Gorresen and Willig (2004) in Paraguay, which concluded that bat community diversity was highest in relatively undisturbed forests, and findings by Estrada and Coastes-Estrada (2001) which concluded that bats within the continuous forest and forest fragments in Mexico had similar species richness.

Guild structure differs between the two forest habitat types, probably indicating the uneven distribution of resources. According to Hodgkinson et al. (2004), the abundance of bats is influenced by the temporal and spatial variation of food resources, which then influence the number of species within a particular habitat (Duchamp et al., 2007; Pinto and Keitt, 2008). While the number of frugivorous bats did not differ significantly between the habitat types, there was a higher proportion of frugivorous bat species in the disturbed habitat than in the undisturbed habitat. This can probably be explained by the presence of many forest tree species such as *Ficus* spp., *Prunus africana*, *Annona senegalensis*, *Borassus aethiopum*, *Hymenocardia acida*, *Nauclea diderrichii*, *Musanga cecropioides*, and *Caloncoba welwitschii*, among species of fruiting trees planted by humans such as *Persea americana*, *Carica papaya*, *Anonidium mannii*, and *Dacryodes edulis*. The presence of more closed-spaced forager insectivorous bat species in the undisturbed habitat can probably be attributed to the nature of their echolocation calls. These species use low-intensity, high-frequency echolocation calls, characterized by low wing



loadings, appropriate for foraging and commuting in cluttered habitats close to vegetation (Law et al., 2011). Therefore, the increase in anthropogenic disturbances can significantly reduce the resource availability for these species (Threlfall et al., 2012). This is consistent with findings by Webala et al. (2019) who captured more closed-space insectivorous bat species in the less-disturbed forest interior with little human disturbance in a Kenyan forest. In addition, the capture of more edge-space insectivorous bat species in the disturbed forest can be attributed to their flexible commuting traits, which enabled them to adapt to cleared environments, including agricultural areas and residential spaces. Thus, these open-adapted species are relatively insensitive to human modification, and in many cases, can exploit man-made structures (Kirsten and Klomp, 1998; Threlfall et al., 2012). Indeed, the fact that some close-space forager insectivorous bat species persist in human-dominated environments is an indication of the versatility and adaptability of some bat species.

In our surveys family, Pteropodidae represented the largest number of captures. This pattern can be attributed both to the high abundance of pteropodid bats in the surveyed area and the use of ground-level mist-netting method, which tends to be more effective at capturing low-foraging frugivorous bats (Meyer et al., 2011). Moreover, it is well documented that fast-flying insectivorous bat species that forage higher at the middle-story and canopy levels, above the height of mist-nets, and adept at detecting and avoiding mist-net due to their very efficient echolocation calls are undersampled in ground-level mist-net surveys, resulting in underestimates of the actual species richness and abundance (Kalko and Handley, 2001; Kalko et al., 2008). This probably explains the absence of molossids, emballonurids, nycterids, and the capture of only a few vespertilionids during our surveys. It is, therefore, imperative to employ different sampling methods such as sub-canopy and canopy nets, acoustic detectors, and harp traps to complement ground-level mist nets for the detection of species that are considered rare or difficult to capture (Kunz and Parsons, 2009; Estrada-Villegas et al., 2010; Fahr and Kalko, 2010) and to obtain more complete inventories of bats (Bergallo et al., 2003; MacSwiney et al., 2008; Furey et al., 2009; Meyer et al., 2011; Silva and Bernard, 2017).

While the majority of bat species were captured in only one habitat type, some species were captured in both the pristine and disturbed habitats, e.g., *Megaloglossus woermanni*, *Myonycteris angolensis*, *Rousettus aegyptiacus*, *Rhinolophus landeri*, *Macronycteris gigas*, *Miniopterus* sp., *Afronycteris nana*, and *Pipistrellus nanulus*. The fact that these species were captured in both habitat types suggested that they are probably generalist species that can tolerate and forage in modified habitats. These species can therefore access additional resources outside of remnant forest patches, such as artificial shelters and food resources (Gehrt and Chelvig, 2003; Duchamp and Swihart, 2008; Loeb et al., 2009; Coleman and Barclay, 2012).

*Megaloglossus woermanni* was mostly recorded in the undisturbed (primary) forest during our surveys. However, a single individual was recorded over a stream at a high elevation site on Mt. Manengouba. This nectarivorous bat is common in closed forests but may enter cultivated areas adjacent to the forest to feed on flowers. It is common in areas where

flowers persist throughout the year. This species has also been recorded in disturbed areas in the Center Region of Cameroon (Waghiiwimbom et al., 2019), as well as in relatively undisturbed forest in the Mpem and Djim National Park by Atagana et al. (2018) and in the Dja biosphere reserve by Bakwo Fils (2009). The fact that this species has been recorded in both habitat types is an indication that it might benefit when natural areas are converted to agricultural landscapes. For example, Weber et al. (2009) captured this species, while it fed on flowers of cultivated bananas around a forested area in Benin.

*Rousettus aegyptiacus* and *Myonycteris angolensis* are large cavernicolous frugivorous bat species that were recorded in both pristine and disturbed habitats. The distribution of these species is largely dependent on the availability of suitable caves as day roost (Weber and Fahr, 2006; Monadjem et al., 2010). These species are known to have a broad habitat tolerance and probably have generalist-feeding habits. The capture of these species at disturbed habitats suggests that they are relatively tolerant to habitat fragmentation and may take advantage of the seasonal fluctuation in fruit production by fruiting trees such fig (*Ficus* sp.), apricot (*Prunus* sp.), peach (*Prunus* sp.), mango (*Mangifera indica*) mostly present in disturbed areas. These species have also been recorded in disturbed areas in Cameroon (Mongombe et al., 2019; Waghiiwimbom et al., 2019; Manfothang et al., 2020, 2021), and undisturbed areas (Bakwo Fils, 2009; Atagana et al., 2018).

The presence of *Macronycteris gigas* in undisturbed forest patches is not that surprising given that this species forages around the edges of clutter, where it often intercepts large flying insects from a foraging perch (Vaughan, 1977). Monadjem et al. (2016) also recorded this species in forested and disturbed habitats in the Guinean Mount Nimba. The presence of *Rhinolophus landeri*, *Afronycteris nana*, and *Pipistrellus nanulus* in both habitat types was not that surprising because these species are associated with primary and secondary forest habitats (Monadjem et al., 2010).

## Conservation and Management Implications

Our surveys suggest that forest loss has strong ramifications on bat species richness and functional richness. In addition, different guilds respond differently to different habitat attributes. These results reveal that disturbed habitats with forest patches are important for the conservation of bat species. Especially those that are adaptable and less sensitive to habitat disturbance, preferring fragmented landscape for commuting and foraging. Therefore, the presence of these habitats around primary forests may support the ecological need of some species as they may provide attractive foraging grounds and roosting sites for edge and open species.

Though disturbed vegetation supports a higher diversity of bats, the conversion of pristine forests to human-dominated landscapes may be detrimental to forest specialists, which are sensitive to human disturbances. Therefore, understanding the habitat needs of species and how human-caused disturbance affects the pattern of species diversity and abundance is essential in determining the degree of sensitivity to fragmentation

and local extinction risk, which in turn could be essential for developing effective species-specific conservation strategies. Furthermore, the observed differences in the bat communities between the two habitat types underscore the significance of maintaining primary forest as a means of avoiding the functional homogenization of the biome by preventing the local extinction of forest species (Cazalis et al., 2020). Finally, the occurrence of at least 10% of bats recorded in Cameroon in the biome indicates the forest remnant needs to be preserved by the local community as a means of safeguarding the local bat diversity.

## 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.

## ETHICS STATEMENT

The animal study was reviewed and approved by the Cameroon Ministry of Scientific Research and Innovation permit (Ref: 0000011/MINRESI/B00/C00/C10/C14).

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## AUTHOR CONTRIBUTIONS

E-MB and BB designed the study. MM, DM, AG-D, and JT conducted the fieldwork. MM and E-MB analyzed the data and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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# Stretching the Habitat Envelope: Insectivorous Bat Guilds Can Use Rubber Plantations, but Need Understorey Vegetation and Forest Buffers

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Envelope: Insectivorous Bat Guilds  
Can Use Rubber Plantations, but  
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Effects of land-cover change on insectivorous bat activity can be negative, neutral or positive, depending on foraging strategies of bats. In tropical agroforestry systems with high bat diversity, these effects can be complex to assess. We investigated foraging habitat use by three insectivorous bat guilds in forests and rubber plantations in the southern Western Ghats of India. Specifically, we monitored acoustic activity of bats in relation to (1) land-cover types and vegetation structure, and (2) plantation management practices. We hypothesized that activity of open-space aerial (OSA) and edge-space aerial (ESA) bat guilds would not differ; but narrow-space, flutter-detecting (NSFD) bat guild activity would be higher, in structurally heterogeneous forest habitats than monoculture rubber plantations. We found that bat activity of all guilds was highest in areas with high forest cover and lowest in rubber plantations. Higher bat activity was associated with understorey vegetation in forests and plantations, which was expected for NSFD bats, but was a surprise finding for OSA and ESA bats. Within land-cover types, open areas and edge-habitats had higher OSA and ESA activity respectively, while NSFD bats completely avoided open habitats. In terms of management practices, intensively managed rubber plantations with regular removal of understorey vegetation had the lowest bat activity for all guilds. Intensive management can undermine potential ecosystem services of insectivorous bats (e.g., insect pest-control in rubber plantations and surrounding agro-ecosystems), and magnify threats to bats from human disturbances. Low-intensity management and maintenance of forest buffers around plantations can enable persistence of insectivorous bats in tropical forest-plantation landscapes.

**Keywords:** insectivorous bat guilds, bat activity, forest cover, rubber plantations, management practices, understorey vegetation, Western Ghats, ecosystem services



## INTRODUCTION

Tropical forest fragmentation caused by agricultural intensification and expansion of commercial agroforestry plantations is a significant threat to biodiversity (Saunders et al., 1991; Raman, 2006; Gardner et al., 2009; Kumar et al., 2010; Canale et al., 2012). Generally irreversible or one-way conversion of primary forest habitat to monoculture plantations is among the main causes of forest fragmentation (FAO and UNEP, 2020). In forest-plantation mosaics, the spatial configuration of land-cover types is an important determinant of species persistence, movement, foraging, and reproductive success (Turner, 1996; Kumar et al., 2002; Henle et al., 2004; Canale et al., 2012). Within land-cover types, habitat use by different species of small mammals, such as insectivorous bats, may be driven by vegetation structure, habitat edges, human land-uses, and management practices (Dauber et al., 2003; Henle et al., 2004; Harvey and Villalobos, 2007). Landscape-scale habitat configuration and alterations in local habitat structure can thus affect the movement and dispersal of insectivorous bats (Erickson and West, 2003; Duchamp and Swihart, 2008; Meyer et al., 2008).

Depending on the dispersal ability and ranging behavior of insectivorous bats, their responses to habitat conversion, local habitat complexity, and landscape context can vary substantially (Gorresen and Willig, 2004; Kusch and Schotte, 2007). Jones et al. (2009) suggest that bats are potential bio-indicators due to their tractable population-level responses (in terms of activity) to land-cover change. Yet, studies on bat responses to land-cover change have yielded equivocal conclusions for different bat species (Estrada-Villegas et al., 2010; Frey-Ehrenbold et al., 2013; Ducci et al., 2015). Insectivorous bat responses to habitat conversion in terms of activity can range from negative (reduced foraging activity: Estrada-Villegas et al., 2010) to neutral (no difference in activity: Davy et al., 2007) to even positive (increased activity; Ethier and Fahrig, 2011). Responses may vary by the type of biome (temperate/tropical: Erickson and West, 2003; Heer et al., 2015), degree and nature of land conversion and agricultural intensification (Gorresen and Willig, 2004; Frey-Ehrenbold et al., 2013), sampling scale (local to landscape: Erickson and West, 2003; Gehrt and Chelvig, 2003; Meyer et al., 2008), and regional species diversity and trait distributions (Duchamp and Swihart, 2008; Meyer et al., 2008; Ducci et al., 2015).

Understanding the influence of land-cover types on insectivorous bats needs an understanding of the diversity of their foraging strategies. Bat foraging strategies can be understood as summaries of functional trait diversity in the local species pool. Insectivorous bat “foraging guilds” can be categorized by echolocation characteristics across bat species (Siemers and Schnitzler, 2004; Denzinger and Schnitzler, 2013).

Accounting for functional trait diversity (and not only species diversity) can help understand the responses of different bat guilds to land-cover change and habitat fragmentation (Siemers and Schnitzler, 2004; Ober and Hayes, 2008; Klingbeil and Willig, 2009; Cadotte et al., 2011; Frey-Ehrenbold et al., 2013). For example, Estrada-Villegas et al. (2010) showed that “forest-dependent” aerial insectivores were affected negatively by forest loss unlike “open-space” foragers that were largely unaffected. Guild-level responses can also be more intuitive to understand and provide an efficient way to monitor land-cover change impacts on ecosystem services from insectivorous bats (Cadotte et al., 2011).

In this study, we assessed the effects of (1) land-cover type (forests, rubber plantations, teak plantations, and settlements) and vegetation structure (stratification, height, and canopy cover) in forests and plantations, and (2) plantation management practices (e.g., clearing of understorey vegetation, pesticide use), on foraging habitat use by three insectivorous bat guilds in the Western Ghats biodiversity hotspot of India. These variables were expected to influence insect abundance, and the ability of bats to navigate, and in turn affect bat activity. We acoustically sampled bat activity in forests, rubber plantations, and adjacent land-cover types (teak woodlands and human settlements) in forest-plantation mosaics. We classified bat guilds as “Open-Space Aerial (OSA)” foragers, “Edge-Space Aerial (ESA)” foragers and “Narrow-Space Flutter Detecting (NSFD)” foragers, based on prey detection ranges and aerospace use (Denzinger and Schnitzler, 2013). OSA bats emit low-frequency echolocation calls with quasi-constant frequency modulations to detect flying insects in open air, ESA bats use mid-range, frequency-modulated calls to detect aerial insect prey mostly along habitat edges, and NSFD bats use mid- to high-range constant frequency calls to detect insects against cluttered vegetation (Schnitzler and Kalko, 2001; Siemers and Schnitzler, 2004; Denzinger and Schnitzler, 2013). As vegetation structure was expected to be more complex in tropical forests than rubber plantations, we expected differential activity of the three bat guilds. Accordingly, we hypothesized that the activity of OSA and ESA bat guilds would not differ between forests and rubber plantations. For NSFD bats, we expected higher activity in forest habitats than rubber plantations. Additionally, we predicted that human management of rubber plantations would alter vegetation structure and influence bat activity. Therefore, we also investigated the processes by which management practices might have affected bat activity within rubber plantations.

## MATERIALS AND METHODS

### Study Area

In India's Western Ghats, a major driver of forest fragmentation has been expansion of commercial plantations (e.g., coffee, rubber, oil-palm; Jha et al., 2000; Kumar et al., 2002; Anand et al., 2010). Our study was conducted in a rubber plantation-dominated agroforestry landscape surrounding the Shenduruney Wildlife Sanctuary (Lat: 8°54.084' N, Long: 77°08.162' E), in the Agasthyamala hills, Kerala, in the Western Ghats. The state of Kerala accounts for the bulk of natural rubber production

**Abbreviations:** OSA, “Open-Space Aerial” foraging bats; ESA, “Edge-Space Aerial” foraging bats; NSFD, “Narrow-Space Flutter Detecting” foraging bats; FmaxE, Frequency with maximum Energy; CF, Constant Frequency; FM, Frequency Modulation; QCF, Quasi-Constant Frequency; GIS, Geographical Information System; OLI, Operational Land Imager; TIRS, Thermal Infrared Sensor; AIC, Akaike Information Criterion; ZIP GLMs, Zero-inflated Poisson Generalized Linear Models.



in India. Mass conversion of forests to rubber plantations in Kerala began about 70 years ago and rubber area expansion has been over 600% in this period (Kumar, 2005). Apart from the major land-cover classes of contiguous and fragmented semi-evergreen/moist-deciduous forests and rubber plantations, the landscape includes teak plantations, fruit and spice orchards, human settlements, and matchwood plantations (**Figure 1**). The forests of this landscape have a remarkable diversity of plants, fishes and amphibians, including many endemics. The study area covers the western slopes of the southern Western Ghats from 65 to 1,300 m above mean sea level, of a topographically complex and rugged horst-and-graben type mountain range. The region receives an average annual rainfall of c. 2,800 mm, with the Indian summer monsoon season duration from June to September (Nair, 1991).

## Study Design

We selected sampling locations corresponding with four land-cover types: forests ( $n = 22$  locations), rubber plantations ( $n = 20$ ), teak woodlands ( $n = 13$ ), and human settlements ( $n = 11$ ). The numbers of locations were roughly proportional to the areal extents (in  $\text{km}^2$ ) of land-cover types in our effective sampling region (forests:  $69.19 \text{ km}^2$ , rubber:  $40.13 \text{ km}^2$ , teak:  $28.63 \text{ km}^2$ , and settlements:  $15.6 \text{ km}^2$ ). Locations were also chosen based on accessibility due to safety-based restrictions, topographic variables (e.g., steep slope), rugged terrain conditions, and thorny vegetation (e.g., canebrakes). Hence, in many forested areas, we had to follow small paths and dirt roads for sampling (**Figure 1**). Location coordinates were logged in a Global Positioning System (Garmin eTrex Vista HCx). We sampled bat activity and habitat variables at replicate points within each location to increase spatial coverage of the land-cover types available there. Sampling was conducted during the dry-season (December to May) on clear evenings in 2011–12, with additional site visits in the dry-season in 2014 and 2019. The dry-season was defined according to the typical duration of the Indian summer monsoon season (see study area section).

## Acoustic Sampling of Bat Activity

The echolocation call rate of insectivorous bats, calculated from recordings of bat ultrasound calls, indicates relative bat activity across different habitats (Vaughan et al., 1997; Davy et al., 2007; Williams-Guillén and Perfecto, 2011). Bat activity is considered a useful index of foraging habitat use as bats generally show site fidelity (Kapfer et al., 2008; Berthinussen and Altringham, 2012). At the selected sampling locations, we recorded bat echolocation calls with a handheld D240X detector (Pettersson Elektronik AB, Uppsala, Sweden<sup>1</sup>) with high-gain automatic detection and  $10\times$  time expansion factor, and stored in a recorder (Edirol R-09HR, Roland). The sampling rate of the detector was 307 kHz and detector frequency range from 10 to 120 kHz. This sampling rate was adequate in resolution for accurate estimation of characteristics of most bat species commonly encountered in the landscape (Brigham et al., 2004). D240X detectors are thought to be highly efficient compared to similar detector types

in their detection range and directionality (Sprong et al., 2012; Kerbirou et al., 2019). Given our financial constraints and for parity with other contemporaneous studies in this region (e.g., Wordley et al., 2014, 2015), this was the best available detector.

Our pilot sampling (at 15 points across land-cover types) with the D240X detector revealed that bat activity was substantially greater in recordings in the dusk and early night hours (1830–2000 h) as compared to later night hours (2000–2230 h) at all sites. Therefore, we focused our effort on the dusk activity peak, post bat emergence from roosts (as done by Hayes, 1997; Davy et al., 2007; Skalak et al., 2012) for sampling the majority of common species in the three guilds. Sampling began half an hour after sunset and was completed over 3 h after sunset (following Berthinussen and Altringham, 2012). Due to work safety issues, overnight sampling was not possible.

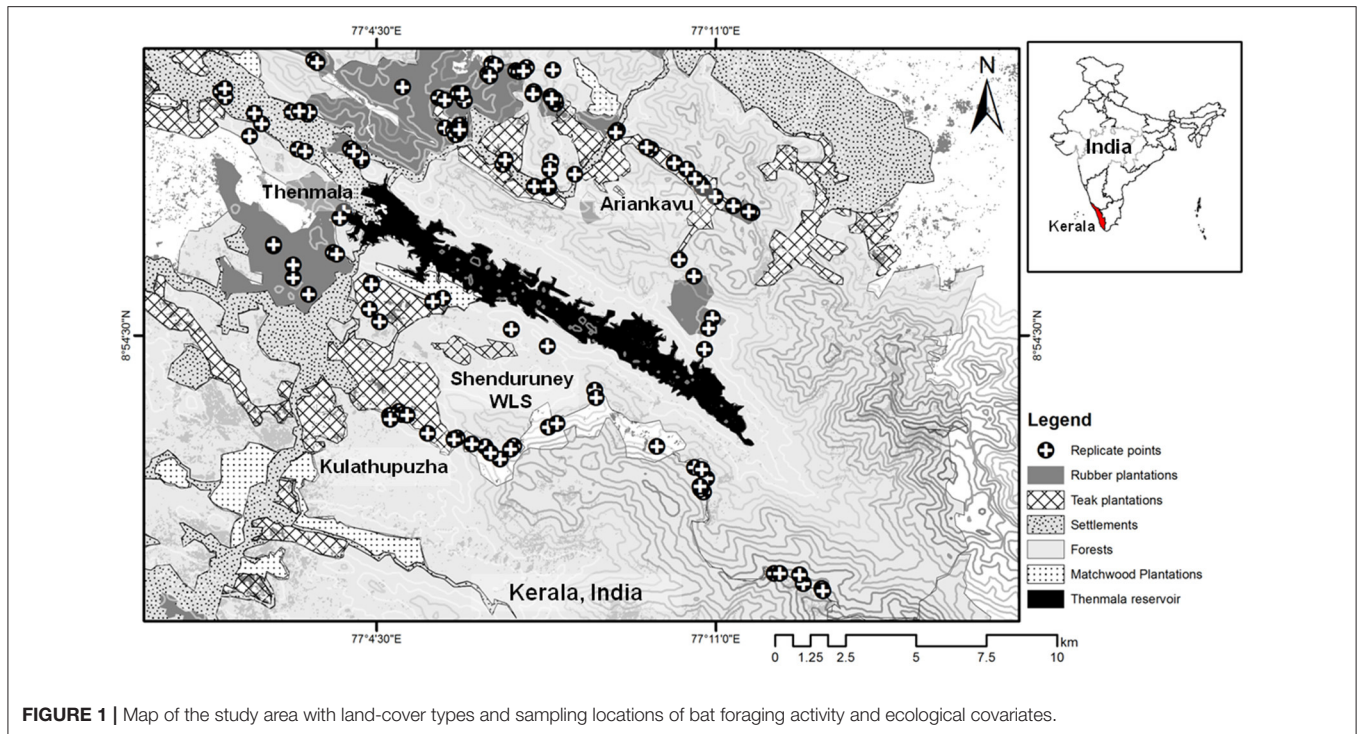
Overall, within the 66 locations across land-cover types, we sampled a total of 157 spatial replicate points. We varied the number of replicate points from 2 to 4 within each location, to avoid potential oversampling of bat calls in small areas and to adequately cover larger areas (Siemers and Schnitzler, 2004; Cel'uch and Zahn, 2008; MacSwiney et al., 2008; Frey-Ehrenbold et al., 2013). The spatial replicate points within each location were at least  $\sim 200 \text{ m}$  apart for independence (Mullin et al., 2020; Yoh et al., 2020), at distances much more than the known detection distances for D240X detectors (Sprong et al., 2012; Kerbirou et al., 2019). Typically, two land-cover types were sampled per night, by staggering the order of sampled points among land-cover types, to allocate similar effort to both. At each point, 10-min recordings were conducted, separated on average by 20-min intervals, which was the time taken to move between points, owing to terrain conditions. Several studies (e.g., Williams-Guillén and Perfecto, 2011; Hogue and McGowan, 2018; Mullin et al., 2020) have conducted replicated recordings of 10–12 min and confirmed this temporal duration to yield reliable estimates of bat activity in habitat mosaics. Thus, we made 367 echolocation call recordings at the 157 points (mean recording time per point = 21.5 min, range 20–40 min, total effort of c. 3380 min over 60 nights).

## Bat Guild Assignments and Acoustic Analyses

We searched and visited bat roosts in the landscape to visually confirm bat species identification based on morphological keys (Bates and Harrison, 1997) and regional checklists (e.g., Korad et al., 2007). We then recorded bat resting frequencies and characteristic in-flight echolocation calls from roosting individuals and emerging bats at flyways near roost exits (Biscardi et al., 2004; Brigham et al., 2004; Fraser et al., 2020). We validated our recorded calls with available information on the peak, start, and end frequencies, inter-pulse intervals, call duration, etc. of Indian bats from previous studies (Neuweiler et al., 1984; Raghuram et al., 2014; Wordley et al., 2014; Deshpande and Kelkar, 2015).

Using acoustic parameters such as Frequency with maximum Energy (FmaxE) and call structure [Constant-Frequency (CF), Frequency-Modulation (FM), and Quasi-Constant-Frequency

<sup>1</sup> www.batsound.com.



**FIGURE 1** | Map of the study area with land-cover types and sampling locations of bat foraging activity and ecological covariates.

(QCF)], calls were identified as representative or reference calls of bat species confirmed at roosts (Schnitzler and Kalko, 2001; Siemers and Schnitzler, 2004; Denzinger and Schnitzler, 2013; Frey-Ehrenbold et al., 2013). Acoustic analyses of individual calls were carried out manually in the software BatSound Pro v.3.32 (Pettersson Elektronik AB, Uppsala, Sweden). All recordings were analyzed using sampling frequency of 44.1 kHz at FFT size of 1,024 samples with 95% overlap in a hanning window. We recorded a total of 25 insectivorous bat species in all sampled foraging locations. From our reference calls, data on 23 species (sample sizes of 51–114 bat calls each) could be used for unambiguous guild assignment. Ambiguous, unclear, or interrupted calls were omitted and only calls with high signal to noise ratio were considered for further analyses. Based on spectral signatures and acoustic detection ranges of different species, we assigned all usable calls to one of three foraging guilds of insectivorous bats: “Open-Space Aerial (OSA)” foragers, “Edge-Space Aerial (ESA)” foragers, and “Narrow-Space Flutter Detecting (NSFD)” foragers (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). In our study, the OSA guild included the families Emballonuridae and Molossidae, ESA included Vespertilionidae and Miniopteridae, and NSFD included Rhinolophidae (details in **Table 1**). For all spatial replicate points in our sampling locations, we manually calculated bat activity (echolocation call rate or bat passes per unit time) for each guild, from the software BatSound Pro.

## Habitat Variables

We defined four land-cover classes as (1) forests, (2) rubber plantations, (3) teak woodlands, and (4) village settlements, based

on ground surveys and supervised classification of bands 2 (blue), 3 (green), and 4 (red) of Landsat OLI TIRS Level-1 images (30 m × 30 m spatial resolution) from April 2014, which was the dry-season after our main sampling period in 2011–12. The reason to not use Landsat images from 2011 to 12 was that they had a striping problem, which would have affected our classification. Our extensive ground surveys from 2011 to 2014 indicated negligible change in land-cover types since 2011 to 12, and helped us accurately classify smaller patches of land-cover types. We also used topographic maps to identify settlements and established rubber estates (1:25,000 cm; Survey of India, surveyed in 1976–77) in the region. For supervised classification, we used a Maximum Likelihood-based method from 50 training sites that were used to generate spectral signatures of forests, rubber plantations, teak woodlands, village settlements, and fruit orchards in Idrisi Selva software (ClarkLabs, 2012). Supervised classification resulted in a user accuracy rate of above 90% for the first four land-cover categories. Fruit orchards were very small in area and for analyses, thus, these locations were assigned mostly to settlements near fruit orchards. Around each acoustic sampling point ( $n = 157$ ), the percent area under the above land-cover types within circular buffers of area 2 km<sup>2</sup> (radius of 0.8 km) was extracted in Quantum GIS 2.4.0 (QGIS Development Team, 2018). The buffer area was chosen to represent approximate average daily foraging ranges of different bat guilds. No tagging studies were available for the three guilds from South or Southeast Asia, so we borrowed information on daily foraging ranges from other studies. We used studies from Europe and Australia on bats from the three guilds (NSFD: Bontadina et al., 2002; OSA: Marques et al., 2004; ESA: Gonsalves et al., 2013). Prakash et al. (2021)

**TABLE 1** | Description of assigned bat foraging guilds according to echolocation call signatures and included species with frequencies recorded from the study area.

Guild assignment <sup>#</sup>	Echolocation call structure (type)	Range of frequency with maximum energy (FmaxE, in kHz)	Family (representative genus)	Species included in the guilds [FmaxE, mean ( $\pm$ SE) in kHz] <sup>^</sup>
Open Space Aerial (OSA) foragers	Quasi-Constant Frequency (QCF)	10–30	Molossidae ( <i>Tadarida</i> ); Emballonuridae ( <i>Taphozous</i> )	<i>Tadarida aegyptiaca</i> (Geoffroy): 18 ( $\pm$ 2); <i>Tadarida teniotis</i> (Rafinesque): 12.5 ( $\pm$ 1.3); <i>Chaerephon plicatus</i> (Buchanan): 23.3 ( $\pm$ 3); <i>Taphozous melanopogon</i> (Temminck): 26.5 ( $\pm$ 3); unidentified <i>Taphozous</i> sp.
Edge Space Aerial (ESA) foragers	Frequency-Modulated Sweep (FM-sweep) and Frequency Modulation with Quasi-Constant Frequency tail (FM-QCF)	25–70	Vespertilionidae ( <i>Pipistrellus</i> ); Miniopteridae ( <i>Miniopterus</i> )	<i>Pipistrellus</i> cf. <i>tenuis</i> (Temminck): 52.5 ( $\pm$ 3); <i>P. ceylonicus</i> (Kelaart): 35 ( $\pm$ 3); <i>P. cf. coromandra</i> (Gray): 44.3 ( $\pm$ 1.7); unidentified species of <i>Pipistrellus</i> and other genera; <i>Miniopterus fuliginosus</i> (Hodgson): 52.5 ( $\pm$ 2.5); <i>M. pusillus</i> (Dobson): 61.5 ( $\pm$ 2.5)
Narrow Space Flutter Detecting (NSFD) foragers	Constant Frequency (CF)	40–105	Rhinolophidae ( <i>Rhinolophus</i> )	<i>Rhinolophus beddomei</i> (Andersen): 44 ( $\pm$ 1); <i>R. rouxii</i> (Temminck): 80.5 ( $\pm$ 2); <i>R. indorouxii</i> (Chattopadhyay, Garg, Kumar, Doss, Ramakrishnan, and Kandula): 89.5 ( $\pm$ 0.8); <i>R. lepidus</i> (Blyth): 102 ( $\pm$ 4)

<sup>#</sup>Guild assignment based on Schnitzler and Kalko (2001) and Denzinger and Schnitzler (2013). We detected, but have not included the families Hipposideridae (NSFD foragers) and Megadermatidae (Narrow-Space Passive-Gleaning or NSPG foragers), and *Myotis* spp. (Edge-Space Trawling bats) in our analyses because of low sample sizes. <sup>^</sup>Species call frequencies identified in this study. See **Supplementary Material** for average species-level activity by habitat type.

tagged insectivorous bats in the Western Ghats (*Megaderma spasma*, not included in our analyses), and found highly localized foraging activity.

Effects of percent land-cover types in surrounding buffers (representing the landscape context) were tested on bat activity recorded at each point in particular habitats (similar to Gili et al., 2020). Variables representing vegetation structure (e.g., overstorey canopy cover, tree height, presence of understorey, and lianas) and habitat edges (e.g., roads, streams, and open areas) were recorded at each acoustic sampling point (details of habitat variable measurements in **Table 2**). These variables were chosen in relation to our guild-specific predictions (see section Introduction). Vegetation measurements were conducted before we began acoustic recordings at dusk. The same observer conducted visual estimation of tree height and canopy cover. Visual estimates were initially calibrated with a clinometer and laser rangefinder for accuracy. Understorey vegetation, lianas, and habitat edges were recorded as categorical variables based on presence or absence, and size (e.g., for roads). At each point, we also extracted data on terrain, elevation, slope, and aspect from toposheets (1:25,000 cm; Survey of India), digital elevation models (ASTER 30 m), and satellite imagery (Landsat OLI TIRS<sup>2</sup>). We expected topographic variables to influence bat activity in interaction with local habitat conditions, so these were included later as additional covariates in analyses.

## Statistical Analyses

We computed species accumulation curves with the Jack-knife II estimator from the cumulative recording effort (Moreno and Halffter, 2000). Species accumulation curves for forests and rubber plantations indicated adequate sampling effort, although

teak plantations and settlements, which were smaller in extent, did not show a clear asymptote (**Figure 2**).

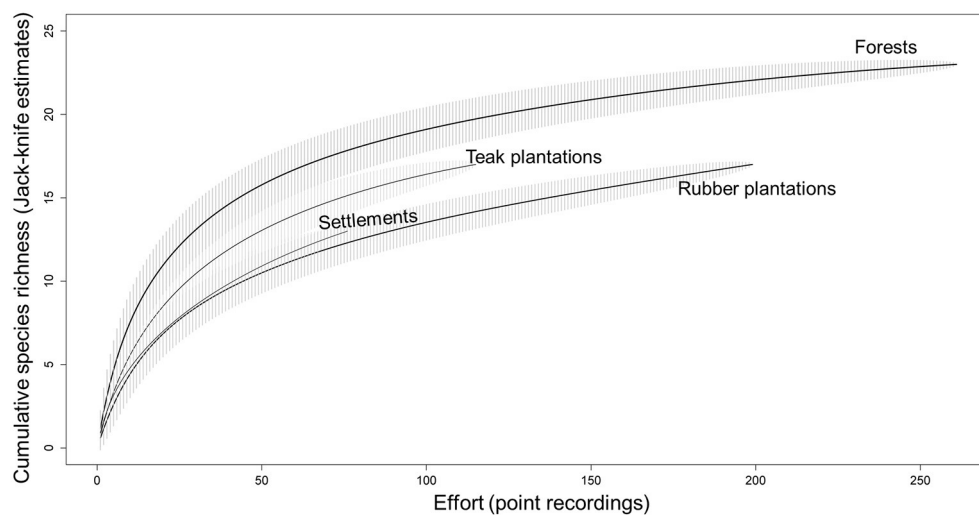
Prior to analyses, we first standardized all point-level data on guild-wise bat activity to 10 min. We also tested for spatial autocorrelation in guild-wise bat activity as a result of proximity of replicate points, by estimating sill and range parameters of omnidirectional variogram models (Fortin and Dale, 2005). Variograms poorly fit bat activity data in relation to distances between recording points, indicating no clear effects of spatial autocorrelation or suggesting spatially localized habitat use by bats. For the three guilds, variogram range was approximately near to or above 2 km (more than twice of our buffer radius). To avoid effects of spatial autocorrelation due to any overlapping buffers, we used a randomized subsampling procedure (generating 100 sub-samples with similar sample sizes from all land-cover types) by first thinning the data to 50% of the sample size by removing points < 1 km apart, and running correlation and regression analyses (Segurado et al., 2006). The poor variogram fits could also be because of the detection range of D240X detectors, and variable detection distances of different species (Kerbiriou et al., 2019) or guilds. So, we separately analyzed guild-wise activity in relation to habitat variables, to avoid biases resulting from differential detection of species upon pooling bat activity across guilds (Kerbiriou et al., 2019).

Proportional or percent (%) cover is a simple but useful indicator that can represent effects of surrounding habitat on species (Watling et al., 2011). We analyzed acoustic activity of bat guilds in relation to percent of land-cover types within buffers (effect of landscape context). We estimated bat activity in (1) rubber plantation points at different % cover of forest in the buffer, and (2) in forest points with different % cover of rubber plantations in the buffer. We performed Spearman's rank-order correlation tests and evaluated correlation coefficients for univariate associations between bat activity and percent cover

<sup>2</sup>www.earthexplorer.usgs.gov.

**TABLE 2 |** Details of habitat variables measured in the study.

Variable name	Interpretation
<b>Terrain and geospatial information</b>	
Location (latitude, longitude)	Degree decimals
Date/time	Date and time of recording
Altitude	Meters above mean sea level
Slope	Percent (%)
Aspect	Directional angle 0–360°
Ruggedness	Percent (%); extracted through analysis of Digital Elevation Model (ASTER DEM)
<b>Land-cover</b>	
Land-cover type	Derived from areas under four land-cover classes (forest, rubber, teak and settlements) in a circular buffer of area 2 km <sup>2</sup> (radius of ~0.8 km) around sampling locations. Areas under land cover types for each buffer were calculated using Quantum GIS software. Landsat Operational Land Imager and Thermal Infrared Sensor (OLI TIRS) (2014) images used to classify the major land-cover types.
<b>Vegetation structure</b>	
Presence of understorey	Presence/absence (1/0)
Presence of lianas	Presence/absence (1/0)
Overstorey canopy cover (density)	Percent (%)
Canopy connectivity	Classified as 1 = Low, 2 = Moderate, and 3 = High based on canopy gaps
Tree height	Tree height estimated visually (in meters)
<b>Habitat edges</b>	
Habitat openness	Open habitat present or absent (1/0)
Stream edge	Stream orders 1 to 4 (as per toposheets of 1:25000 scale), normalized to form a single continuous variable
Stagnant water edge	Categorical: 1-ditch/pond, 2-village tank, 3-large storage tank, 4-dam reservoir; normalized to form a single continuous variable
Road edge	Categorical: 1-mud road, 2-village road, 3-district road (tarred), 4-metalled road (highway); normalized to form a single continuous variable

**FIGURE 2 |** Species accumulation curve based on Jack-knife II estimation of species sampled across different land-cover types.

for consistency in sign, magnitude, and statistical significance. We then ran multiple regression models to estimate the effects of different covariates on guild-wise bat activity. Model covariates included landscape context (% cover in 2 km<sup>2</sup> buffer), vegetation structure (canopy, understorey, and tree height), and habitat edge variables (roads, streams, and open areas) measured at

recording locations within habitat types. Only combinations of uncorrelated covariates (correlation < 0.30) were included in the model. We found high occurrence of zeroes in bat activity data (50–90%), arising both from “absence” (structural zeroes) and “no detection” of bat calls at sites (He et al., 2014). Hence, we chose zero-inflated generalized linear models with Poisson errors



(ZIP GLMs). ZIP GLMs achieved better model convergence and fit over other candidate models, e.g., Poisson, negative binomial, or zero-inflated negative binomial GLMs. Model fit was additionally calculated using the Cox-and-Snell Pseudo- $R^2$  statistic (Williams, 2019), which provides an absolute measure of model improvement after adding covariates to a null model (i.e., model without covariates). ZIP GLMs were run in the package “pscl” in the software R 3.2.3 (R Core Team, 2018). Model selection was based on Akaike weights of models calculated from the Akaike Information Criterion (AIC; Burnham and Anderson, 2002). Models with lower AIC values were selected, if the difference between AICs of the two best comparable model AICs was  $>2$ . We combined the use of pseudo- $R^2$  and AIC for careful model selection, so that we could compare among models for their absolute fit (as improvement over null models) as well as relative fit and parsimony.

### Effects of Plantation Management on Vegetation Structure and Bat Activity

We surveyed 30 rubber plantations in 19 locations to compile qualitative categorical information on the varieties of rubber planted (new: high-yielding, and mixed: new + old), and management intensity. We recorded directly visible indicators of management intensity as: (1) presence or absence of understorey vegetation, indicating frequency of clearing or removal of natural vegetation and weeding, and (2) pesticide use, from direct field observations as well as through information provided by plantation managers and workers. Based on the above factors, we classified rubber plantations as low-management, moderate-management, or high-management, reflecting management intensity. A low-management plantation was typically one with relatively intact understorey vegetation and no pesticide use, medium-intensity plantations had any one of the two indicators or intermediate levels of both (e.g., thinner understorey and occasional pesticide use), and high-management plantations had both indicators of intensive management at high levels. Pesticide application frequency and rubber tapping frequency were both higher in high-management plantations. We then compared guild-wise bat activity between these plantation management categories, using non-parametric Kruskal–Wallis tests and Dunn tests.

## RESULTS

### Effects of Land-Cover Type on Guild-Wise Bat Activity Within Buffers (Landscape Context)

Average activity of NSFD bats was almost 10 times greater in forests (10.06 passes/h) than in all other land-cover types (Table 3). Average ESA bat activity was higher in forests (34.1 passes/h) as compared to rubber (26.2), teak plantations (19.9), and settlements (18.7 passes/h; Table 3). Average OSA bat activity was highest in settlements and teak plantations (14 and 9.4 passes/h), followed by forests and rubber plantations (4.28 and 2.54 passes/h; Table 3). Activity of all bat guilds was positively correlated with percent forest cover and negatively with percent

**TABLE 3 |** Bat activity (mean  $\pm$  SE of bat passes per hour) of the three guilds across the four land-cover types.

Guild	Forests	Rubber	Teak	Settlements
OSA	4.28 $\pm$ 1.41	2.54 $\pm$ 2.71	9.4 $\pm$ 4.25	14 $\pm$ 6.34
ESA	34.1 $\pm$ 6.9	26.2 $\pm$ 9.26	19.9 $\pm$ 6.3	18.7 $\pm$ 8.24
NSFD	10.06 $\pm$ 2.87	1.08 $\pm$ 0.84	0.15 $\pm$ 0.11	0.0 $\pm$ 0.0

**TABLE 4 |** Associations (Spearman's rank correlation coefficients) of bat guild activity with land-cover extent (\*\* $p < 0.001$ , \* $p < 0.01$ ,  $p < 0.05$ , and NS = Not Significant), indicating positive association with % forest cover and negative association with % rubber plantation and % settlement area in 2 km<sup>2</sup> buffers.

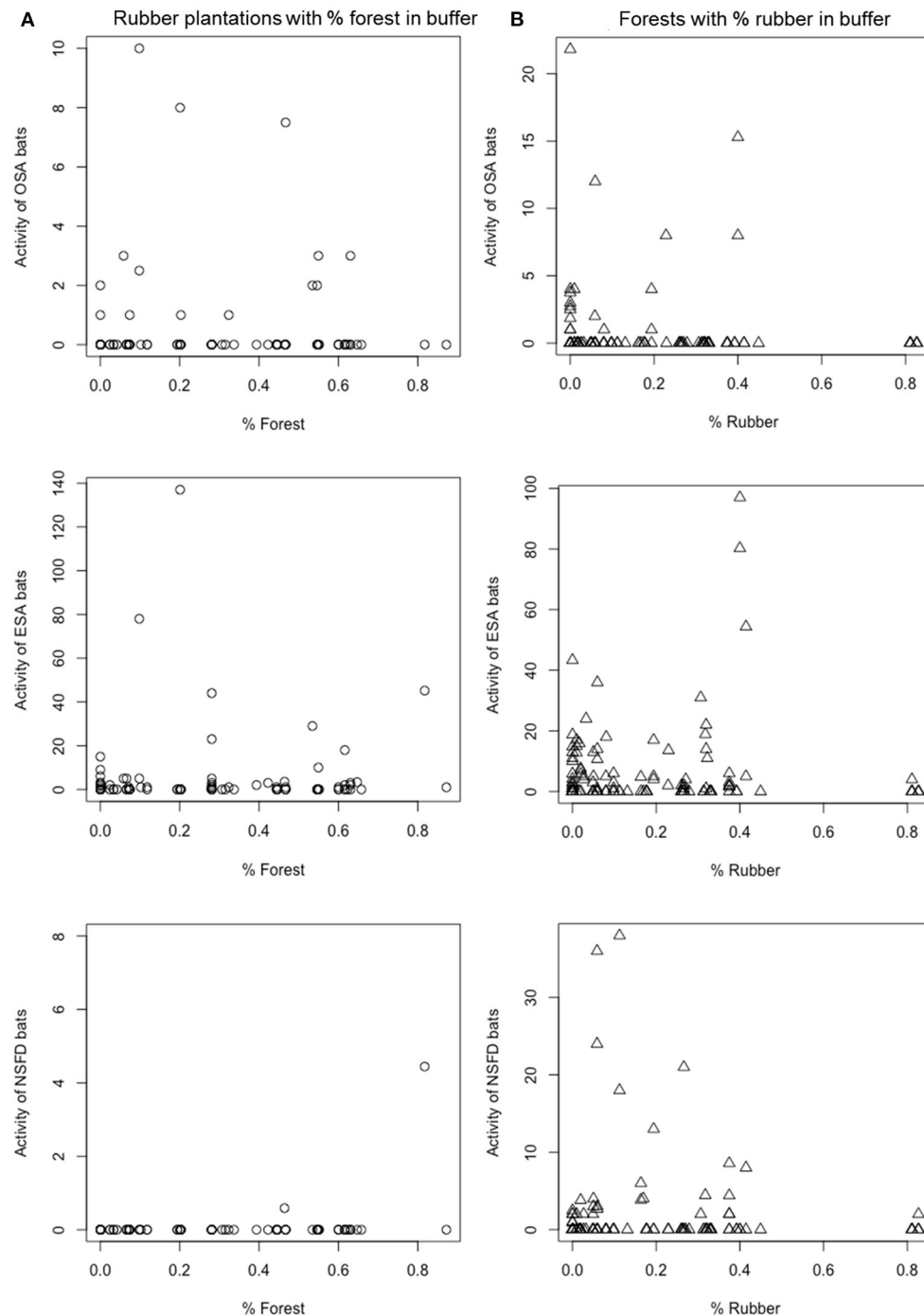
Guild	% Forest	% Rubber	% Teak	% Settlement
OSA	0.10*	−0.11**	0.07 <sup>NS</sup>	0.01 <sup>NS</sup>
ESA	0.24***	−0.20***	0.02 <sup>NS</sup>	−0.11**
NSFD	0.29***	−0.13**	−0.06 <sup>NS</sup>	−0.25***

rubber in the surrounding buffers of 2 km<sup>2</sup> (Table 4). Average OSA and ESA activity was highest (1.25 and 5.2 passes/h, respectively) in buffers with forest cover  $>25\%$  and  $<75\%$  (Figure 3). For NSFD bats, 97% of total activity was recorded in areas with  $>75\%$  forest cover in buffers (Figure 3). NSFD activity was present in rubber plantations only if the buffer had over 80% forest cover (Figure 3). In contrast, if buffers had more than 50% rubber plantation cover, low bat activity was recorded (OSA: 1.1 passes/h, ESA: 14.7 passes/h, and NSFD: 0.23 passes/h).

### Effects of Vegetation Structure and Habitat Edges on Guild-Wise Bat Activity

Bat activity of all guilds, irrespective of the association with forest cover, was positively associated with the presence of understorey vegetation (Table 5; Figure 4). Across all land-cover types, OSA, ESA, and NSFD bat activity levels were thrice, twice, and 5.5 times higher in the presence of understorey vegetation (mean  $\pm$  SE: 6.4  $\pm$  1.5, 30.5  $\pm$  5.6, and 5.5  $\pm$  1.5 bat passes/h, respectively) than in its absence. Forest understorey was structurally heterogeneous (multi-layered) with mostly native plant species, whereas rubber understorey was homogenous (single-layered) and often composed of one or two invasive plant species like *Lantana camara* and *Chromolaena odorata*. The high activity of NSFD bats in forests with understorey vegetation was as expected, but the response of OSA and ESA bat activity to understorey vegetation was a surprise finding. Effect sizes of understorey vegetation on bat guilds varied as NSFD  $>$  ESA  $>$  OSA (Figure 4). NSFD bat activity was positively associated with old-growth forests with tall trees and dense canopy cover (Figure 4). NSFD bats were absent in open habitats such as settlements (Table 5; Figure 4), as expected. OSA and ESA bat activity were negatively associated with tree height (Table 5; Figure 4). ESA activity was positively associated with habitat edges, especially streams and small roads in forests and plantations (Table 5).





**FIGURE 3 |** Time-standardized activity (bat passes per 10 min) of insectivorous bat guilds in rubber plantations (A) and forests (B) in relation to landscape context, i.e., % forest (A) and % rubber (B) cover in the surrounding buffer.

## Effects of Rubber Plantation Management Practices

Almost no activity of OSA bats (mean  $\pm$  SE:  $1 \pm 0.16$  bat pass/h) was recorded in the 30 rubber plantations selected

to test the effects of management practices. Total ESA bat activity was higher in low- ( $144 \pm 62$  bat passes/h) and moderate-management rubber plantations ( $120 \pm 30.5$  passes/h) than those with high-management intensity ( $27 \pm 10.6$  passes/h).

**TABLE 5 |** Summaries of selected zero-inflated Poisson (ZIP) generalized linear models (GLMs) with effect sizes (parameter estimates) of habitat variables on bat activity of OSA, ESA, and NSFD bat guilds.

Guild	Covariates	Parameter estimates Mean (SE)	Model fit (Cox and Snell's Pseudo- $R^2$ )	AIC (compared to AIC of null model)	AIC weight
Open Space Aerial Foragers (OSA)					
Count model	Intercept	0.72 (0.31)*	0.18	395.0 (AICnull = 423)	0.60
	Understorey	1.34 (0.31)***			
	Openness	0.56 (0.22)**			
	Tree height	−0.05 (0.015)***			
	Aspect	−0.002 (0.0009)#			
Zeroes-model	Intercept	1.32 (0.20)***			
	%Rubber	1.79 (0.90)*			
Edge-Space Aerial Foragers (ESA)					
Count model	Intercept	−1.49 (0.73)*	0.28	1,587.4 (AICnull = 2162)	0.80
	Stream Edge	2.10 (0.72)*			
	Understorey	1.80 (0.14)***			
	Openness	0.94 (0.08)***			
	Road Edge	0.60 (0.13)**			
	Tree height	−0.06 (0.005)***			
Zeroes-model	Intercept	−0.39 (0.18)*			
	% Rubber	1.71 (0.59)**			
Narrow-Space Flutter-Detecting Foragers (NSFD)					
Count model	Intercept	−3.69 (1.15)***	0.44	360.0 (AICnull = 496)	0.92
	Understorey	3.21 (1.14)**			
	% Forest	0.96 (0.24)***			
	Canopy density	0.07 (0.004)***			
	Tree Height	0.047 (0.01)***			
Zeroes-model	Intercept	1.16 (0.26)***			
	Openness	1.25 (0.5)*			

Count model covariates predict recorded bat activity and the zeroes-model covariates predict recorded absences. Significance levels of parameter estimates (\*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p \leq 0.05$ , and # $p > 0.05$ ), model fit (Pseudo- $R^2$  values) and evaluation with respect to null model (based on AIC weights) are also shown.

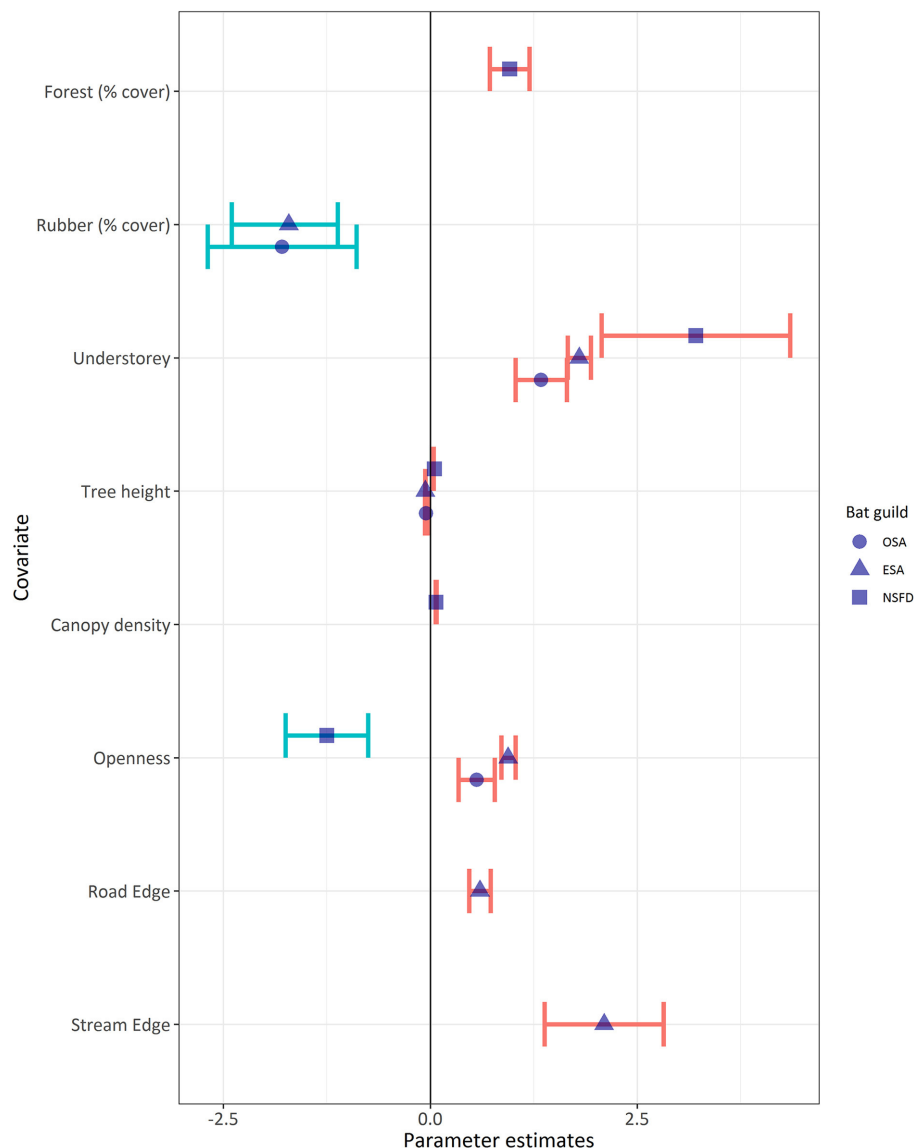
Here, the difference between moderate- and high-management intensity categories was statistically significant [Kruskal–Wallis (K–W) test:  $\chi^2 = 3.79$ ,  $df = 2$ , and  $P = 0.15$ ; Dunn's test: moderate vs. high,  $P = 0.03$ ]. Total NSFD bat activity was greater in low- ( $17.5 \pm 4.1$  passes/h) and moderate-management ( $11 \pm 2.8$ ) than high-management rubber plantations ( $0.75 \pm 0.39$ ), and differences were statistically significant (K–W test:  $\chi^2 = 5.94$ ,  $df = 2$ ,  $P = 0.05$ ; Dunn test: low vs. high:  $P = 0.02$ ; moderate vs. high:  $P = 0.01$ ; low vs. moderate:  $P = 0.40$ ). Importantly, NSFD bats showed activity in rubber plantations only when understorey vegetation was present. Total ESA bat activity was higher when understorey was present in rubber ( $138 \pm 43.4$  passes/h) than in its absence ( $60 \pm 23.7$ ), but differences were not statistically significant (K–W test:  $\chi^2 = 0.675$ ,  $P = 0.41$ ). About 61% of the rubber plantations removed understorey vegetation during weeding operations. Total ESA activity was also significantly higher (K–W test:  $\chi^2 = 1.74$ ,  $P = 0.04$ ) in rubber plantations without pesticide use ( $206.4 \pm 49.5$  passes/h) than those with regular pesticide use ( $65 \pm 4.1$ ). Total ESA and NSFD bat activity was on average much greater in plantations with mixed planting of old and new rubber varieties (162 and 18 passes/h), than in monocultures of new rubber varieties alone (97.8 and 9 passes/h).

## DISCUSSION

### Consistent Positive Effects of Forest Cover on Activity of Bat Guilds

Activity of all bat guilds was consistently higher in forests than in rubber plantations in the Shenduruney Wildlife Sanctuary landscape of Kerala's Western Ghats. Similar positive effects of forest cover have also been reported on insectivorous bats in other plantation agroforestry regions of the Western Ghats. For instance, Molur and Singh (2009) reported higher bat activity in forest fragments than coffee plantations in the Western Ghats of Kodagu. In the Anamalai hills, Wordley et al. (2015) also reported lower bat activity in tea plantations as compared to shade-coffee plantations and natural forests. Tea plantations with forest fragments had higher activity than tea plantations without, in their study.

Commercial rubber plantations have been a major driver of forest loss in tropical Asia (Kumar, 2005; Tata, 2010; Warren-Thomas et al., 2015, 2020; Chakraborty et al., 2018). Studies from Southeast Asia have reported mostly negative effects of commercial rubber plantations (Tata, 2010; Phommexay et al., 2011; Warren-Thomas et al., 2015, 2020) and oil palm (Struebig



**FIGURE 4 |** Comparison of effect sizes (mean  $\pm$  SE of parameter estimates: **Table 5**) of habitat variables on bat activity of the OSA, ESA, and NSFD guilds.

Understorey vegetation positively influenced activity of all bat guilds, but other variable effects differed. Variables explaining zero bat activity are denoted by blue error bars, and variables influencing non-zero bat activity are shown with red error bars.

et al., 2008, 2011; Mullin et al., 2020) on insectivorous bats. In Thailand, forest-dependent understorey-foraging bats (NSFD guild) were more diverse and abundant in forest fragments than rubber plantations (Furey et al., 2010; Phommexay et al., 2011; Warren-Thomas et al., 2015). Our findings for NSFD bats were very similar. But our hypothesis that activity of OSA and ESA bats would not differ between natural forests and plantations was not supported. This result contrasted with that of Heer et al. (2015), who reported indifferent or positive effects of rubber plantations on similar bat guilds in Brazil. This difference could be because of the much higher diversity of Neotropical bats, and also due

to the structurally complex nature of secondary vegetation in “rubber-forest plantations” and mixed rubber-cacao plantations, in their study. In contrast, most rubber plantations in our study area were monocultures.

In the observed general tendency of preference for natural forests and avoidance of rubber plantations, the landscape context mattered. Different bat guilds showed variable activity across habitat types in relation to the percentage of forest cover in surrounding buffers. Responses of insectivorous bats to individual habitat types depend on whether the surrounding landscape context is bat-friendly or not (Harvey and Villalobos,

2007; Williams-Guillén and Perfecto, 2011). Faria et al. (2007) found that shade coffee and cocoa plantations in the neotropics, when adjacent to forests, supported greater bat foraging activity. Our results for NSFD and ESA bats were similar to those of Weier et al. (2021), who reported low activity of narrow-space foraging bats in macadamia monocultures of South Africa and more use of macadamia plantations with natural edges by edge-space foraging bats. In the same landscape, open-space foragers used more human-modified habitats. For rubber-dominated regions in Southeast Asia, preserving forest cover in the surrounding landscapes had positive effects on biodiversity (He and Martin, 2015; Sreekar et al., 2016).

## Positive Effects of Understorey Vegetation on All Bat Guilds

Bat activity across the three guilds was generally higher when understorey vegetation was present in forests or plantations. This result is interesting and also surprising, because it highlights the importance of understorey vegetation for all bat guilds, irrespective of their foraging modes. Warren-Thomas et al. (2020) reported a strong positive effect of maintaining understorey in rubber plantations on multiple biodiversity elements. Such an overwhelming influence of understorey vegetation on bat activity across guilds could be due to higher insect abundance in undergrowth. Although, we could not sample insect abundance, understorey vegetation might significantly increase the abundance of insect prey for bats (Holloway et al., 1992; Phommexay et al., 2011). In Panama, in the dry-season, understorey vegetation had higher insect abundance than in clearings (Richards and Windsor, 2007). Rodríguez-San Pedro and Simonetti (2015) found that dense understorey in pine plantations supported higher bat activity along track edges. Understorey vegetation could lead to an aggregative effect on bats that may respond to concentration of insect prey in these habitats (Müller et al., 2012). Habitat types with understorey vegetation would thus support higher bat activity in turn. This was confirmed by our analysis of effects of rubber plantation management. Rainho et al. (2010) found that in spite of higher insect abundance in ground vegetation, dense vegetation cover might not allow bats to access insect prey in the undergrowth. Therefore, perhaps, rubber plantations that maintained moderate management levels and understorey shrub growth had higher bat activity than intensively managed plantations in our study.

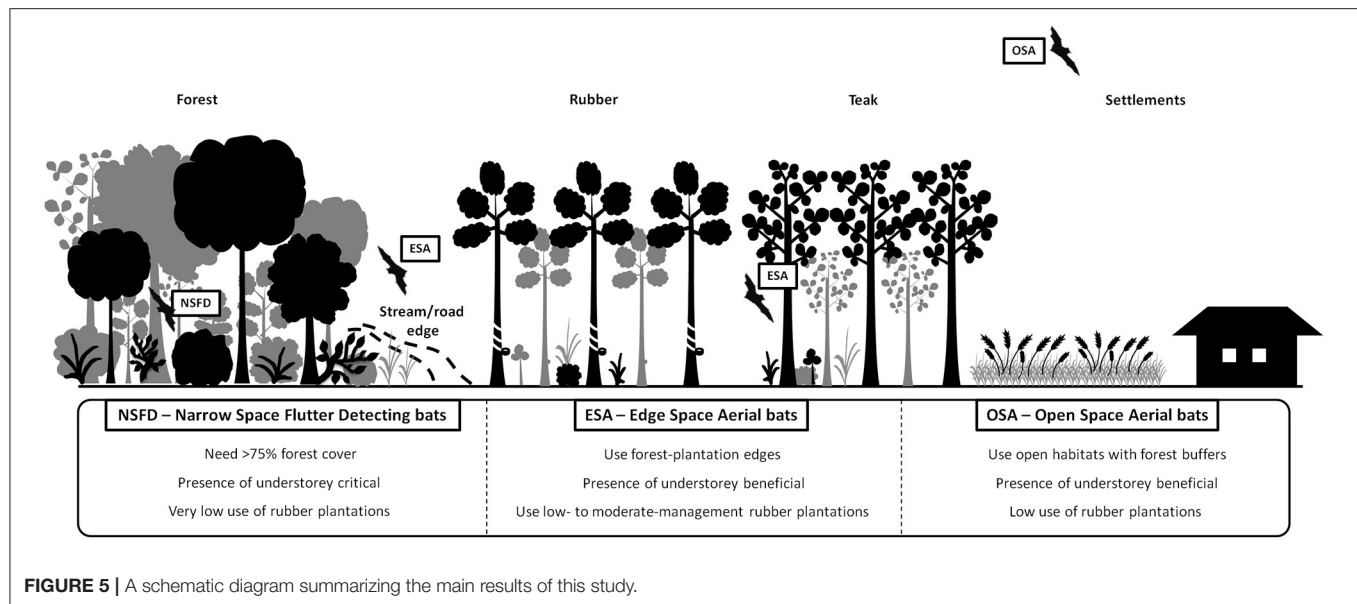
## Effects of Local Habitat Structure on Activity of Different Bat Guilds

OSA bats (families Emballonuridae and Molossidae) had higher activity in open habitat patches concurring with our hypothesis, but at the local scale. At the landscape scale, OSA activity was higher in buffers of high forest cover. This was not expected, although our result resonated with Frey-Ehrenbold et al. (2013), who found that even high-flying “long range echolocators” (similar to OSA) might be associated with vegetation structure in the landscape. We found that ESA bats (families Vespertilionidae and Miniopteridae) had the highest activity along stream

or road edges at forest-plantation boundaries, vindicating their description of being edge-space foragers (Denzinger and Schnitzler, 2013). ESA bats prefer streams at plantation edges due to the high abundance of riparian insect prey (Fukui et al., 2006; Ober and Hayes, 2008). They also use thinned plantations and clearings along plantation edges (Humes et al., 1999; Hein et al., 2009; Obrist et al., 2011; Lentini et al., 2012). Ambivalent responses of the ESA bat guild to local habitat structure could also be due to the high species diversity within the Vespertilionidae. Future guild-based studies can benefit from more detailed analysis of species-level responses particularly for ESA bats (Siemers and Schnitzler, 2004). NSFD bats (family Rhinolophidae) totally avoided open habitats but used deciduous teak plantation belts along forest edges. NSFD bats are generally known to occur along wooded edges of forests (Davy et al., 2007; Goiti et al., 2008). These results together suggest variable effects of vegetation structure and habitat edges on different bat guilds (Gehrt and Chelvig, 2003; Ducci et al., 2015), despite the consistent positive effects of forest cover at the landscape scale, and of understorey at the local scale (Figure 5).

## Influence of Plantation Management Practices on Bat Activity in Fragmented Landscapes

Obrist et al. (2011) found insectivorous bat activity to be higher in managed orchards than unmanaged ones, indicating a favorable effect of plantation management. Wickramasinghe et al. (2003) reported higher bat activity in organically managed than conventional farms. Lentini et al. (2012) and Williams-Guillén and Perfecto (2011) found that lower levels of plantation management benefited bat activity, which our results concur with. Frequent removal of understorey might have contributed to low bat activity due to poor availability of insect prey in intensively managed rubber plantations (as reported by He and Martin, 2015). Intensive plantation management might have also accelerated forest fragmentation by expansion of roads and village settlements, causing disturbances to movement corridors of bats (Berthinussen and Altringham, 2012). Management practices prevalent in rubber plantations have been intensifying in our study area (authors' observations). This may negatively affect potential ecosystem services from insectivorous bats for rubber plantations. It is also likely that bats avoiding rubber plantations might forage more in adjacent forests and agro-ecosystems, resulting in positive effects in terms of insect pest control services to the latter habitats. Conversely, the spread of intensively managed rubber monocultures could also depress existing bat activity and potential for insect pest control in other habitats. Anecdotal reports from local villagers in our study area indicated higher mosquito abundances in rubber plantations. Bat activity might also be important to control mosquito abundances (Gonsalves et al., 2013) and have potential implications for associated disease risks to people. Our results thus indicate that maintaining low to moderate levels of management might enable reductions in pest activity, while allowing bats to use rubber plantations with overall low environmental impacts. Such management can maximize commercial benefits from rubber



while securing insectivorous bat-generated ecosystem services (Häuser, 2016).

## Implications for Bat Conservation in Forest-Plantation Landscapes

Our paper contributes evidence that forest habitats and understorey vegetation may enhance bat activity in agroforestry plantation landscapes dominated by rubber monocultures. Despite the fact that the bulk of our data was collected in 2011–12, our study remains relevant given the current state of knowledge on impacts of land-use change from forests to rubber plantations on insectivorous bats. At present there are no studies from India on this issue, even though rubber plantations are expanding in many regions (Chakraborty et al., 2018). Our study may be one among only a few to identify criteria that may allow bat guilds to use rubber plantation-dominated regions, in relation to percent of remnant forest cover in the landscape, and maintenance of understorey vegetation in rubber plantations (Figure 5). By linking management practices to bat guild activity, our study provides an understanding of the conditions that may help sustain bat foraging and habitat use even in commercial rubber plantations. In Brazilian forest-rubber mosaics, intensively managed rubber-cacao plantations surprisingly had high bat diversity and abundance (Heer et al., 2015), possibly due to the mixed nature of these plantations. In our study area, plantations maintaining old rubber varieties along with new high-yielding varieties showed higher bat activity than rubber plantations with only new varieties (authors' field observations). To mitigate negative impacts of rubber plantations on bats, we suggest modification of management practices at multiple levels, including (1) protection of forest habitat buffers around rubber plantations, (2) maintenance of understorey vegetation in large, intensively managed rubber plantations, and (3) inter-cropping and organic management

practices in plantations. Insectivorous bats could also benefit if their ecosystem services toward controlling insect pests are valued in eco-certification for rubber plantations (Gouyon, 2003; Tata, 2010; Warren-Thomas et al., 2020). Hence, quantifying insect pest control (especially of beetle and moth pests) by insectivorous bat guilds in rubber plantations will be important in future studies. In conclusion, our findings emphasize that ecologically sensitive management of commercial agroforestry plantations can help conserve insectivorous bats and secure bat-generated ecosystem services to tropical agroforestry landscapes (Fitzherbert et al., 2008; Häuser, 2016).

## 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 animal study because the study was based on non-invasive acoustic sampling of insectivorous bats. To do this study, we had obtained research permits from the state Forest Department where we worked.

## AUTHOR CONTRIBUTIONS

KD: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft, writing – review and editing, visualization, project administration, and funding acquisition. NK: methodology, formal analysis, writing – review and editing, and visualization. JK: writing – review and editing, visualization, supervision, and resources. MS: methodology, writing – review and editing, visualization,



supervision, and resources. 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/fcsc.2021.751694/full#supplementary-material>

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# Sex-Biased Habitat Use by Phyllostomid Bats on Riparian Corridors in a Human Dominated Tropical Landscape

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Some animal species exhibit sex-specific patterns as an adaptation to their habitats, however, adaptability to a human-dominated landscape is commonly explored without considering intraspecific sexual differences. Differences between males and females lead to a sexual segregation in habitat use. In southern Mexico, we explored sex-specific responses to landscape modification of six common species of phyllostomid bats: *Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga soricina*, and *Platyrrhinus helleri* using riparian corridors within continuous forest and cattle pastures. Furthermore, we explored sex related responses to vegetation attributes (i.e., tree height and basal area) and seasonality (i.e., wet and dry seasons). Overall, capture rates were significantly skewed toward females and riparian corridors in pastures. Females of *G. soricina* exhibited a strong positive relationship with greater tree height and basal area. Seasonality was important for *A. lituratus* and *S. lilium* females, only. The results indicate a sexual driven response of bats to habitat modification. The high energetic demands of females associated to reproduction could lead to foraging into riparian corridors in pastures. The presence of large trees along riparian corridors in pastures may help maintaining a diverse and dynamic bat community in modified tropical landscapes.

**Keywords:** forest disturbance, bats, riparian corridors, tropical forests, sex ratio

## INTRODUCTION

The configuration of tropical landscapes is highly dynamic as a consequence of changes in land-use and cover (Mayaux et al., 2005; Fagan et al., 2013). A common feature in tropical agricultural landscapes is the presence of relict natural vegetation along streams which persists even when being exposed to long-term agricultural practices and small-scale land use changes (Lundy and Montgomery, 2010). Habitat disturbance can alter the spatial arrangement of critical resources for animals within a given landscape, potentially resulting in disrupted demographic patterns (e.g., sex-ratio, abundance, age classes, etc.) among habitat patches. The degree to which habitat disturbance



alters the demography of animal populations, however, should vary as a function of the behavioral plasticity of individual species (Bender et al., 1998; Nupp and Swihart, 2000).

Males and females of the same species may differ in several aspects of their biology (e.g., sexual dimorphism, different thermoregulatory strategies), which may result in sexual segregations of habitat use (Lintott et al., 2014) and/or between sex competition (Lemaître et al., 2014; Benítez-Malvido et al., 2016). Sexual segregation can be broadly categorized into the following types: habitat segregation and social segregation. Habitat segregation occurs where the sexes differ in the use of the physical environment, whilst social segregation when a species tends to form single-sex groups (Wearmouth and Sims, 2008). Habitat segregation hypothesis suggests that inherent sexual differences in reproductive strategies i.e., reproductive energy demands, breeding period and predation risk (Dietz et al., 2006; Nardone et al., 2015; Beerman et al., 2016; Benítez-Malvido et al., 2016) result in females trading off habitat quality in favor of offspring safety (Wearmouth and Sims, 2008).

Most studies on the effects of human-modified landscapes on bat communities have focused at the species level responses, while the potential importance of intra-specific differences are often ignored (Lintott et al., 2014). Bats are an ideal taxon for studying sexual segregation, since sexual dimorphism in bats is rare but sexual segregation is widespread (Senior et al., 2005). Seasonal and maternal sexual segregation have been documented for many bat species (Sgroi and Wilkins, 2010; Encarnação, 2012; Diamond and Diamond, 2014). In many tropical bat species, females in resource-rich habitats roost in groups with few or no males present (harem groups) (Ortega and Arita, 1999; McCracken and Wilkinson, 2000; Altringham, 2011). Particularly due to reproductive and parental costs, females have higher energy requirements, so they are less abundant in habitats with limited food resources (Racey et al., 1987; Ramos Pereira et al., 2010). Sex should be considered separately whenever possible in the study of bats because males and females of the same bat species may have different seasonal distribution and roosts with different characteristics (Broders et al., 2006; Safi et al., 2007; Weller et al., 2009). For instance, the response of two Neotropical frugivorous bats to local and landscape scale attributes were sex and seasonally specific; females were more abundant than males in edge and matrix habitats, and females seem to increase their foraging movements during pregnancy and low fruit availability (Rocha et al., 2017). In another study, bats showed sexual differences in the habitat use within urban landscapes, with males being more widely distributed and females more abundant in highly connected areas. Moreover, access to water was a limiting factor in determining female distribution (Lintott et al., 2014; Patriquin et al., 2019). The importance of fine-scale spatiotemporal and demographically precise data is essential for effective conservation strategies (Hutson et al., 2001; Russo et al., 2010; van Toor et al., 2011).

Habitat loss and fragmentation are important threats to bat populations as they eliminate or reduce suitable foraging habitats and forest structures for roost (Kingston, 2010). Information on the abundance and sex ratios of bat populations throughout the year is important for understanding their ecology in

periods of resource scarcity (Perry et al., 2010). Therefore, obtaining sex-specific information on the behavior and habitat requirements of bats should be one of the primary goals in conservation efforts (Weller et al., 2009; Perry et al., 2010). In order to understand the mechanisms by which some bat species are affected by habitat loss, it is necessary to determine not only if habitat disturbance affects life-history parameters, but also if habitat loss generates changes in their social structure. In this study we assessed six common species of phyllostomid bats to identify sex-related patterns within a human-dominated landscape. Our study provides insights into the importance of habitat type on sex ratio and on sex distribution throughout the year. The objective of this study was to determine if habitat affects bat sex ratio in a human dominated landscape in Southern Mexico. For this, we sampled individuals from six abundant bat species in conserved continuous forests and cattle pastures along and away from riparian corridors. We expected that because riparian corridors provide food, water and roosts, capture rates of females would be greater along them (Naiman et al., 2000). We hypothesized that sex specific differences in habitat use will be caused by the reproductive energetic demands in females (i.e., pregnancy and lactation). At the local scale, vegetation attributes such as tree height may affect female abundance, because females are frequently restricted to high-quality habitats for foraging (Lintott et al., 2014).

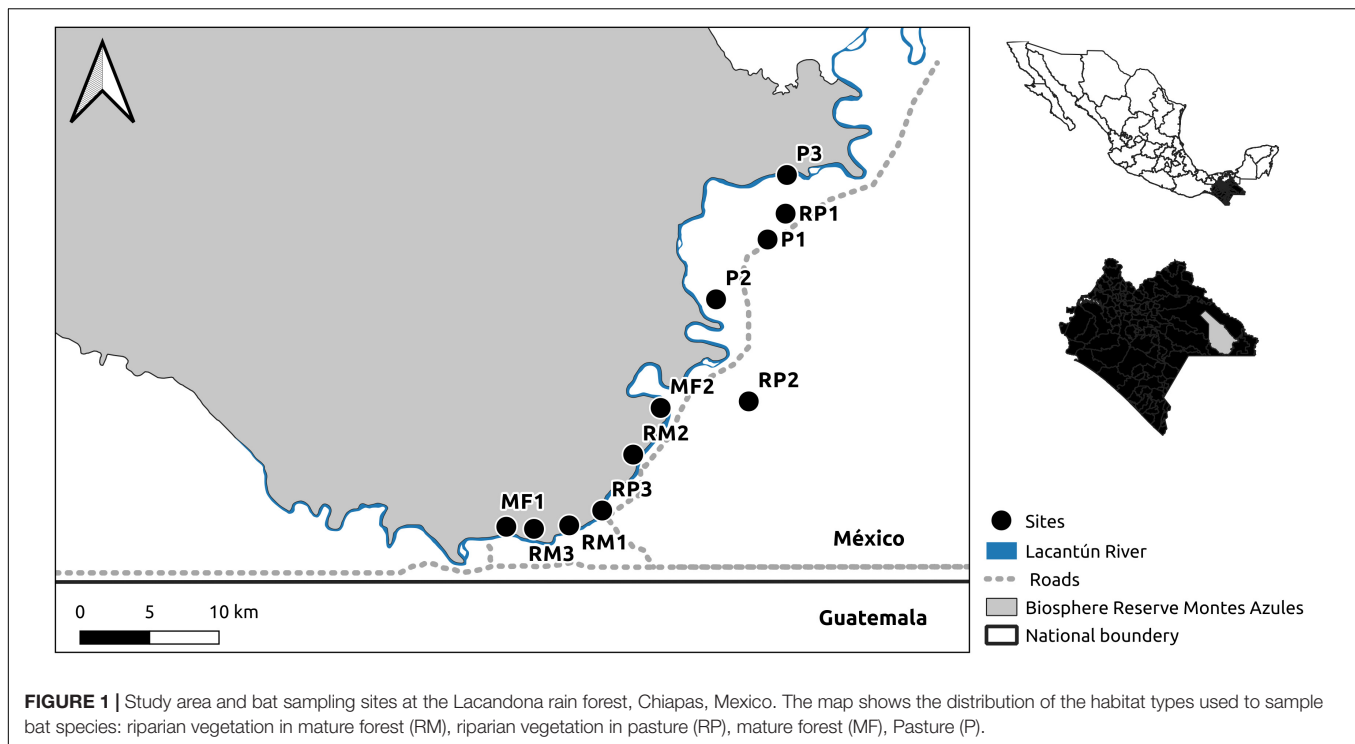
## MATERIALS AND METHODS

### Study Area

The study was carried out in the tropical region of Lacandona, south of the state of Chiapas, Mexico. The original vegetation consists mainly on lowland tropical rain forests. Deforestation of the region began in the 1970's, resulting in the reduction of old-growth continuous forest from 95% in 1976 to 56% in 1996 (De Jong et al., 2000); only 36% of the original old-growth continuous forest remains today (Carabias et al., 2012). Currently, the main land-use practices in the region consist of cattle pastures, the cultivation of maize and other crops (De Jong et al., 2000; Zermeño-Hernández et al., 2015). The resulting landscape comprise a mosaic of human-modified habitats that include semi-urban settlements, agricultural land, open pastures for cattle, riparian zones, patches of secondary and old-growth forests of various sizes. The region has a mean annual temperature of 24°C; average annual rainfall is 3,000 mm with June to October as the wettest months (551 mm month<sup>-1</sup>) and February to April as the driest months (<100 mm month<sup>-1</sup>) (Comisión Federal de Electricidad, 2006; van Breugel et al., 2006).

Four different habitat types were selected for this study including the following: (i) riparian habitat within old-growth continuous forest (RM); (ii) riparian habitat in active cattle pastures (RP); (iii) old-growth continuous forest 1,000 m away from riparian vegetation (MF); and (iv) active cattle pastures (P) 1,000 m away from riparian vegetation. For a total of 12 sampling sites. Each habitat type was replicated three times and study sites were at least 1.5 km away from each other (**Figure 1**).





Streams were all permanent (although with variable amounts of running water throughout the year) while stream width varied from 2 to 8 m. Study sites in pastures were active cattle pastures, although these sites were predominantly devoid of a tree cover, all sites had isolated trees and a few trees that serve as live fences. It is common that isolated trees are left standing to provide shade for cattle, firewood for cooking, or for aesthetic reasons (Galindo-González et al., 2000). The cattle pastures were located in the Marqués de Comillas municipality, on the south side of the Lacantún River. Old-growth continuous forest sites were located in the 330,000 ha Montes Azules Biosphere Reserve (MABR) on the north side of the river (16°04' N to 90°45' W; INE, 2000, Figure 1).

## Bat Sampling

Sampling of bats was conducted twice during the dry season (December to May) and twice during the wet season (June to November) for 3 consecutive years (2011, 2012, and 2013), using a standardized method of four nights per site. A previous study in the same locations showed that over 70 sampling nights, 34 during the dry season and 36 during the rainy season, a total of 1,752 individuals belonging to 28 species of Phyllostomidae were captured (de la Peña-Cuéllar et al., 2015). For this study however, we considered the six most abundant species of phyllostomid bats in the region, including the following: *Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Carollia perspicillata*, *Glossophaga soricina*, and *Platyrrhinus helleri*, the minimum number of captures needed to be considered in the study were one capture per habitat per season, species abundance cut off of  $n = 60$ .

Five nets (12 m long  $\times$  2.6 m high) were set at ground level and were opened at dusk (1800–1830) for four consecutive

hours, which corresponds to the peak foraging time for most phyllostomid species (La Val, 1970). The bat sampling nets were arranged according to habitat type: (1) in the riparian habitats (including continuous forest and pastures), nets were located parallel and/or diagonally across the stream, depending on site characteristics; (2) in continuous forest, nets were positioned across natural flying corridors; (3) in active pastures, nets were located under the canopy of isolated trees. In all sites we searched for similar physical characteristics that allow the same mist net arrangement, this is one individual net and two pairs of nets in an “L” shape (two nets connected perpendicularly). Nets were located ca. 50 m apart. Nights with a full moon or heavy rain were avoided during bat sampling in order to prevent variation in capture success associated with these conditions (Morrison, 1978). Captured individuals were temporarily stored in cloth bags and identified to species following Medellín et al. (2011). For all captured bats, we determined sex by inspecting genitalia (Racey and Speakman, 1987). In females, we detected pregnancy by palpation (Racey and Speakman, 1987), and lactation by the occurrence of enlarged nipples surrounded by a hairless skin area and by extruding milk with a gentle finger pressure on the nipple base. Sex ratio was calculated as the ratio of males to females in each site (Russo et al., 2010).

There is a risk of exposure to some significant zoonotic agents for any person handling bats in the field, following biosecurity recommendations (Newman et al., 2011). For this, all participants that sampled bats were appropriately trained to handle bats; bites and scratches were avoided by using leather gloves, previous anti-rabies vaccination and hand washing before and after bat manipulation.

## Vegetation Structure

To determine the influence of vegetation structure on the abundance of male and female bats, for each site we recorded all trees  $\geq 10$  cm diameter at breast height (dbh) within a 0.1 ha (20 × 50 m) plot (Gentry, 1982). Transects were located along streams in riparian continuous forest and riparian pasture habitats and randomly located in continuous forest and pasture habitats. We considered the following vegetation attributes: density of individuals, species richness, forest basal area, and tree height.

## Data Analyses

First, we compared capture rates for each sex among habitat types by using a standardized capture rate (captures/1,000 mist net hour) that compensated for differences in number of nets, size of nets and length of time nets were open (Perry et al., 2010). We compared capture rates using analysis of variance on ranks (ANOVA). Data were checked to meet assumption of homoscedasticity and normality. We performed non-metric multidimensional scaling analyses (NMDS) based on the identity and abundance of tree species occurring in the sampling sites, to obtain a continuous synthetic variable summarizing dissimilarity patterns among vegetation species composition. The matrix used in the analysis was built using the Bray-Curtis index (Magurran, 2004). This iterative method of ordination has the advantage of properly handling non-linear species response of any shape (Oksanen, 2013) and has a good performance even when beta diversity is high (McCune and Grace, 2002). It is one of the preferred ordination methods for analyzing community data (McCune and Grace, 2002). The scores of axis 1 were used as an explanatory variable for evaluating differential sex response to tree species composition. Second, we fitted a general linear mixed model (GLMM) for each species separately with binomial error distribution and logit link function to determine the influence of vegetation traits on male and female abundance. In order to assess the relative effects of the explanatory variables on males in comparison to females, the model was run with the proportion of females to males per night ( $n = 70$ ) as the response variable, with “site” as a random factor (Lintott et al., 2014). We considered the following explanatory variables: habitat type; season (dry and rainy), Vba, forest basal area per site; Vab, total number of trees; Vrich, trees species richness; Vh, average tree height; Vspcomp, scores of NMDS axis 1 (see **Supplementary Tables 1, 2**). For each model, we calculated Akaike’s information criterion (AICc) corrected for small sample size following (Burnham and Anderson, 2004). This approach allowed us to select the most plausible models from a set of models. The set of models considered for every response variable, at each scale, included the null model (without explanatory power) and other models that considered each explanatory variable independently. We compared the model using  $\Delta i$ , which is the difference of AICc between a given model and the best (lowest AICc) model. We also calculate the AIC weights ( $w_i$ ) for each model. The  $w_i$  represents the weight of the evidence that a certain model is the best model given the data and the set of candidate models. The 95% confidence set of the best models was defined by summing the

$w_i$ , from the largest to the smallest, until the sum is = 0.95. Only models with an AICc lower than the null model were considered to define the 95% confidence set of plausible models.

All analyses were performed with R v. 1.0.136 (R Core Team, 2019).

## RESULTS

### Sex Proportion

We completed 70 nights of capture effort, 34 during the dry season, and 36 during the rainy season, resulting in a total capture effort of 180 net hours in RM, RP, and P, and 140 net hours in MF habitats. The total number of captures of the six most common bat species was 1,365 individuals (78% of all captures) including the following: *Artibeus jamaicensis* ( $n = 199$ , 11%), *Artibeus lituratus* ( $n = 396$ , 23%), *Sturnira lilium* ( $n = 521$ , 30%), *Carollia perspicillata* ( $n = 60$ , 3%), *Glossophaga soricina* ( $n = 109$ , 6%) and *Platyrrhinus helleri* ( $n = 81$ , 5%). These species were also present at all study sites. Overall, 43% of the sampled individuals from the species considered were males, while 57% were females, 1.131 proportion of females to males. The capture rates were significantly skewed toward females ( $F = 5.282$ ,  $P < 0.001$ ) (**Figure 2**). Riparian pasture, was the habitat with the highest female capture rates (433 individuals, 2.14 capture rate), followed by riparian continuous forest (152, 0.75) and active pasture (141, 0.69). Continuous forest was the habitat with the lowest female capture rates (50, 0.28) (**Figure 2**).

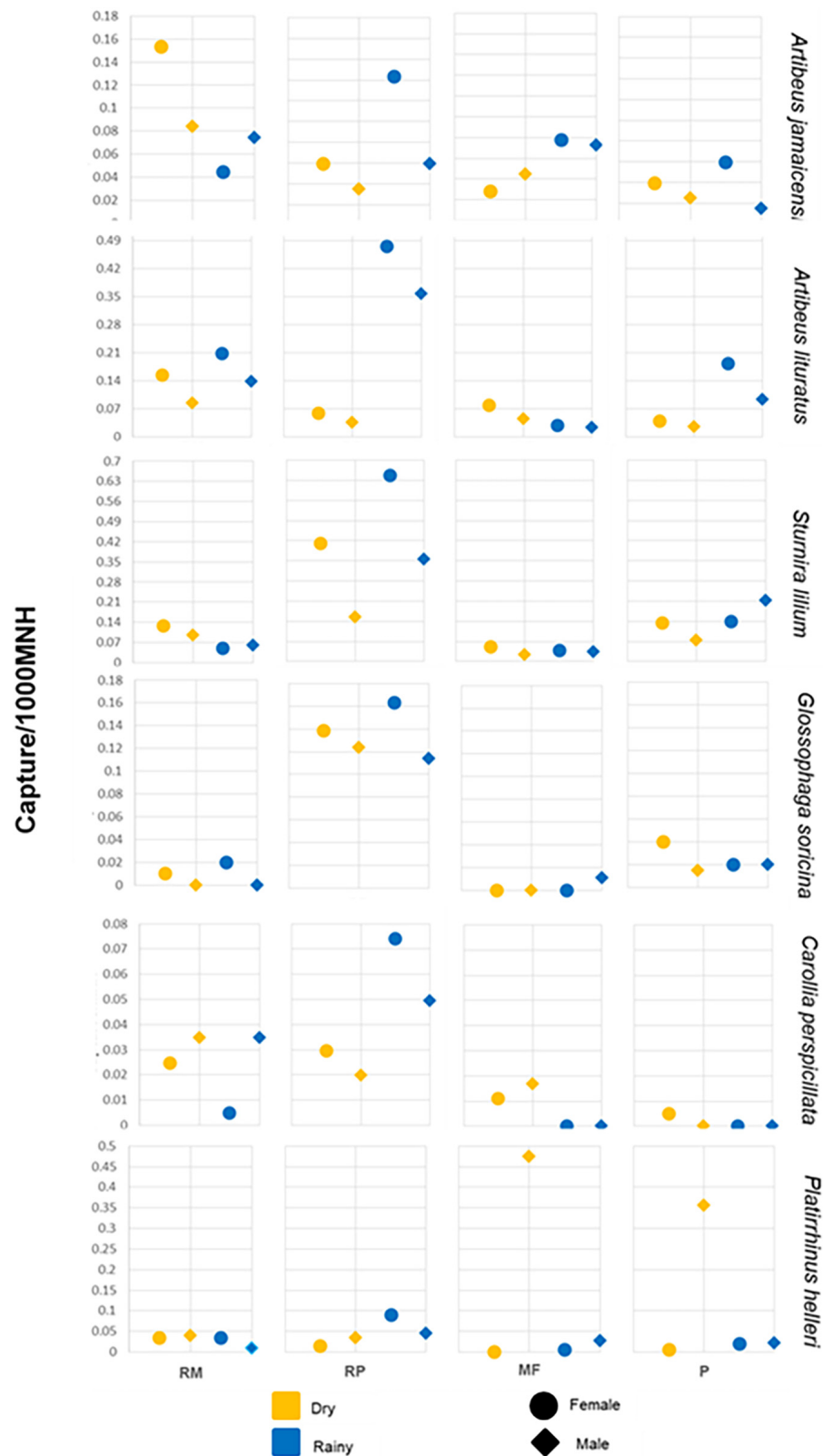
### Vegetation Attributes and Seasonality Response

Riparian habitats in mature forests (RM) and pastures (RP) showed higher vegetation structural complexity than non-riparian habitats. Despite of the fact that RM contained more trees than RP, these habitats showed similar average canopy height (**Table 1**), whereas the lowest canopy height was recorded in pastures. On the other hand, basal area was greater in riparian habitats than in non-riparian habitats, in both old-growth forests and pastures (**Table 1**). The biplot resulting of NMDS ordination is in **Supplementary Figure 1**.

Seasonality and habitat type were the best explanatory variables describing the presence of *A. lituratus* females; while for *S. lilium*, tree species composition and seasonality appeared as the most important variables explaining the incidence of females. In the case of *G. soricina* we found that the presence of females was positively related to vegetation structure including forest basal area and average tree height (**Table 2**). The results for all species are in **Supplementary Table 3**.

## DISCUSSION

Overall, the results showed that males and females of the selected bat species cope differently with habitat disturbance. Sex ratio was skewed toward females, which is an expected pattern for harem species (*A. jamaicensis* and *A. lituratus*) (de Mello and Fernandez, 2000). Furthermore, the results provide insights into



**FIGURE 2 |** Capture rate (bats/mist net hour) of males and females of six bat species across different habitat types at the Lacandona rain forest during the dry and rainy seasons.

**TABLE 1 |** Tree community attributes in four different tropical habitat types replicated three times, Chiapas, Mexico.

Vegetation attributes	Riparian vegetation in mature forest (RM)	Riparian vegetation in pasture (RP)	Mature forest (MF)	Pasture (P)
Number of individuals	182	101	55	37
Number of species	46	46	29	17
Average basal area (m <sup>2</sup> ha <sup>-1</sup> )	25639.51	20285.77	6241.88	8561.030
Average tree height (m)	13.63	13.12	10.69	9.70

The values correspond to 10, 50 × 2 m transects (0.1 ha) per site per habitat type. Only trees with diameters at breast height > 10 cm were considered.

**TABLE 2 |** Results of Akaike information criterion (AIC)-based model selection, assessing the association between the proportion of females to males of three bat species with seasonality and vegetation attributes.

Bat species	Factor	K	logLik	AICc	Δi	wi
<i>Artibeus lituratus</i>	Season	3	-72.49	151.35	0.00	1
<i>Sturnira lilium</i>	Tree species composition	3	-86.88	180.12	0.00	0.88
	Season	3	-89.03	184.42	4.30	0.10
<i>Glossophaga soricina</i>	Total forest basal area	3	-26.45	59.27	0.00	0.63
	Average height of trees	3	-28.23	62.82	3.55	0.11

Confidence set of plausible models (95%) explaining the variation in the response variables. Only highest ranked models explaining gender variation for each species are shown.

K, number of estimated parameters; logLik, log-likelihood; AICc, sampled-sized adjusted Akaike information criterion; Δi, Akaike differences; wi, Akaike weights. Response variable: proportion of females to males per night. Explanatory variables: habitat, season (rainy, dry), tree species composition (using scores of NMDS axis), total forest basal area at each site, average height of trees at each site.

the relative importance of habitat type for a specific sex. Except for mature forest, overall capture rates of females were greater than those of males, for the six studied species implying that during reproductive period, females of some bat species, may increase their activity in these habitats (e.g., foraging and/or drinking). Female bats can show changes in foraging activity probably due to lactation when energy and water requirements increase (Adams and Hayes, 2008; Barclay, 2012).

Unlike males, females need to return at night to the maternity roosts to nurse their young which probably limits female foraging areas and restricts foraging females to the rewarding areas located in the proximity of their roosts (van Toor et al., 2011). Moreover, males may have greater survival than females (Keen and Hitchcock, 1980; Kurta and Matson, 1980), because males are not subject to the additional energetic pressures associated with pregnancy and lactation. For instance, in arid environments the drinking passes of lactating female bats were significantly higher than those of non-reproductive adult females, thus, survival of reproductive female bats seems to be conditioned to the availability or frequent and uninterrupted access to free-standing water sources (Adams and Hayes, 2008). We found that capture rates in active pastures were predominately toward females. The prevalence of females may be related to the high energy demanding of flying in cluttered habitat than flying in more open areas (Grodzinski et al., 2009), due to the elevated energetic costs

associated with higher vegetation complexity might represent a particularly high burden for females during pregnancy and while nursing, males otherwise prefer sites with greater vegetation cover possibly related to roost defense (Henry and Kalko, 2007; Rocha et al., 2017).

## Sex Ratio and Vegetation Structure

Contrary to our hypothesis, we found that females of *A. lituratus* did not exhibit relationship with habitat quality. The largest species of Stenodermatinae is *A. lituratus*, and as in other mammals, larger species could be more sensitive to human habitat disturbance (Lande, 1987). Nevertheless, the high number of females in this bat species, reflects selective foraging in a resource rich environment and higher roost availability in forested habitats. Even though *Artibeus* species may cross inhospitable matrix areas in fragmented landscapes, covering different vegetation types and flying distances ranging from 5 to 10 km (Galindo-González, 1998), females of *A. lituratus* might locally depend on temporal foliar roosts, and prefer larger trees within the dense and shaded mature forest that can provide energetic and thermal requirements to leave the young while foraging (Evelyn and Stiles, 2003; Bianconi et al., 2006; Arnone et al., 2016). For the same study area, *A. lituratus* has shown to select roosts with high humidity located in trees with the greatest basal areas (Ortiz-Ramírez et al., 2006).

Furthermore, some studies have argued that Glossophaginae are resilient to land use change (Willig et al., 2007). Our data indicate that the presence of *G. soricina* females is significantly and positively correlated to vegetation attributes such as tree height and forest basal area, supporting the idea that the species is an habitat specialist (Aguilar et al., 2014). The association between females of *G. soricina* with large trees could be due to the fact that large trees provide greater availability of roosts and foraging opportunities (Evelyn and Stiles, 2003; Ortiz-Ramírez et al., 2006). There is evidence showing food differentiation between specimens of *G. soricina* in the same areas where females preferred a plant food item different from males (Alvarez and Sánchez-Casas, 1999). During pregnancy and breeding seasons females might feed on the nearest available resource, whereas males fly larger distances in search of other feeding areas (Sosa et al., 1996). This foraging behavior might reduce the activity of *G. soricina* to habitats with high resource availability limiting its activity to small home ranges increasing its susceptibility to local extinction (Arita and Santos-del-Prado, 1999). This increases the importance of vegetation traits associated to the reproductive energetic demand (pregnancy, lactation and roost defense) (Charles-Dominique, 1991; Klingbeil and Willig, 2010).

Tree species composition was the strongest predictor variable for *S. lilium*, this frugivorous bat is known for its preference for understory shrubs and pioneer tree species, females of *S. lilium* are able to forage among forest elements as a result of non-random distribution of resources across the landscape (Loayza and Loiselle, 2008). Moreover, frugivorous bats like *S. lilium* which can visit different vegetation types can be considered as indicator taxa of habitat change in riparian vegetation, rather than highly specialized taxa in which population decline rapidly under environmental changes (de la Peña-Cuéllar et al., 2015).



## Sex Ratio and Seasonality

The importance of seasonality for *A. lituratus* and *S. lilium* females might reside on differences in abundance and diversity of food resources between the wet and dry seasons. Seasonal fluctuations in rainfall influence phenology of fruiting plants and affects productivity in tropical forests (Ramos Pereira et al., 2010). In tropical regions, usually the rainy season corresponds to greatest fruit abundance than the dry season (Smythe, 1986). Even, many tropical bats timing their reproductive phenology to match periods of peak food availability, female bats may be constrained by the energetic requirements associates with reproduction, which might force them to alter their foraging behavior (Lintott et al., 2014). Resource availability due to seasonality can result in shortened flights during the exploration for food and shelter, whereas during the dry season when food resources are often scarce, females respond to local-scale vegetation structure increasing foraging movements into resource-rich pioneer fruiting plant species areas like secondary forests, while males tend to select areas close to old-growth forests (Rocha et al., 2017).

## Implications for Conservation

Our results show that responses of bat to human disturbance are sex-specific. Taking into account sex ratios of bat populations may help to a better understanding of the pervasive consequences of habitat loss and fragmentation. Sex-specific studies are important for bat conservation practices in order to promote habitat conditions favorable for both, females and males (Perry et al., 2007). Vegetation attributes like three height and basal area reflect the age and vertical complexity of forest, and more varied niche opportunities for bats, enhancing greater taxonomic and phylogenetic biodiversity (Martins et al., 2017). Our results suggest that the structural complexity of the vegetation and large trees influence the presence of females of *G. soricina*. In this sense, management efforts should promote riparian vegetation cover with large forest basal areas, important for the conservation of the entire bat community. Even though our analysis was restricted to six common bat species, we assumed that the maintenance of habitats that favor habitat generalist species should also benefit bat species that are habitat specialists (Istvancko et al., 2016; Rocha et al., 2018). Therefore, we encourage the inclusion of species of sensitive trophic guilds (gleaning insectivores and carnivores) and particularly roosting habits emphasizing adequate protection of females in conservation plans. Conservation actions toward female protection are particularly important due to their high level of parental investment associated with rearing pups (Istvancko et al., 2016). Management decisions that do not guarantee the protection of the habitat frequently used by female bats would likely have detrimental long term consequences on their reproduction, jeopardizing the dynamics and long-term persistence (van Toor et al., 2011; Frank et al., 2016).

In human dominated landscapes, the presence of isolated trees in pasture promote bat flights across pasture and increase bat detectability (Galindo-González et al., 2000), based on foraging behavior frugivorous bats travel across pastures and visit isolated trees while foraging, and use canopies for roosts

or to decrease predation risks (Galindo-González, 1998), also isolated trees in pastures act as stepping stones for traveling across fragmented landscapes to different forest remnants (Guevara et al., 1989). However, pastures cannot sustain the same species richness of bats as old-growth forest and riparian vegetation (de la Peña-Cuéllar et al., 2015). Moreover, land use change in tropical landscapes seems to have considerable effects on bat population dynamics, for instance evidence suggests that forest-adapted insectivorous species are particularly sensitive to habitat conversion (Medellín et al., 2000; Williams-Guillén and Perfecto, 2010). Furthermore, frugivorous bats respond to matrix quality in different manners, whereas studies have found that frugivorous abundance was positively associated with the proportion of high quality habitats (Pinto and Keitt, 2008; Avila-Cabadilla et al., 2012; de la Peña-Cuéllar et al., 2015), some other studies have shown that frugivorous bat richness and abundance are higher in moderately fragmented landscapes than in old-growth forest (Willig et al., 2007; Klingbeil and Willig, 2009). Overall agricultural intensification may cause detrimental effects on bats and thus presumably on the ecosystem services they provide (Williams-Guillén et al., 2015). Additional research is needed to directly examine the effects of pregnancy and lactation on habitat selection by bats. We encourage radio-tracking studies that can show specific habitat use of males and females (roost and foraging areas) and if there is temporal segregation between sexes; this could provide information about how different habitats have an impact in the demography of bat 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

Ethical review and approval was not required for the animal study because the handling was very brief and we did not perform animal sacrifices.

## AUTHOR CONTRIBUTIONS

EP-C and JB-M conceived and designed the experiments, contributed reagents, materials, and analysis tools, wrote the manuscript, and revised the manuscript. EP-C performed the experiments and analyzed the data. Both 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.2021.741069/full#supplementary-material>

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# Anthropogenic Light, Noise, and Vegetation Cover Differentially Impact Different Foraging Guilds of Bat on an Opencast Mine in South Africa

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Bats are known to be sensitive to changes in their environment. The impact of natural vegetation cover, artificial light intensity and noise (dBA) were investigated on the bat community on the opencast Venetia diamond mine using mixed-effects models. Clutter-feeding bats were virtually absent compared to surrounding natural habitats, suggesting the negative impact of vegetation removal and/or light and/or noise pollution. Mixed-effect models revealed that natural vegetation was the most important factor impacting species richness and overall bat activity. In general, bat activity of both open-air and clutter-edge foragers was negatively impacted over areas close to mining operations that were devoid of vegetation cover. Artificial light only significantly affected feeding activity with less feeding activity in the lit areas. Anthropogenic noise had no significant impact on bat activity and species richness. Our study highlights the importance of vegetation cover and the complexity of the interaction between bats and the environment incorporating anthropogenic factors (artificial lighting, continuous noise, and habitat degradation) and natural factors such as minimum temperature, moon phase, and season that confound trends in bat species richness and responses in relation to opencast mining.

**Keywords:** chiroptera, anthropogenic light, noise, bat behaviour, opencast mining, bat ecology

## INTRODUCTION

Anthropogenic developments expose bats to habitat alterations and a range of pollutants, to which bats are known to be sensitive (Jones et al., 2009; Naidoo et al., 2016; Frick et al., 2019). Opencast mining allows the study of the effects of habitat degradation due to the physical removal of natural habitat and continual noise and nighttime light pollution. It is generally accepted that bats exhibit trait-based responses to these habitat-specific environmental changes based on morphology, such as differences in wing shape and associated echolocation call (Aldridge and Rautenbach, 1987; Schoeman, 2015; Jung and Threlfall, 2018), as well as sensitivities of audiological and visual systems (Schaub et al., 2008; Eklöf et al., 2014; Luo et al., 2015; Haddock et al., 2019; Finch et al., 2020), and by shifts in behaviour and community structure due to differential roosting and feeding

preferences of different foraging groups: open air, clutter edge, and clutter (Norberg and Rayner, 1987; Bader et al., 2015; Monadjem et al., 2020). Combined, these aspects governing responses of bats to alterations in their environment could result in physiological changes. For example, bats that benefit from foraging around artificial light sources have shown higher blood metabolite levels ( $\beta$ -hydroxybutyrate) early in the evening compared to species that do not forage around lights (Cravens and Boyles, 2019).

Many studies have focused on the impacts of noise and light individually on bat behaviour, predominantly in a laboratory setting, focusing on a single or select few species. Some exceptions have investigated these impacts in the field in habitats that are naturally dark and lit for experimental purposes (Stone et al., 2009; Minnaar et al., 2014; Bailey et al., 2019) or areas that experience temporary lighting depending on human activities, e.g., at stadiums (Schoeman, 2015). The response of bats to light and noise in their environment is species-specific (Schaub et al., 2008; Stone et al., 2009).

Artificial night time lighting delays and reduces the number of bats emerging from their roosts (Boldogh et al., 2007), influences species-specific foraging behaviour (Minnaar et al., 2014; Stone et al., 2015; Lewanzik, 2017; Bailey et al., 2019; Salinas-Ramos et al., 2021), affects commuting behaviour (Stone et al., 2009, 2015; Gaston et al., 2013; Lewanzik, 2017), interferes with navigation (Lewanzik, 2017; Lewanzik and Voigt, 2017), and could affect the stability of bat communities through competitive exclusion (Arlettaz et al., 2000; Stone et al., 2015). If adults have to forage further afield from maternity roosts, the resulting higher energetic cost and decreased foraging time could negatively impact the growth rates of young bats (Stone et al., 2015; Lewanzik, 2017). Artificial lighting can thus create “barriers” that may limit the effective dispersal of species, isolating habitat patches and populations from immigration and reduce the connectivity of habitats in the landscape, e.g., *Rhinolophus hipposideros* (Stone et al., 2009; Gaston and Bennie, 2014). Many bat species appear to be intolerant of light and avoid lit areas, particularly slow-flying highly manoeuvrable species that feed within cluttered spaces (clutter foragers) of the genera *Rhinolophus* and *Hipposideros* (Lewanzik and Voigt, 2017). In general, they are accepted to be intolerant of light and avoid lit areas due to the sensitivity of their eyes to light (and ultraviolet) that may lead to potential vision impairment in lit areas (Jones et al., 2009; Lewanzik, 2017).

Bats are known auditory specialists (Lattenkamp et al., 2020), with excellent hearing over several octaves, with the greatest sensitivity in species-specific high-frequency ultrasonic echolocation call spectral ranges, although there is evidence for aural sensitivity to lower frequency sounds to eavesdrop on prey-generated sounds or to hear low-frequency isolation calls of pups, e.g., *Rhinolophus ferrumequinum* (Bohn et al., 2006). Foraging success can be impeded by auditory conflicts resulting from anthropogenic or natural noise that has spectral ranges similar to that of any given species of echolocating bat or species that rely on the sounds produced by prey (mating calls and movement) (Simmons et al., 1978; Schaub et al., 2008; Gomes et al., 2016). Sounds that overlap with bats auditory cues, and sounds with

properties (including loudness and intensity) that fall within the sensitive auditory range of bats could be intolerable to bats and are avoided. These sounds can cause stress, reduce attention, disrupt biological processes (e.g., communication) and mask auditory perceptions (acoustic masking) (Bunkley and Barber, 2015; Luo et al., 2015; Gomes et al., 2016; Geipel et al., 2019).

The response of bats to noise seems to be not only species and individual specific but is also dependent on the behavioural context (Schaub et al., 2008; Luo et al., 2014, 2015). For example, under laboratory conditions, *M. myotis* avoided the playback sound stimulus and actively avoided foraging areas that were heavily impacted by noise (Schaub et al., 2008). Conversely, during rest (torpid period), *M. myotis* quickly habituated to anthropogenic noise exposure (Luo et al., 2014). Species that rely on passive listening to locate prey are expected to avoid foraging habitats degraded by anthropogenic noise such as *M. blythii*, *M. evotis*, *M. septentrionalis*, *Eudermis maculatum*, and species from the genera *Plecotus* and *Corynorhinus* (Schaub et al., 2008; Bunkley and Barber, 2015). Few field studies show how traffic noise (Luo et al., 2014; Finch et al., 2020) and noise associated with natural gas extraction (Bunkley et al., 2015) impacts bat ecology. Ambient noise (less than and greater than 20 kHz) can provide a greater challenge for insectivorous bats which have been shown to actively avoid noise stimulus even if the noise characteristics does not overlap with echolocation calls, resulting in reduced foraging activity (Luo et al., 2015; Finch et al., 2020).

Studies on the effects of large-scale opencast mining activities on bat communities in tropical regions are scant and few exist for temperate regions (see Armstrong, 2010; Duarte et al., 2015; Theobald et al., 2020). Factors shown to influence total bat activity and species richness included distance from the boundary of the mine, woodland cover, climatic variables (Theobald et al., 2020) and machinery noise negatively impacting soundscape complexity (Duarte et al., 2015).

We investigated the impact of artificial lighting, noise and natural vegetation cover on bat activity and behaviour in relation to opencast diamond mining at Venetia Mine in the Limpopo River Valley. Compared with most studies which investigate light and noise separately, we investigated the effects of light and noise together in the field, taking vegetation structure, moon phase, minimum temperature ( $^{\circ}\text{C}$ ) and season into account. Based on the literature above, we predicted that clutter and clutter-edge forager bats might avoid well-lit, noisy areas with low vegetation cover. In contrast, we expect open-air foragers that fly above the canopy may be unaffected by noise and low vegetation cover but that they might increase feeding activity over well-lit areas due to an increase in insects attracted to lights.

## MATERIALS AND METHODS

### Study Site

The study was conducted on the footprint of the opencast Venetia diamond mine ( $-22.427708^{\circ}$ ,  $29.324158^{\circ}$ ) over 21 nights during March 2019 (early autumn) and September 2019 (early spring). The Venetia diamond mine is situated in the northern Limpopo River Valley, approximately 60 km north of

the Soutpansberg mountain range (**Figure 1**). Mining-related activities began in 1984 and the mine was fully operational since 1992.<sup>1</sup> Mining operations are active 24 h a day. The mine is located in the Limpopo Ridge Bushveld (Mucina and Rutherford, 2011) and is restricted to a kimberlite pipe containing the diamonds (Brown et al., 2009). The Limpopo Ridge Bushveld is dominated by Mopane (*Colophospermum mopane*), Red Bushwillow (*Combretum apiculatum*), and Purple-pod Cluster-leaf (*Terminalia prunoides*) with a handful of other iconic tree species such as Knobthorn (*Senegalia nigrescens*), Marula (*Sclerocarya birrea*), and Baobab (*Adansonia digitata*) (Mucina and Rutherford, 2011). The area is considered subtropical and semi-arid. The climate is characterised by hot dry winters and hot summers with mean annual precipitation between 300 and 400 mm falling predominantly during the summer (Mucina and Rutherford, 2011).

## Light Transect Location and Luminosity Measurements

The *in situ* lighting on the mine was used to identify the impact of light along a gradient. Six SM4BAT FS recorders (Wildlife Acoustics, Inc., Maynard, United States) with SMM-U1 ultrasonic microphones mounted approximately 6 m above the ground and fitted with two 64 GB SDXC cards were placed approximately 100 m apart along a light gradient. The transect began from the floodlights near several workshops and the processing plant and extended in a straight line from the mine into darker areas (**Figure 1**). The specific positioning of the transect ensured that the effect of water was eliminated to prevent an over-representation of activity at a given site. Bats are known to be attracted to artificial water points in semi-arid regions in the absence of larger, natural water sources (Taylor et al., 2020). Bat detector 01 was placed in an area that was exposed directly to a harsh white light from the workshop buildings as well as an orange floodlight from a nearby conveyer belt system (~36 m away). Bat detector 02 was positioned in an area that was exposed to direct light from an orange floodlight at the processing area. Bat detector 03 was placed on the edge of the processing plant in an open-air storage area. Bat detector 04 was placed at the edge of the mining footprint to the southwest of the processing plant. Bat detectors 05 and 06 were placed furthest away from the processing plant extending into natural vegetation.

Light intensity (maximum luminosity) at each site was recorded and presented as the measurement lux using a handheld digital lux meter (ME-GM1020 Digital Lux Meter) held ~2 m above the ground with the light-sensitive sphere pointing toward the light source. Maximum luminosity was recorded as this would in effect be what the bats are exposed to when flying through lit patches. At bat detectors 04, 05, and 06, spill-over light was measured in lit areas within the vegetation as the vegetation had effectively created dark spots where luminosity was recorded as 0.0 lux. Due to logistic constraints, light measurements could not be taken each night. Light intensity readings (maximum lux) were recorded on the initial nights of the transect installations during

March and September 2019 after the sun had set and the horizon no longer had the glow of the setting sun.

## Noise Frequencies and Sound Pressure Levels

The primary source of noise that bats would be exposed to was the constant noise from the processing plant (crusher and conveyor systems). There would also be intermittent noise from trucks and earth-moving plant (engine noises, reverse alarms) and loading and offloading of material. From the recorded bat call files, the continuous noise levels that the bats would have been exposed to at each bat detector per night were extracted from all the .WAV files. The Noise Analysis tool in Kaleidoscope Pro<sup>2</sup> was used to determine the maximum sound pressure level (SPL) of the mine at each bat detector from the .WAV files. The analysis was followed in accordance with the guidelines suggested by Wildlife Acoustics.<sup>3</sup> We selected the standard A-weighted frequency band (covering the audible frequency range from 20 Hz to 20 kHz) to be analysed, as this would provide a frequency response curve typical to how a human ear would perceive the ambient noise of the mine and is considered ideal for bat hearing ranges (Bunkley and Barber, 2015). We required the scale of the SPL output results to be in relation to the international reference pressure (auditory threshold) of 0 dB (SPL) = 20  $\mu$ Pa (sound pressure), where 1 Pa is equal to 94 dB relative to 20  $\mu$ Pa, thus 94 dB was entered in the dB adjustment field (Bruneau, 2006). Taking into account the microphone sensitivity gain of +12 dB entered into the settings of the SM4BAT, the software applied a correction factor of 81 dB. From here on, SPL will be referred to as noise (dBA). The noise frequency along the transect that the bats were exposed to was measured in BatSound from sound files with a timestamp as close to 19:00 as possible on each night. The frequency of the background noise was determined over a 2,000 ms period and the mean and standard deviation was calculated.

To determine the acoustic intensity ratio ( $z$ ) between the “quietest” and “loudest” points along the transect, the equation  $\Delta L = 10 \log_{10}(z)$  was used.  $\Delta L$  is the difference between two relative intensities and  $z$  is the ratio of one sound to another, thus  $z = 10^{\Delta L/10}$ . To calculate the perceived change in loudness or level change ( $x$ ), the equation  $\Delta L = 10 \log_2(x)$  was used, thus  $x = 2^{\Delta L/10}$  (equations by Sengpiel Audio, 2014).

## Percentage of Natural Vegetation Estimation

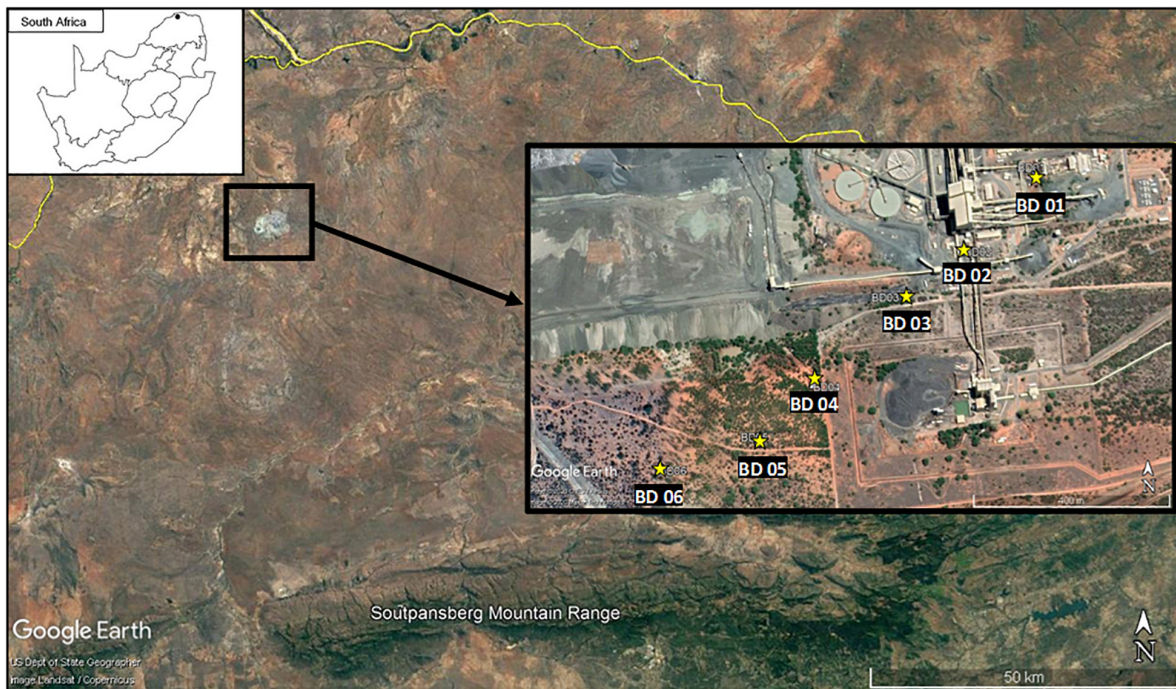
Natural vegetation cover was visually estimated and recorded as a percentage; bat detectors 01 and 02: 0% (completely devoid of vegetation; no trees and no grass), bat detector 03: 25% (in a cleared lay-down area; on the edge of a stand of trees but no grass), bat detector 04: 50% (on the edge of a wooded area bordered by a road and open grass area) and bat detectors 05 and 06: 100% (unaltered natural vegetation). For the mixed-effects model analysis and resulting graphical outputs, each percentage

<sup>2</sup>www.wildlifeacoustics.com

<sup>3</sup><https://www.wildlifeacoustics.com/resources/video-tutorials/kaleidoscope-pro-software/en/kaleidoscope-pro-software-noise-level-analysis-english>

<sup>1</sup><https://www.debeersgroup.com/the-group/our-history>





**FIGURE 1 |** The location of the study site in the northern Limpopo River Valley (dot on map insert) and placement of the bat detectors (★) on the Venetia diamond mine. BD01 was situated at a workshop, BD02 was at the processing plant itself, BD03 was on the edge of a laydown (open-air storage) area, BD04 was placed along the edge of a road opposite the sorting area, BD05 and BD06 were placed furthest from the noise and light of the active mining areas in natural vegetation.

was assigned a letter to ensure it was treated as categorical: A = 0%, B = 25%, C = 50%, D = 100%.

## Call Analysis

Kaleidoscope Pro (version 4.5.5, Wildlife Acoustics, Inc.) was used to convert sound files (.WAV) into zero-crossing files (ZC). AnalookW (version 4.5z, Chris Corben) and BatSound (version 3.31, Pettersson Elektronik AB) were used to identify all bat calls. A minimum of four pulses per 15 s was initially filtered from the data set. The filtered sound files were then bulk sorted to species level using filters designed in AnalookW based on call parameters from Taylor et al. (2013) and Monadjem et al. (2020) and were refined using the bat calls recorded on site (**Supplementary Table 1**). Due to the overlap in call parameters (particularly peak frequencies, durations and bandwidths), all calls were manually checked and adjusted as necessary if the filters had incorrectly identified the calls.

Several bat species could not be confidently differentiated from each other due to the degree of overlap in call parameters. *Chaerephon pumilus* and *Mops condylurus* are known to occur on the mine, even sharing the same roosts (pers. Obs.) but could not be reliably distinguished from each other acoustically and thus were placed in the same call group but considered as one species for the analyses. *Chaerephon cf. ansorgei* and *Molossid 19 kHz* (possibly *Tadarida ventralis*) exhibit overlapping call parameters and were grouped as one species. The same procedure was followed for *Pipistrellus rusticus* and *Neoromicia anchietae*,

and *Laephotis capensis* and *P. rueppellii* with each species group counted as a single species for the analysis.

Three categories of bat behaviour were recognized: non-feeding (commuting/searching), feeding attempts (feeding buzzes) and socialising. Feeding buzzes were manually identified from the ZC files and were validated using the associated WAV file in BatSound since these types of behavioural calls are challenging to confidently classify based on the ZC file. The identification of each echolocation call to bat behavioural category was important to determine if the artificial lighting on the mine provided feeding opportunities. All calls were organised into foraging guilds according to Monadjem et al. (2020); open-air foragers (OAF) that fly and forage above the vegetation (Molossidae and Emballonuridae), clutter-edge foragers (CEF) that forage near/along the edge of vegetation (Vespertilionidae and Miniopteridae) and clutter foragers (CF) that forage within cluttered spaces, often close to the ground (Rhinolophidae and Hipposideridae). All bat passes were standardised to Activity Index (AI) based on Miller (2001). Activity Index was thus represented as one call per specific species over a 1-min interval. The same was done for behaviourally-categorised subsets of calls with special attention paid in instances where conspecifics were performing two types of behaviours during the same 1-min interval, thus no identified calls were lost.

Detectability of the bats across the site does need to be considered. However, the proposed correction factor by Monadjem et al. (2017) was not applied due to several concerns around sample size, bat detector brand and methodology. Until



**TABLE 1** | Average and standard deviation of maximum luminosity (lux), noise frequency (kHz), and sound pressure level (SPL, dBA) recorded at each bat detector with the associated percentage of natural vegetation cover indicated in brackets. Distribution of activity index (AI) of all bats across the transect indicating behaviours and foraging guilds with the AI per behaviour and foraging guild presented in brackets.

Bat Detector (% vegetation cover)	Luminosity <sub>max</sub> (lux ± SD)	Noise Frequency (kHz ± SD)	SPL (dBA ± SD)	# of nights (n)	# Species	Behaviour (AI)			Foraging Guild (AI)		
						Foraging (3481)	Communing/ searching (28040)	Social (42)	Clutter forager (3)	Clutter-edge forager (6896)	Open-air forager (24664)
BD01 (0%)	6.31 ± 0.60	8.76 ± 1.48	55.57 ± 4.90	21	11	30	869	0		123	776
BD02 (0%)	14.19 ± 0.25	8.40 ± 0.70	57.63 ± 2.91	21	7	18	233	0		120	131
BD03 (25%)	2.26 ± 0.09	8.26 ± 2.29	54.25 ± 2.67	21	15	620	6,233	6		622	6,237
BD04 (50%)	2.58 ± 1.77	4.15 ± 4.54	53.40 ± 4.16	21	18	1517	10,681	25	1	4385	7,837
BD05 (100%)	0.47 ± 0.82	3.97 ± 5.01	52.58 ± 5.05	21	16	725	5,930	8		856	5,807
BD06 (100%)	1.12 ± 4.56	3.36 ± 4.06	51.01 ± 6.19	21	20	571	4,094	3	2	790	3,876

more research has been conducted in this field with new technologies, we are hesitant to apply a correction factor to the current data as it will undoubtedly distort the data (see Taylor et al., 2020 where this detection factor over-compensated for clutter-feeding bats).

## Statistical Analysis

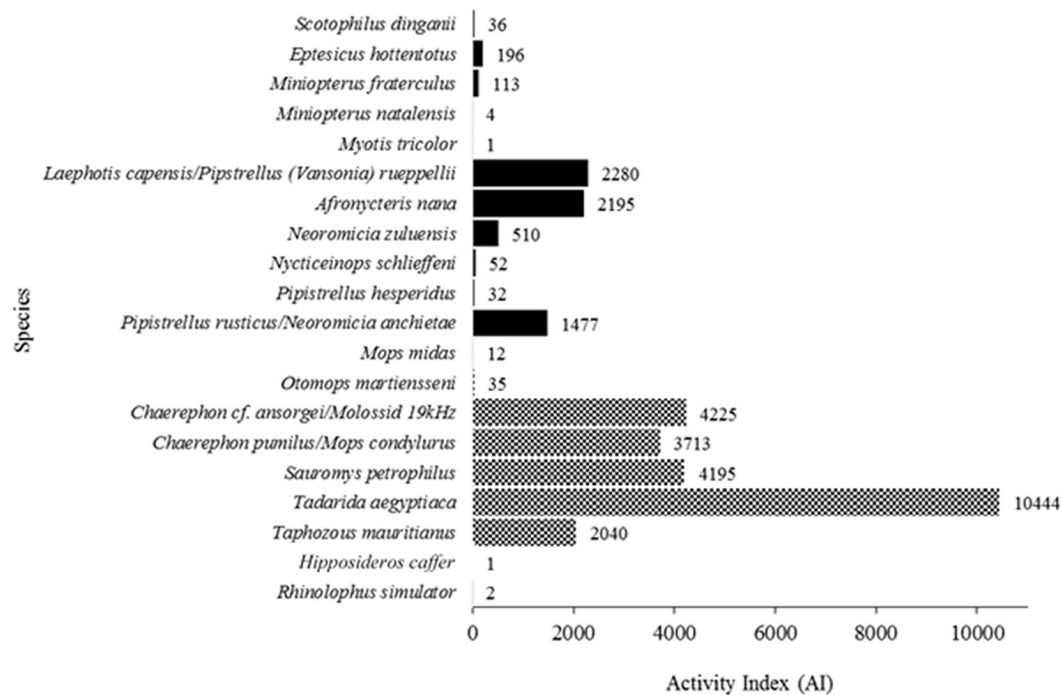
R version 3.6.3 and packages “car,” “pscl,” “lme4,” “MuMIn,” “multcomp,” and “mgcv” were used to perform the statistical analyses. Significant differences in artificial light and noise (dBA) between six bat detectors were explored using one-way ANOVAs since these two main variables of particular interest were expected to be significantly different between the bat detectors. Linear mixed-effects models (lmer) and a generalised mixed-effects model (glmer) were used to determine which factors and associated models were most likely responsible for the observed differences in AI (total AI, AI per foraging guild and AI associated with specific behaviours) and species richness along the transect. Date and bat detector was set as the random factor to account for pseudo replication. The fixed factors were light intensity (lux), noise (dBA), minimum temperature ( $T_{\min}$ , °C), percentage of natural vegetation cover, moon phase and season. All AI data were log-transformed to normalise the data suitable for lmer with the exception of feeding. In this instance, a glmer (family Poisson) was used to determine the best fit model. Best-fit models were selected based on the calculated corrected Akaike Information Criterion values (AICc) and associated delta AICc ( $\Delta AICc$ ) values < 2. Collinearity between the fixed factors was tested using the variation of inflation factor (VIF) function in R. As suggested by Fox and Monette (1992), we used generalised VIF ( $GVIF^{1/2*df}$ ) instead of GVIF. If the  $GVIF^{1/2*df} < 5$ , the association between the factors was deemed weak and were included in the mixed-effects models.

Type II Wald Chi-square tests (Anova: lme4) were used on each mixed-effects model (lmer and glmer) to determine any significant differences in the means of the independent variables; moon phase,  $T_{\min}$  (°C), maximum luminosity (lux), noise (dBA) and percentage of natural vegetation cover in relation to the dependent variables; AI and species richness across the six bat detectors. The Wald Chi-square test was chosen as it is not bound by a specific distribution and is thus a suitable non-parametric test that can be used for non-normal variable distributions in mixed-effects models.

Percentage AI of OAF and CEF species was used to determine the dominant species along the transect. One-way ANOVAs were used to explore the differences in AI of the dominant species along the transect in relation to bat detector and percentage natural vegetation cover.

## RESULTS

A total of 35,327 files recorded over the 21 nights were identified (species level and activity type) using a combination of AnalogW and BatSound to analyse zero-crossing and wave files, respectively, resulting in a total of 42,028 bat passes. Since zero-crossing files lose intensity and harmonic information, BatSound



**FIGURE 2 |** Species identified with the associated sum of behavioural AI categories. Solid filled bars indicate clutter-edge foragers and the checkered bars indicate open-air foragers. *Rhinolophus simulator* and *Hipposideros caffer* are clutter foragers but were represented in such low numbers that a fill is not visible.

was used to verify feeding buzzes and identifications where zero-crossing files viewed in AnalookW were unclear or ambiguous. The total activity index was calculated to be 31,563 (Table 1).

## Species Richness and Activity Index

Overall, 19 (potentially 23) bat species/species-groups were acoustically identified (Figure 2). Bat species richness varied along the transect (Table 1). The highest species richness was recorded where percentage natural vegetation cover was 50% and at the end of the transect (18 species), and the lowest species richness was recorded at the beginning of the transect (seven species). For all analyses, 19 species or species-groups were used as listed in Figure 2.

Total AI, AI per foraging guild and behaviour (feeding attempts, non-feeding, and social) were all significantly different along the transect (all  $P < 0.05$ ; Supplementary Figure 1). Open-air foragers (OAF) accounted for the highest overall AI (24,664), as well as AI associated with social (29), feeding (2,594) and non-feeding (22,041) activity (Table 1 and Supplementary Figure 1). Total OAF AI was dominated by *T. aegyptiaca* (42.35%), *cf. C. ansorgei/Molossid 19 kHz* (17.13%), *Sauromys petrophilus* (17.01%), and *C. pumilus/M. condylurus* (15.05%). Clutter-edge foragers (CEF) accounted for the second-highest overall AI (6,896), social (13), feeding (887), and non-feeding (5,996) activity (Table 1 and Supplementary Figure 1). *Laeophotis capensis/P. rueppellii*, *A. nana*, and *P. rusticus/N. anchietae* dominated with 33.08, 31.83, and 21.42% of the total CEF AI, respectively. Finally, clutter foragers (CF) were poorly

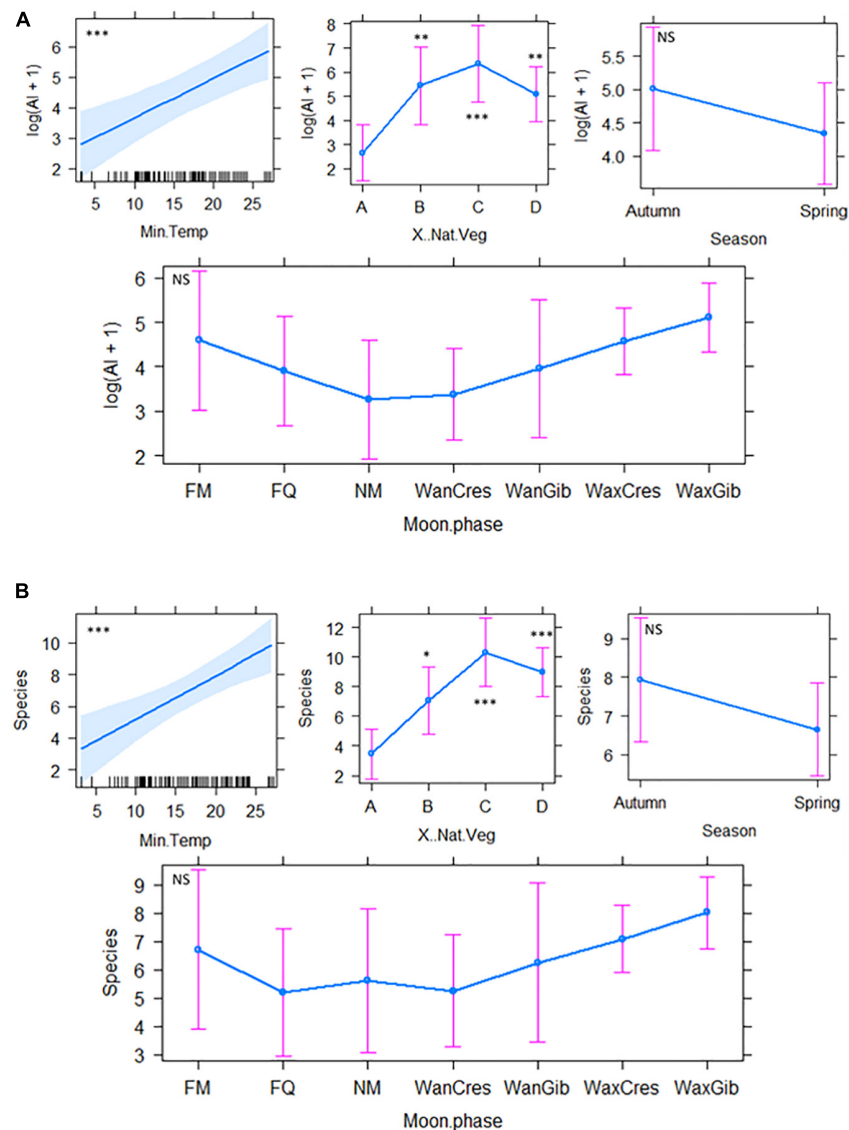
represented with only three recorded bat passes (Table 1) of two individuals of *R. simulator* and a single *H. caffer*.

## Artificial Light and Anthropogenic Noise

Light intensity and noise (dBA) were significantly different along the transect ( $P < 0.05$ ), decreasing both with distance away from the mine and the percentage of natural vegetation (highest at BD01 and BD02 with zero cover and lowest at BD05 and BD06 with 100% cover (Table 1). All noise (dBA) fell into the range that would be considered to be moderate to seriously annoying, particularly to humans (Berglund et al., 2000). Noise frequencies that were recorded at the beginning of the transect at and near the processing plant could have only overlapped with *O. martiensseni*, which is known to produce a narrow bandwidth ( $6.4 \pm 2.3$  kHz) and long duration ( $24 \pm 14.8$  ms) echolocation calls with a peak frequency of  $10.8 \pm 2$  kHz (Monadjem et al., 2020). With only 35 calls recorded of *O. martiensseni*, noise frequency was not used in any of the analyses since the chance of acoustic masking of the remaining species of bats would be negligible to absent.

## Tests of Collinearity, Analysis of Variance, and Mixed-Effects Models

The tests of collinearity on each linear and generalised mixed-effect regression model (lmer and glmer) showed that all factors had fairly weak associations when considering GIVF<sup>1/2\*df</sup> since all values were  $<5$  (Supplementary Table 2). The results of the analysis of variance (Anova: lme4) are presented

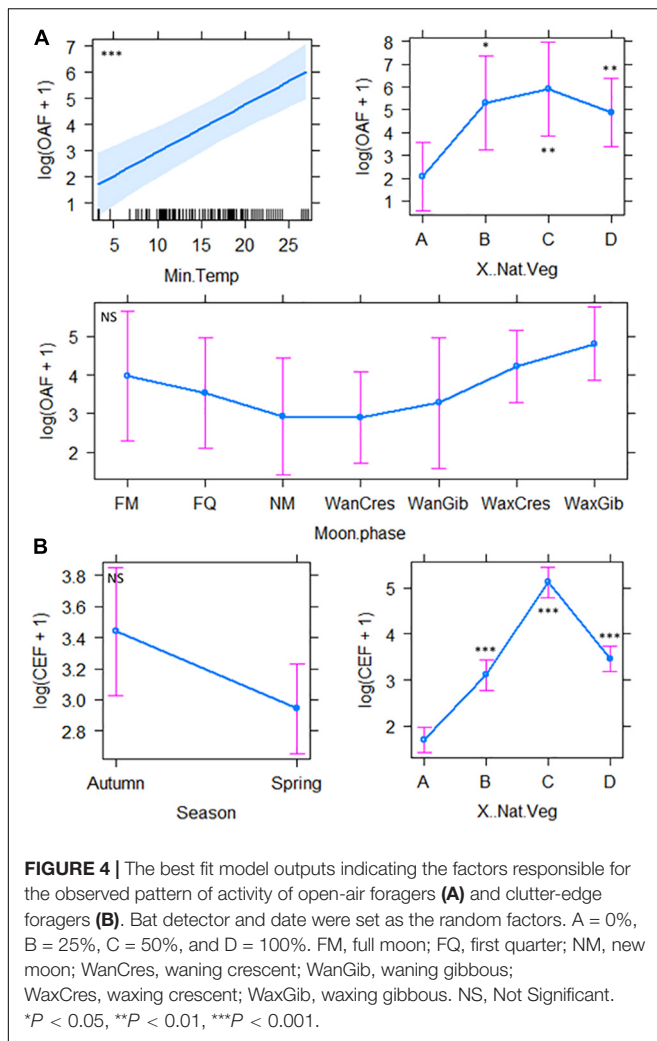


**FIGURE 3 |** The best fit model outputs for **(A)** AI (model #2) and **(B)** species (model #1) showing the influence of season, maximum luminosity, noise (dBA), percentage of natural vegetation cover and moon phase on bat richness and activity. Bat detector and date were set as the random factors. Codes in graphs: A = 0%, B = 25%, C = 50%, D = 100%. FM, full moon; FQ, first quarter; NM, new moon; WanCres, waning crescent; WanGib, waning gibbous; WaxCres, waxing crescent; WaxGib, waxing gibbous. NS, Not Significant. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

in **Supplementary Table 2** indicating the effect of light intensity (lux), noise (dBA),  $T_{\min}$  ( $^{\circ}\text{C}$ ), percentage of natural vegetation cover (% Nat. veg), moon phase and season on the dependent variables.

The best fit model selection, model estimates and associated cftest results are presented in **Supplementary Table 3**. The percentage of natural vegetation cover was significantly important for all 12 best-fit models, with significantly higher AI, species richness, forager guild activity and specific activities of different behaviour over 25, 50, and 100% natural vegetation cover than areas devoid of natural vegetation (**Supplementary Table 3**). Differences in AI were best explained by three best-fit models which included, in addition to percentage of vegetation

cover and  $T_{\min}$ , moon phase, season and light intensity (lux) (**Figure 3A**). Species richness was best explained by two best-fit models which showed a significant increase with percentage vegetation cover  $\geq 25\%$  and increasing  $T_{\min}$  ( $^{\circ}\text{C}$ ), and was affected by moon phase and season, although not significantly (**Supplementary Table 3** and **Figure 3B**). Open-air forager activity was best explained by two best-fit models indicating significant effects of  $T_{\min}$  and percentage vegetation cover as well as non-significant effects of moon phase, season, and noise (dBA) (**Supplementary Table 3** and **Figure 4A**). Clutter-edge forager activity was shown only to be significantly affected by percentage of natural vegetation cover in both best-fit models although season (not significant) was included in the first model



from the best-fit selection table (Supplementary Table 3 and Figure 4B). Light intensity, percentage natural vegetation cover, moon phase and season were all significant factors that described feeding activity by a single best-fit model (Supplementary Table 3 and Figure 5A) with higher feeding attempts during early autumn over the dimly lit areas that were exposed to spill-over from the lights of the mine, had natural vegetation cover  $\geq 25\%$  and during periods of darker moon phases (Table 1 and Supplementary Table 3). Lastly, three best-fit models indicated that  $T_{\min}$  and percentage natural vegetation cover were significant factors for bats non-feeding behaviour with the inclusion of light intensity in the third model (Supplementary Table 3 and Figure 5B). Moon phase and season were included in the models but did not have a significant effect on non-feeding behaviour (Supplementary Table 3).

## DISCUSSION

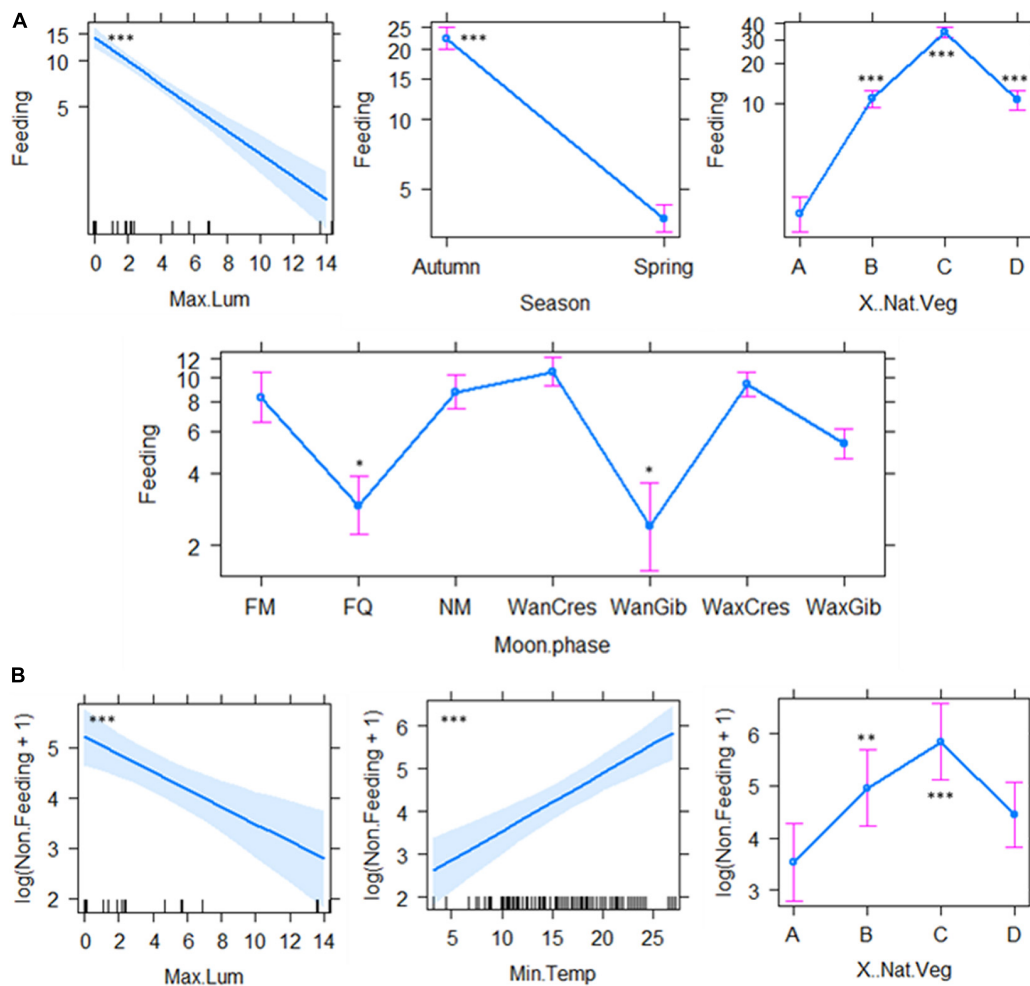
Species richness recorded along the transect on the Venetia diamond mine is comparable with the species richness recorded

by Taylor et al. (2020) from the surrounding area. However, compared to the study of Taylor et al. (2020) conducted only about 14–30 km from Venetia Mine, clutter-feeding bats were conspicuously scarce ( $AI = 3$ ) in our study. While the activity of clutter feeders was significantly related to the proximity of water bodies and riparian vegetation by Taylor et al. (2020), it is unlikely that the proximity of water accounted for the absence of these bats in our study since a dam used by bats was located close to the sample sites on the mine property. Furthermore, a much higher activity of clutter feeding bats ( $AI = 150$ ) was recorded during the duration of this study on an undisturbed game farm close to the mine in the same vegetation type (Limpopo Ridge Bushveld) by Cory Toussaint (2021). Thus, we conclude that, as we predicted, these sensitive, clutter-dependent bats have been excluded from our study transect by vegetation removal, light pollution and noise pollution or a combination of these factors. It is known that Rhinolophidae and some Vespertilionidae are sensitive to light (Schoeman, 2015; Stone et al., 2015; Rowse et al., 2016; Azam et al., 2018). Stone et al. (2009) showed that artificial lighting negatively affected *R. hipposideros* (lesser horseshoe bats) and disrupted commuting routes when hedges were lit (53.09 lux). The unlit side of the hedge (4.17 lux) was also avoided and 0.45 lux was considered to be too bright. Thus the range of light along our transect may have been too bright for the clutter foragers.

With the clutter-edge and open-air feeding guilds, conclusions were less clear-cut. However, the percentage of natural vegetation was the most important factor affecting observed patterns of bat activity. Total AI, foraging guild activity, species richness, feeding and non-feeding behaviour were highest where vegetation cover was at least 50%, as we expected for clutter-edge but not for high-flying open-air bats. Both open-air bat activity in general and that of particular molossid species (see “Results”) were associated with 100% of natural vegetation (furthest from the mine) which was surprising, especially since two of these species are known to roost in buildings on the mine property. It is possible that the low number of open-air feeding bats in well-lit open areas close to the mine infrastructure could have been due to these bats navigating visually using the artificial illumination of the mine. Orientation by sight is not implausible since molossids generally commute and forage in the open, fairly high above the ground where the risk of collision with stationary objects is low. It has been shown that vision takes priority over echolocation when bats are travelling far distances (commuting or migrating) and in instances where a bat may be receiving conflicting information from its sight and echolocation calls (Eklöf, 2003; Gorresen et al., 2015; Liu et al., 2015; Rowse et al., 2016).

As expected for open-air but not clutter-edge feeding bats, neither light nor noise levels had a significant impact on the activity of clutter-edge and open-air feeding bats, separately or combined. A similar pattern was observed by Bunkley et al. (2015) for the open-air feeding molossid, *T. brasiliensis* where their activity was higher over quieter areas of natural gas extraction. With the clutter-edge feeders, it is possible that habituation to noise has occurred; Bunkley et al. (2015) found that *Myotis lucifugus*, *M. californicus*, *M. cillolabrum*, and *Parastrellus hesperus* were not affected by noise associated with natural gas extraction. Since they rely more on echolocation





**FIGURE 5 |** The factors to best explain the observed patterns of feeding (A) and non-feeding (B) activity. Bat detector and date were set as the random factors. A = 0%, B = 25%, C = 50%, D = 100%. FM, full moon; FQ, first quarter; NM, new moon; WanCres, waning crescent; WanGib, waning gibbous; WaxCres, waxing crescent; WaxGib, waxing gibbous. NS, Not Significant. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

to detect and capture prey as opposed to listening for acoustic cues from prey, noise possibly did not impact them in the manner that it would affect gleaner bat species. For example, *M. myotis*, a gleaner, habituated to traffic noise during torpor but was negatively impacted by traffic noise during foraging activity (Jones, 2008; Schaub et al., 2008; Luo et al., 2014). Organisms can adapt to a particular disturbance regime (Grindal and Brigham, 1998). Since the Venetia diamond mine has been operational since 1992 (27 years at the time of data collection), we assume that the bats inhabiting and using the resources of the Venetia Diamond mine have possibly adapted to a degree to changes in the landscape (including habitat clearing) and possibly habituated to the nightly artificial light and the persistent anthropogenic noise from the mining.

There is no evidence from the current study indicating that either open-air or clutter-edge feeding bats used the flood lights as feeding opportunities. Some species of fast-flying bat species belonging to the genera *Tadarida*, *Myotis*, *Eptesicus*, *Pipistrellus*,

and *Vespertilio* to name a few, benefit greatly from increased feeding opportunities around street lamps as the bats preyed on insects that were attracted by shortwave light (Rydell, 1992; Stone et al., 2009, 2015; Schoeman, 2015). In fact, our results show an opposite trend where foraging activity (of open-air and clutter-edge feeding bats combined) is significantly inversely correlated with light intensity. The observed pattern may have been influenced by the early spring and late summer sampling periods when insect abundance could expectedly be low.

The observed pattern of activity in response to  $T_{min}$  and moon phase is well known and well documented in the literature (Ciechanowski et al., 2007; Appel et al., 2016; Pech-Canché et al., 2018; Pretorius et al., 2020). Reduced bat activity has often been associated with the energetic costs of flight, reduced prey availability and maintaining stable body temperatures during cooler temperatures and unfavourable weather conditions (Erickson and West, 2002; Bender and Hartman, 2015). Moon phase was shown to be important in our best-fit models but only

significantly so for feeding activity where feeding activity was significantly lower during the first quarter, waning gibbous and waxing gibbous (**Figure 5A**). Whether bats were experiencing true lunar phobia during foraging activities or relying more on visual cues is yet to be investigated.

To our knowledge, no study has simultaneously incorporated the impact of ecological light pollution and continuous noise from mining operations on bat species. The study of bats on the Venetia diamond mine highlights the anthropogenic factors (artificial lighting, noise and habitat degradation) and natural factors that influenced bat activity. As the first case study of the impacts of opencast diamond mining in South Africa (and globally), we hope that the study highlights the need for rigorous scientific studies, inspires students, researchers and consultants alike to investigate the impacts of large-scale developments, particularly mines. It is crucial to understand how African bats respond or adapt to mining developments in the field.

## 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 animal study was reviewed and approved by Research Ethics Committee, University of Venda, Thohoyandou.

## AUTHOR CONTRIBUTIONS

DC-T and PJT contributed to conception and design of the study. DC-T wrote the first draft of the manuscript, organised the database, and performed the statistical analysis with assistance from PJT. Both authors contributed to manuscript revision, read, 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.2022.752665/full#supplementary-material>

**Supplementary Figure 1** | AI across the transect for the two main foraging guilds, open-air foragers (right bar) and clutter-edge foragers (left bar), and for two different behaviours, foraging (lower bars) and commuting (upper bars). The activity index of the clutter foragers and social activity were excluded from the current plot as clutter forager activity social calls were minute in comparison to the other two foraging guilds and activity types (see **Table 1** for detail).

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# Ecosystems Services Provided by Bats Are at Risk in Brazil

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Ecosystem services (ES) are essential for human society worldwide. ES originate from ecological processes commonly occurring in well-preserved regions. Bats play an essential role in providing such services, primarily insect suppression, plant pollination, and seed dispersal. Human activities have affected Earth's systems, compromising species and ecosystems and, consequently, the ES provision. Brazil is a country with many bat species but is also one of the world's leaders in deforestation. Here we aimed to identify regions with high potential for bats ecosystem services provision, assuming that the predicted presence of the species represents the existence of the services. First, we used a Maximum Entropy algorithm to model the distribution of 128 bat species, which correspond to 71% of the Brazilian species. We classify all species into 10 different groups, which resulted from a combination of three body sizes and four predominant trophic guilds (i.e., frugivores, insectivores, nectarivores, and carnivores). The guilds were associated with services of seed dispersion, pest control, pollination, and animal control. Then, we created a 0.5 × 0.5-degree grid to represent an index of ES per guild, which is defined by the sum of the product of the bat's size weight (1, 2, or 3) by the area occupied of each species in each cell. For comparison, the index was normalized and scaled from 0 to 1. Finally, we used a map of current land use to compare the effects of natural area suppression on the provision of ES in each cell. Our results indicate a substantial reduction in the provision of ES by bats in extensive parts of the central and eastern parts of Brazil, but changes in ES varies among biomes. While the loss of species is an important factor affecting the provision of ES in the Atlantic Forest and the Cerrado, the reduction of species occurrence is most important factor in Amazonia, Caatinga, or Pantanal regions. We suggest that degraded area restoration should be promoted in areas with high ES values and areas near cities and croplands and that a precautionary approach of promoting the conservation of high provider richness should be applied to protect the continuation of bat's ES.

**Keywords:** Chiroptera, feeding guilds, functional diversity, habitat loss, species distribution models

## INTRODUCTION

Through land-use change processes habitat loss has been pointed to as a major driver of biodiversity loss worldwide (Foley et al., 2005; Newbold et al., 2015). The human ecological footprint is such that biologically and ecologically intact landscapes devoid of anthropogenic disturbances stand for only 23% of Earth's terrestrial surface (Watson et al., 2016). About 40–50% of occupied areas have been

converted to near homogeneous urban or agriculture-dominated landscapes (Chapin, Zavaleta et al., 2000; Barnosky et al., 2012). Such simplified landscapes support less diverse communities than those originally present in the native systems (Tscharntke et al., 2005; Schipper et al., 2008; Flynn et al., 2009). Consequently, human's indiscriminate interventions interfere with both structure and functioning of ecosystems (Hooper et al., 2012), often resulting in less adaptive systems that are highly vulnerable to disturbances and changing environmental conditions (Folke et al., 2002).

Stability is a desirable characteristic when considering our dependence on the current state of functioning of ecosystems. Stability is often associated with resilience, which relates to a system's reorganization capacity after disturbance without disrupting crucial ecosystem processes and characteristics (Holling, 1973). One way species diversity contributes to resilience is through mechanisms of redundancy. Redundancy relates to a situation where the same function is performed by multiple species (Walker, 1992). Thus, ecosystem processes are safeguarded against loss of function through local extinctions (Yachi and Loreau, 1999; Oliver et al., 2015). Effects of redundancy on function stability are more significant if the species of interest differ in their responses to environmental change (Mouillot et al., 2013; Oliver et al., 2015), which implies the need for diversity within the group of species sharing ecological roles. Such view benefits from the reunion of species into functional groups representative of a suite of organisms with similar functional traits related to their shared ecological role (Luck et al., 2009).

Bats form the second most speciose order (Burgin et al., 2018). Most of this diversity is concentrated in the Neotropics, where bats gather in ecologically diverse assemblages critical for ecosystems (Medellín et al., 2000; Meyer and Kalko, 2008). Their contribution results from the diversity of ecological roles performed by bat species. Through morphological and sensorial adaptations, they can explore a various of resources such as fruit, nectar, pollen, insects, small vertebrates, and even blood (Fenton, 1992). These give bats a place in almost every trophic level. While acting as seed dispersers, pollinators, and predators, bats' roles in the ecosystem can be translated into services (Kunz et al., 2011; Aguiar et al., 2021).

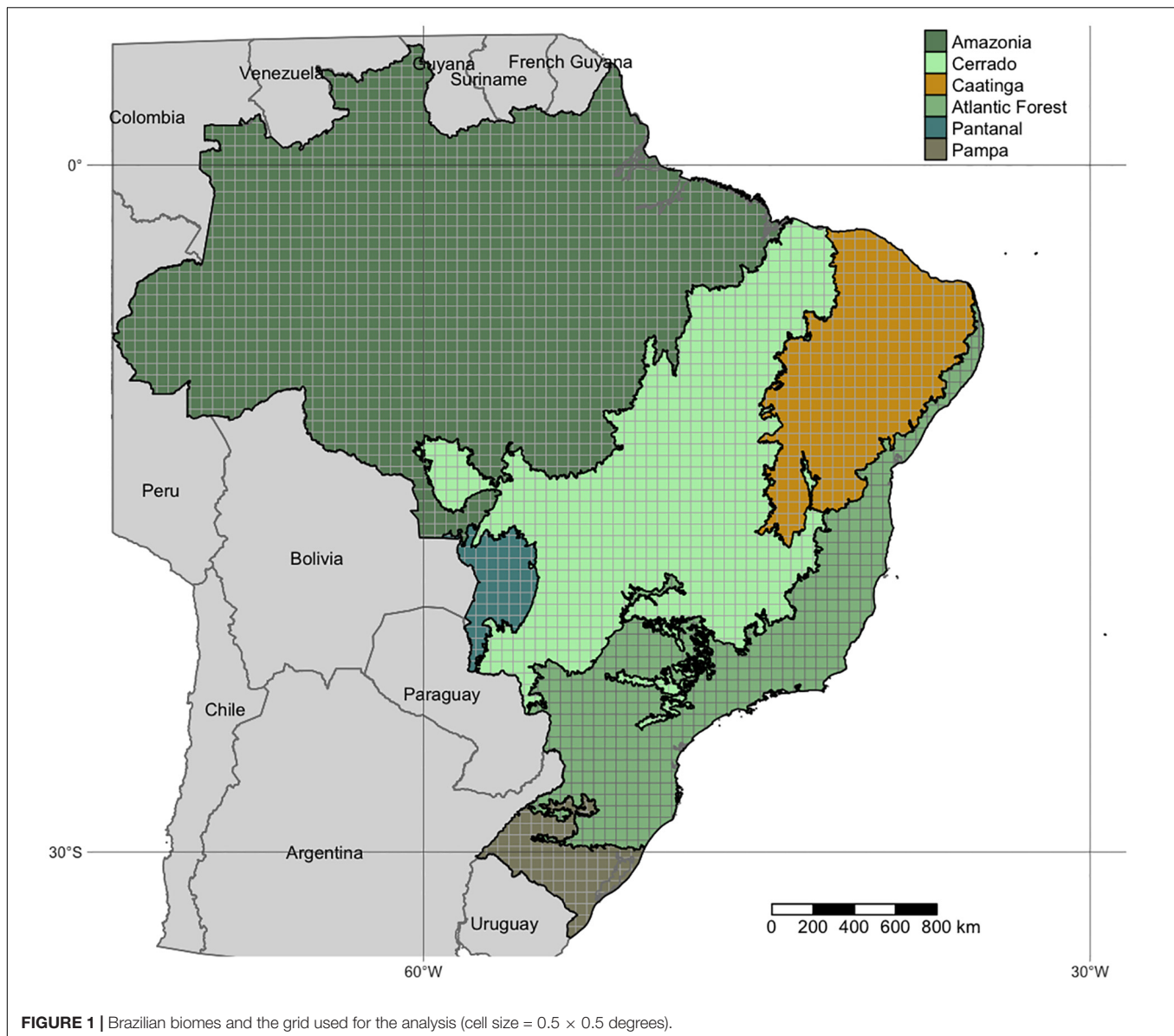
Bats build on nature's contributions to people (Díaz et al., 2018) as ecosystem services (ES) providers (Luck et al., 2009). Bats sustain plant diversity (Wang and Smith, 2002) by acting as mobile agents of seed and pollen for hundreds of species (Kunz et al., 2011), facilitating tropical forest succession and accelerating the regeneration of degraded areas such as abandoned pastures (Galindo-González et al., 2000; Muscarella and Fleming, 2007). From a more direct perspective of human welfare, bats play essential roles in agriculture by acting as biological agents of pests suppression in crucial crops, reducing plant damage, and increasing crop yield (Maine and Boyles, 2015; Taylor et al., 2017; Aguiar et al., 2021). Bats also interact mutualistically with economically essential species associated with the

survival and cultural reproduction of many social groups (Chávez-Pozo and Ortiz, 1997; Aguiar and Antonini, 2008; Scanlon et al., 2014; Aziz et al., 2017).

Despite the ubiquity of bats and the relative ease of spot one flying by in disturbed and undisturbed areas, their nocturnal and volant habits make diversity relatively inconspicuous and ongoing declines considerably less evident. Nonetheless, bat communities in heterogeneous native habitats can differ substantially in abundance and composition from those found in adjacent occupied areas such as urban and agricultural landscapes (Medellín et al., 2000; Frank et al., 2017; Gonçalves et al., 2017; Jung and Threlfall, 2018). This indicates that habitat conversion, translated into the simplification of landscapes, results in simplified communities remaining to support the ecological functions bats offer for humans' benefit. This is a worrisome scenario given that diverse communities are key to the delivery stable functions (Tilman, 1999) and services (Isbell et al., 2011; Bartomeus et al., 2013).

Bat research has a long history of studies relating form to function (Vaughan, 1959; Norberg, 1972; Barclay and Brigham, 1991; Muscarella and Fleming, 2007) and grouping bats into body size classes is a common approach. Bat body size is known to influence resource use, with larger bats being able to use a greater diversity of resources and with greater intensity (Bonaccorso, 1979; Barclay and Brigham, 1991; Fleming, 1991; Kalko et al., 1996; Wendeln et al., 2000; Houston et al., 2004; Bonaccorso et al., 2007; Esbérard and Bergallo, 2009). Although the relationship between body size and its importance on ES provision is a theoretically valid assumption (Peters, 1983) it requires more conclusive testing. Nevertheless, these aspects are expected to differentiate larger, medium, and smaller bats in terms of how each size group potentially participates in providing associated ecosystem services. Furthermore, body size is also a well-established response trait indicating vulnerability to disturbances like habitat fragmentation among bats (Schulze et al., 2000; Farneda et al., 2015).

Without proper planning, we may reduce to fragments areas with the potential to harbor great diversity and potentially sustain stable services through high provider richness (Isbell et al., 2011). The present study aims to determine for Brazil, a large-scale neotropical country, the negative impacts of habitat conversion on bat diversity and associated services, considering their functional roles and the importance of the habitat areas lost for sustaining such diversity and services. We apply a broad definition of ES that considers ecosystem functions (Isbell et al., 2011; Ceașu et al., 2021). We employ species distribution models (SDMs) to depict the environmental suitability of sites within each species' distribution. We use guilds as a way of assembling bats within functional groups (Simberloff and Dayan, 1991) associated with their ecological functions (ca. frugivores, nectarivores, insectivores, and carnivores) and account for the diversity of species performing similar functions (ca. "guild diversity," see Elmquist et al., 2003) by classifying bats within each guild according to body size. Thus, we assume traits are



associated with the relative importance of individual species for ES provision (Ceașu et al., 2021) and use body size as a best-available proxy for a large-scale assessment of bat contribution to ES.

As our working hypothesis, we expect that the loss of native areas will affect the feeding bat guilds differently, being more significant in guilds with a low level of redundancy (than in guilds with higher redundancy). Thus, we expect groups with less redundancy (lower species richness, such as carnivores and nectarivores) will be more impacted by deforestation than frugivores and insectivores. Likewise, we expect the loss of ecosystem services will follow the species' body size, being more significant in large species than in medium and small species. Finally, understanding diversity can buffer ES provision loss through compensation mechanisms, and we test for the role of species richness and redundancy on ES persistence in the face of

natural habitat suppression. We expect ES will persist in altered areas, although reduced, unless redundancy is completely lost.

## MATERIALS AND METHODS

### Study Area

We considered the Brazilian territory in the study as its 8.5 million km<sup>2</sup> makes it the largest country in Latin America (5th in the world), ranging from various climatic zones from the humid tropics in the north to temperate areas in the south. Those climatic differences led to the formation of the following distinct biogeographic regions: the Amazon and Atlantic Forest (rainforest), the Pantanal (floodplain), the Cerrado (Neotropical savannah), the Caatinga (tropical dry forest), and the Pampa (natural grasslands) (Figure 1).



**TABLE 1** | Forearm length intervals corresponding small, medium, and big size classes for each trophic group considered.

Classes	Forearm interval (mm)			
	Insectivory	Frugivory	Nectarivory	Carnivory
Small (1)	(28.5, 42.0)	(28.5, 41.5)	(30.7, 36.2)	(61.5, 71.0)
Medium (2)	(42.0, 56.8)	(41.5, 54.0)	(36.2, 39.4)	(71.0, 93.0)
Large (3)	(56.8, 80.0)	(54.0, 71.5)	(39.4, 40.3)	(93.0, 101.0)

Groups were obtained by an unsupervised kmeans classification.

## Species Distribution Models

### Species Occurrences

We gathered occurrence data throughout all of South America for the 181 bat species currently recognized to occur in Brazil (available at <https://www.sbeq.net/lista-de-especies>, Nogueira et al., 2018). The dataset consisted of 7,730 records describing the geographical distribution of bats within Brazil (Aguilar et al., 2020) and 28,496 records obtained from the Global Biodiversity Information Facility—GBIF<sup>1</sup> complementing the data with a representation of bat records across South America (Supplementary Figure 1). The Brazilian dataset was assembled from museum vouchers, published literature, and fieldwork by the Laboratory of Bat Biology and Conservation at the University of Brasília, coordinated by L.M.S. Aguilar.

The GBIF collected occurrences were then subjected to an examination of taxonomic and spatial errors. We followed the taxonomy adopted by Nogueira et al. (2018), and spatial issues of spatial autocorrelation and sampling bias were assessed separately (Syfert et al., 2013). First, the Clark-Evans index (Clark and Evans, 1954) for all species showed some level of sample clustering, so a general spatial thinning was done to maintain unique records for any locality within a 10 km radius (Phillips et al., 2009). Second, now considering the distribution of point density along with the map (Fithian and Hastie, 2013; Renner et al., 2014), we performed the balanced design described at Kramer-Schadt et al. (2013), aiming to balance the representation (i.e., point density) of sampled areas and to avoid over-representation of certain aspects of the environmental space due to artifacts of sampling bias (see Supplementary Material 2 for detailed method). All analyses were conducted in R 3.4.1 (R Core Team, 2021). We used the package *dismo* (Hijmans et al., 2011) and *rangeBuilder* (Rabosky et al., 2016) for the general spatial filter and the *sf* (Pebesma, 2018), *lwgeom* (Pebesma, 2020), and *dplyr* (Wickham et al., 2021) packages for the balanced design. The data treatment described above resulted in a dataset of 12,058 occurrences, from which 128 species were considered to have sufficient records (10 or more observed presences) for distribution modeling (Wisz et al., 2008; Varela et al., 2014).

### Environmental Variables

We extracted environmental information from the bioclimatic variables available at the WorldClim database<sup>2</sup> (Hijmans et al., 2005). We first considered the 19 bioclimatic

current variables at 2.5 arc min resolution (ca. 5 km), all derived from monthly temperature and rainfall values. We tested the correlation between pairs of groups of variables (i.e., temperature bio1 to bio11 and precipitation bio12 to bio19) by using the Pearson's test (Supplementary Tables 1A,B). In each group, we kept only one of the variables each variable when pairs showed values of over 70% of correlation. This resulted in the selection of eight bioclimatic variables described as annual mean temperature (BIO1), mean diurnal temperature range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), the maximum temperature of the warmest month (BIO5), annual precipitation (BIO12), precipitation of the driest month (BIO14), and precipitation seasonality (BIO15), as used to model bats distribution in Aguilar et al. (2016).

### Species Distribution Model—Species Distribution Model—Building

We used the MaxEnt software Version 3.4.0 (Phillips et al., 2017), a widely used presence-background algorithm. MaxEnt derives a species' distribution by comparing the environmental conditions within the area where the species is known to occur with the conditions along with the background (i.e., area of unknown presence or absence) and then projects this environmental relation to the geographical space (Phillips et al., 2006). For model construction, we initially used the geographic extent of South America and subsequently cropped the results to the boundaries of Brazil and within the country, for each biome. As a rule, 10,000 points were randomly sampled as background, and we randomly set aside 10–20% of the data for internal model testing. The test/train ratios depended on the number of records available for each species. We used the latest MaxEnt's complementary log log (cloglog) output, which carries the same advantages as the previous logistic output, but with greater theoretical support for its interpretations (Fithian et al., 2015; Phillips et al., 2017).

We used a regularization multiplier of 2.5, a magnitude proper for fitting less complex and more general models (Elith et al., 2010; Radosavljevic and Anderson, 2014). Finally, we assessed model accuracy with True Statistic Skill—TSS (Allouche et al., 2006), a threshold-dependent measure unaffected by prevalence and validation dataset size. It considers omission and commission errors and ranges from  $-1$  to  $+1$ , where values below zero indicate a performance no better than random. We established a TSS threshold value of 0.6 to determine whether a model presented satisfying predictive performance or not. Classifying bats

The species distribution modeling results are represented in a continuous surface of values ranging from 0 to 1, showing areas where species are potentially more likely to occur due to their environmental suitability. These distribution models were reclassified to produce a discrete distribution map for each species. Our maps were then grouped into 10 categories resulting from a combination of four bat guilds (e.g., frugivores, insectivores, nectarivores, and carnivores) and three size classes (e.g., small, medium, and large). We placed omnivorous species into all guilds their feeding habitats are

<sup>1</sup><http://www.gbif.org>

<sup>2</sup><http://www.worldclim.org>



**TABLE 2** | Provision values (mean, median, and standard deviation) of ecosystem services associated with bat's feeding guilds in Brazil per biome.

		Brazil	Amazon	Cerrado	Caatinga	Atlantic forest	Pantanal	Pampa
All bats	Mean	0.542	0.536	0.575	0.576	0.509	0.582	0.415
	Median	0.563	0.532	0.663	0.623	0.579	0.688	0.395
	s.d.	0.259	0.234	0.270	0.286	0.267	0.327	0.270
Frugivory	Mean	0.529	0.561	0.558	0.426	0.513	0.564	0.415
	Median	0.578	0.548	0.631	0.409	0.582	0.644	0.416
	s.d.	0.264	0.579	0.288	0.288	0.250	0.321	0.276
Insectivory	Mean	0.565	0.237	0.592	0.605	0.510	0.621	0.527
	Median	0.586	0.554	0.682	0.675	0.533	0.708	0.569
	s.d.	0.253	0.221	0.278	0.268	0.252	0.350	0.300
Nectarivory	Mean	0.421	0.561	0.454	0.516	0.386	0.409	0.378
	Median	0.451	0.401	0.509	0.546	0.361	0.459	0.202
	s.d.	0.220	0.180	0.232	0.225	0.250	0.240	0.315
Carnivory	Mean	0.465	0.398	0.475	0.609	0.557	0.514	0.388
	Median	0.394	0.308	0.481	0.715	0.576	0.632	0.369
	s.d.	0.320	0.304	0.282	0.370	0.341	0.297	0.281

known to contribute to, and we excluded hematophagous species from further analysis because of their small representation in our validated models.

## Classifying Bats

We classified the species within each guild according to the body size classes of small, medium, and large bats. Our approach used mean forearm length as a proxy for body size, which is an adequate classification method since forearm measures are precise and associated with bat's body length and mass content (Meng et al., 2016; Thiagavel et al., 2017). We gathered the morphological data from published literature (**Supplementary Table 2**). With a *kmeans* clustering analysis, we identified intervals of mean forearm lengths that represented small, medium, and large categories for each guild separately. These were then attributed to the values of 1, 2, and 3, respectively.

The hierarchical classification expresses the decrease in the number of species for a potential replacement with increased body size. Further, it also expresses the broader functional range of larger species, which are less limited by morphology in performing their ecological functions (Fleming, 1991; Kalko et al., 1996; Houston et al., 2004). Thus, we attributed greater value to larger species due to their rarity and potential functional uniqueness within their guilds.

## Ecosystem Services Potential Analysis

We considered all species indicated by the modeling process in each biome separately for this stage. We analyzed the potential contribution of bats to ecosystem service in each major Brazilian biomes, which were divided in a regular grid of cells with a resolution of  $0.5 \times 0.5$  decimal degrees (**Figure 1**). Within each grid cell we calculated a diversity index of provider richness (hereafter Index of Potential Ecosystem Services Provision or ES index) like the one applied in Ceaușu et al., 2021. This was done by summing the area occupied by a species within the same guild multiplied by their class

size (i.e., 1, 2, or 3). The grid cell values were normalized by dividing each cell value by the maximum value found among cells for each biome separately. This resulted in values ranging from 0 to 1 representative of the cell's importance for providing of each guild's associated services. We repeated this analysis using all bats independent of the guild in each biome and considered the scenarios with and without natural habitat suppression.

## Impacts of Natural Habitat Suppression

We wanted to test how habitat conversion has affected the potential provision of ecosystem services by bat species in Brazil, identifying regions with different loss of ecosystem service provision.

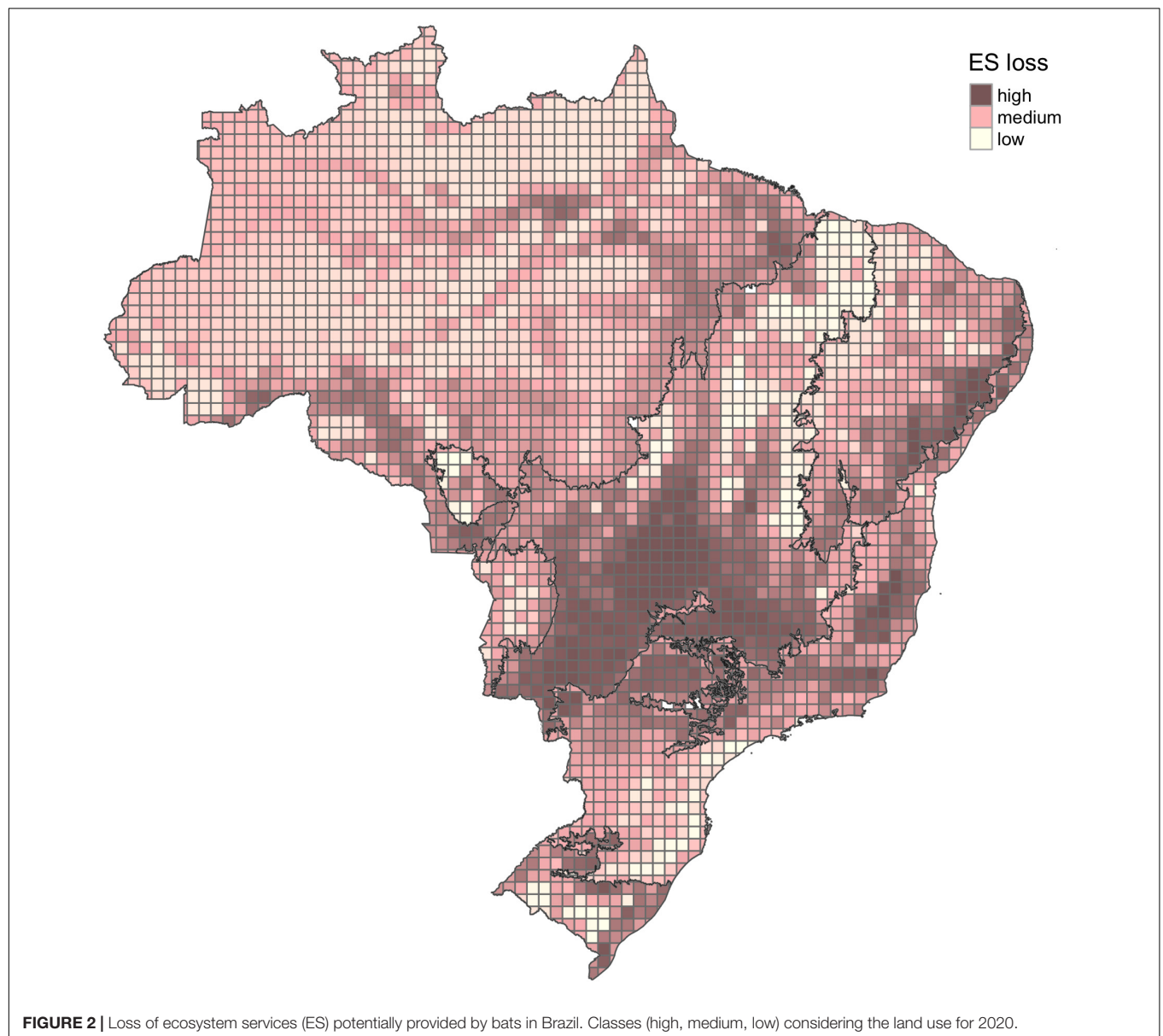
For the representation of land conversion, we used the MapBiomas version 5 land cover product,<sup>3</sup> representing the year 2020. The map is presented at a 30 m resolution and features several landcover classes. We resampled it to the same spatial resolution as our models (ca. 2.5 arc min resolution). We created a binary map of natural vegetation remnants, which included all classes of forest and non-forest natural formations as remnants. All areas occupied by pastures, agriculture, urban infrastructure, and water bodies became zero-valued. Thus, this mask was used to suppress suitable areas within the species' potential distribution. With it, we could compare the potential for ES provision prior to and after natural area suppression. With this approach, we assume that diversity, its functions, and associated services depend on the existence of natural remnants. This means we followed the notion of "supporting systems" suggested in Kremen (2005) and Tschardt et al. (2005), i.e., any diversity present in altered landscapes depends upon the support of the surrounding native landscape. All spatial analyses were conducted in the R software (R Core Team, 2021), using the packages *raster* (Hijmans, 2021) and *sf* (Pebesma, 2018).

<sup>3</sup><http://mapbiomas.org/>

**TABLE 3 |** Mean value of the ecosystem services index provide by bats considering the original (column ORI) and remaining native (column Dev) in Brazil and biomes.

	All bats			Frugivory			Insectivory			Nectarivory			Carnivory		
	Ori	Dev	Diff	Ori	Dev	Diff	Ori	Dev	Diff	Ori	Dev	Diff	Ori	Dev	Diff
Brazil	52.36	46.70	−5.66	54.81	45.27	−9.54	53.00	49.88	−3.12	54.11	49.03	−5.08	45.59	40.75	−4.84
Amazon	50.81	49.74	−1.07	53.93	50.98	−2.95	49.61	48.36	−1.25	57.20	52.16	−5.04	40.30	39.05	−1.25
Cerrado	60.99	41.61	−19.38	58.50	39.92	−18.58	60.88	41.14	−19.74	60.64	41.49	−19.15	50.41	46.37	−4.04
Caatinga	55.52	40.98	−14.54	48.25	40.98	−7.27	54.94	48.83	−6.11	54.94	52.32	−2.62	55.23	43.02	−12.21
Atlantic forest	52.83	34.72	−18.11	60.00	35.28	−24.72	53.77	35.09	−18.68	46.41	32.23	−14.18	51.32	31.13	−20.19
Pantanal	54.44	51.89	−2.55	53.16	51.89	−1.27	55.62	54.44	−1.18	54.43	54.43	0.00	54.43	54.43	0.00
Pampa	44.44	38.88	−5.56	50.00	39.81	−10.19	56.48	39.81	−16.67	33.98	31.48	−2.50	39.81	34.23	−5.58

The column "Diff" represents the mean loss of ecosystem services up to 2020. Ori, proportion related to the original area; Dev, proportion related to the devegetated area; Diff, loss of potential proportion area after devegetation.



**TABLE 4 |** Magnitude of ecosystem services in Brazil and its biomes per feeding guilds.

	Carnivory	Frugivory	Insectivory	Nectarivory	Order of impact	KW test
Brazil	−0.160	−0.188	−0.197	−0.119	INS > FRU > CA > NEC	391.49***
Amazon	−0.043	−0.079	−0.078	−0.037	FRU > INS > CA > NEC	691.92***
Cerrado	−0.201	−0.324	−0.336	−0.190	INS = FRU > CA = NEC	196.35***
Caatinga	−0.220	−0.141	−0.194	−0.125	CA = INS > FRU = NEC	55.75***
Atlantic Forest	−0.405	−0.336	−0.336	−0.243	CA = FRU = INS > NEC	74.77***
Pantanal	−0.088	−0.092	−0.112	−0.039	INS = FRU = CA > NEC	22.821***
Pampa	−0.179	−0.165	−0.210	−0.158	INS = CA = FRU = NEC	3.91( <i>ns</i> )

KW, Kruskal–Wallis rank test. \*\*\**p*-value smaller than 0.001. *ns*, non-significant.

## Statistical Analysis

### Species Contributions and Redundancy for Ecosystem Services Provision Magnitude of Losses

We compared each biome's loss of ecosystem services with a Kruskal-Wallis test since the distribution pattern was not normal (Shapiro test  $W = 0.8061$ ,  $p < 0.001$ ). Then we used the function *kwAllPairsNemenyiTest* from *PMCMRplus* package (Pohlert, 2021) to perform a non-parametric pairwise comparison between all biomes.

We used a binomial proportion test (two proportions *z*-test) to test our hypothesis. Proportion tests were performed between guilds to see whether we would observe a gradient of losses following the expected pattern of carnivory > nectarivory > frugivory > insectivory. Another set of tests was performed between size classes within the guild and within all bats to ascertain whether proportional losses were associated with bat's body size in the respective order: large > medium > small. All analyses were conducted in the R software (R Core Team, 2021).

### Species Contributions and Redundancy for Ecosystem Services Provision

We were interested in identifying which features of diversity work to maintain the ecosystem service provision within grids where natural habitat suppression has occurred. We applied generalized linear models (GLM) with Gaussian distribution using the ES index values after deforestation as our response variable and remnant area occupied by species plus the number of lost species of the same size class as our explanatory variables. We only consider insectivores, frugivores, and nectarivores for this stage because of their number of species. This was done separately for each guild within each biome separately.

## RESULTS

### Bats Species Distribution Models and Classification

We generated 128 generated models with good predictive performance. TSS values ranged from 0.6 to 0.97, with 53 species validated with scores between 0.6 and 0.69 and 60 species

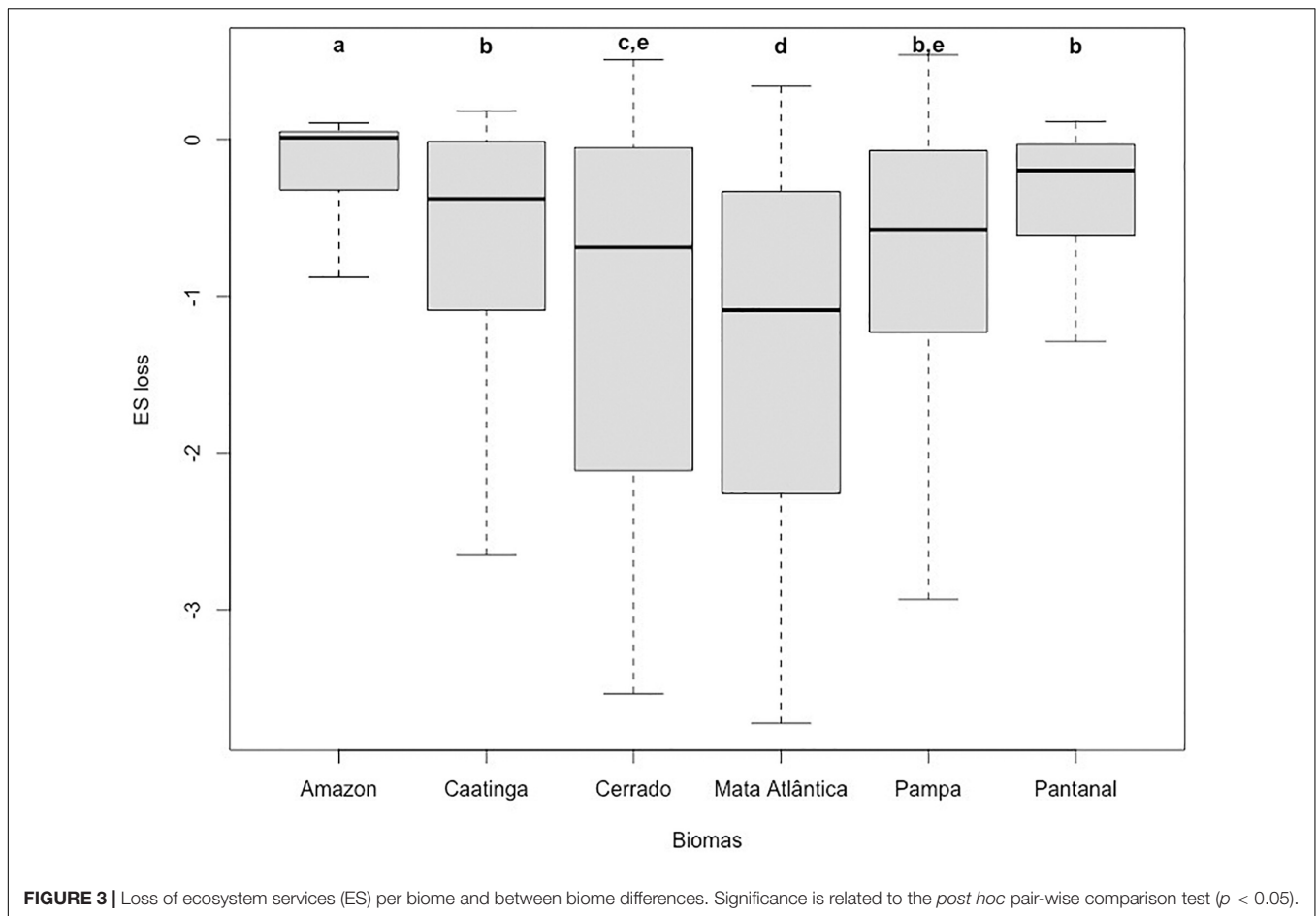
validated between 0.7 and 0.97. Five species were removed from the study due to unsatisfactory model results after a visual inspection. Thus, all results presented here are based on 128 bat species, of which 76 were identified as insectivores, 36 as frugivores, 12 as nectarivores, and four as carnivores (Supplementary Table 2).

We calculated for each trophic guild three mean forearm lengths intervals (small, medium, and large) using *kmeans* clustering (Table 1). Overall, there were 63 small, 38 medium, and 27 large bat species. Size differences were most marked for insectivorous and frugivorous bats (Table 1) and after specialist consultation we decided to keep only small and medium classes for nectarivores and only medium and large for carnivores. Overall, most species within each guild were classified as small (Supplementary Table 2).

### Provision Potential of Ecosystem Services Associated to the Brazilian Bat Fauna

For Brazil and for each biome, values of the corresponding potential for the provision of ES were identified (i.e., disregarding natural area suppression). Overall, the values of the ES index varied among biomes, indicating differences in species compositions between regions (Table 2). Cerrado was the only biome that presented mean ES index values greater than the national average for all guilds (Table 2). The potential for insectivores' associated services is predicted to be greater in the Pantanal, Caatinga, and Cerrado biomes (Table 2). Nectarivores species presented higher values for the Amazon and Caatinga, on average. Frugivory seems to be well distributed across Brazil, with the weakest potentials predicted for Caatinga and Pampa (Table 2). Finally, carnivory potential is predicted to be distributed toward Pantanal, Atlantic Forest, and Caatinga (Table 2).

Knowing the potential provision scores for a country or region is not the only way of assessing a place's likelihood of providing or sustaining specific ecosystem services. A complementary approach is to see how these values are distributed in space. The Cerrado, for instance, has 60.99% of its original cells, i.e., without considering area suppression, presenting ES index values greater than the national average. The other biomes have 55.52% (Caatinga), 54.44% (Pantanal),



**FIGURE 3 |** Loss of ecosystem services (ES) per biome and between biome differences. Significance is related to the *post hoc* pair-wise comparison test ( $p < 0.05$ ).

52.83% (Atlantic Forest), 50.81% (Amazon), and 44.44% (Pampa) (Table 3).

## Ecosystem Services Provisioning Potential Losses

With the historical occupation of Brazil, biomes' ES provisioning potential eroded. The Atlantic Forest biome is an extraordinary case, with a total loss of more than 70% of its original area (ca.1.1 million km<sup>2</sup>). Another striking case is the one of Cerrado, which had lost more than 1 million km<sup>2</sup> of its native area. Considering a threshold of 50% of remaining native areas, the percentage of cells below such limit is 74.53% for Atlantic Forest, 59.39% for Pampa, 55.65% for Cerrado, 27.84% for Pantanal, 27.62% for Caatinga, and 16.05% for Amazon.

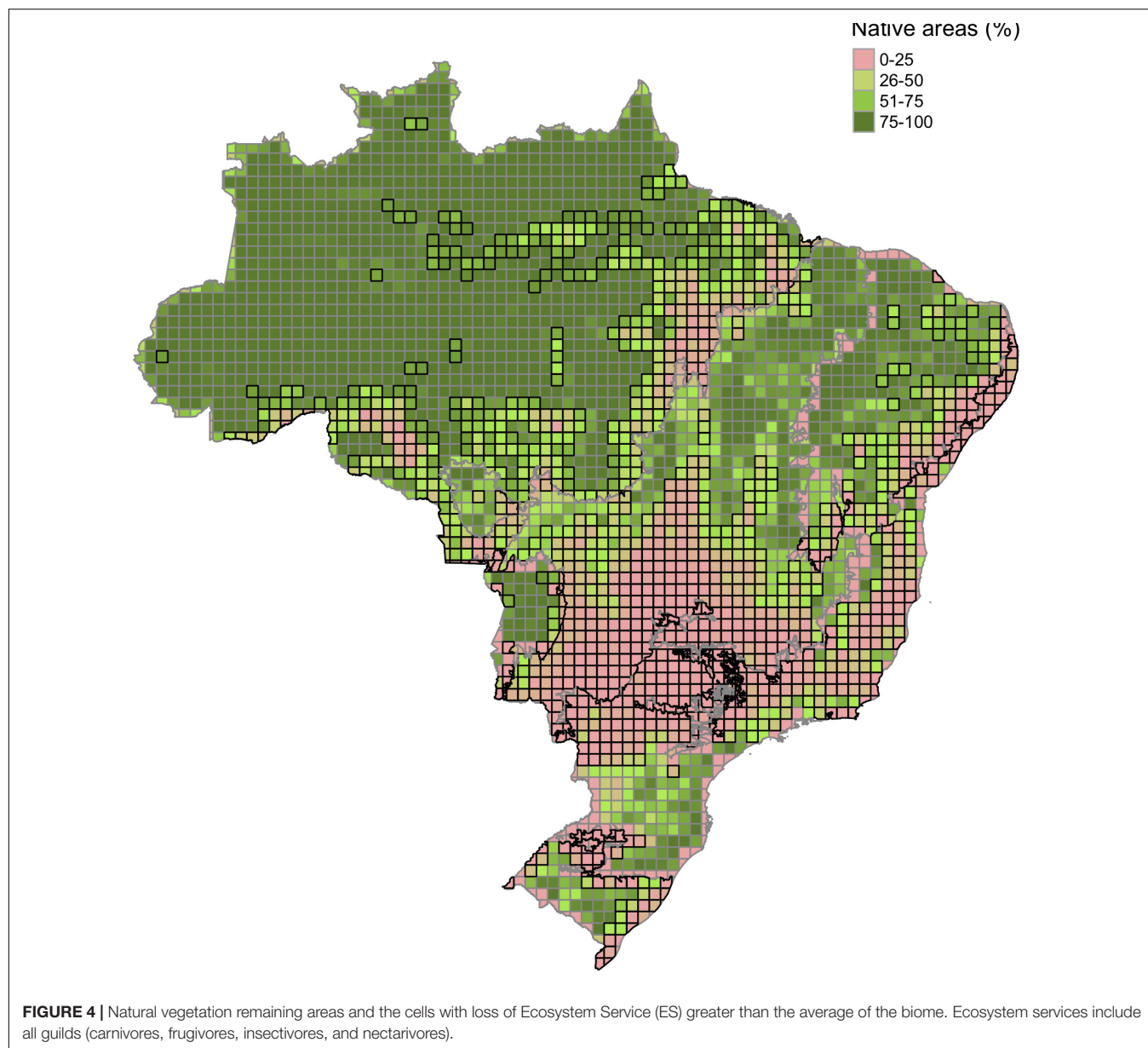
The land conversion process observed up to 2020 has impacted the provision of ES differently in each biome and, on average, the Cerrado, Atlantic Forest, and Caatinga, were the biomes with the highest losses (Table 3 and Figure 2—Mapa de perda de ES). Most of central-southern Cerrado, central Atlantic Forest, and eastern Caatinga had heavily lost the provision potential of ES. When comparing the absolute loss of ES potential, i.e., the values resulting from the difference of the original provision by the remaining provision after

natural area suppression, Atlantic Forest is the biome with the highest loss, followed by Cerrado, Caatinga, and Pampa, and Amazonia (Kruskal-Wallis  $\chi^2 = 685.81$ ,  $p < 0.001$ ) (Figure 3). The proportion of cells with expressive loss of ES is 62.26% for Atlantic Forest, 50.77% for Cerrado, 44.44% for Pampa, 33.72% for Caatinga, 24.05% for Pantanal, and 16.31% for Amazonia. Considering the cells with ES index equals or greater than the national mean, only 28.3% of essential areas for ecosystem services provision stand in Brazil (Figure 4). This proportion changes among the biomes, being 7.9% for Atlantic Forest, 16.7% for Pampa, 19.6% for Cerrado, 24.5% for Caatinga, 39.8% for Amazonia, and 50.1% for Pantanal.

## Guild's Responses to Land Conversion

The negative impacts of natural area conversion in Brazil varied among guilds and regionally. The general pattern for Brazil is a decrescent and significant impact of devegetation on insectivores, frugivores, carnivores, and nectarivores (Kruskal-Wallis  $\chi^2 = 391.49$ ,  $p < 0.001$ ) (Table 4). However, the pattern of impacts on different guilds varied per biome. The frugivores were more impacted in the Amazon, while insectivores and frugivores were more impacted in the Cerrado and Pantanal. In Atlantic Forest, there was no





**TABLE 5 |** Order of magnitude of impact on loss of ecosystem services by classes size of each guild.

	All guilds	Carnivory	Frugivory	Insectivory	Nectarivory
Brazil	$\underline{L} > M = S$	$L = M$	$\underline{\underline{L}} > \underline{M} > \underline{S}$	$L > M = S$	$S > M$
Amazon	$\underline{L} > M = S$	$L = M$	$L = M = S$	$L > S > M$	$S > M$
Cerrado	$\underline{L} > M = S$	$M > L$	$\underline{L} > \underline{M} > \underline{S}$	$\underline{L} > M = S$	$S > M$
Caatinga	$L = M = S$	$\underline{L} > M$	$L = M > S$	$\underline{L} > M = S$	$S > M$
Atlantic forest	$\underline{L} > \underline{M} > \underline{S}$	$\underline{L} > M$	$\underline{L} > \underline{M} > \underline{S}$	$\underline{L} > \underline{M} > \underline{S}$	$S > M$
Pantanal	$L = M = S$	$L = M$	$L = M > S$	$\underline{L} > M = S$	$S > M$
Pampa	$L = M = S$	$L = M$	$\underline{L} > M = S$	$S > L = M$	$S > M$

The “equal” symbol means no statistical difference between groups. The “greater than” symbol means a statistical difference for  $p < 0.05$  (Nemenyi’s non-parametric test). Cells marked with double underline show the sequence of impacts according to our working hypothesis. Cells marked with single underline show the sequence of impact partially according to the working hypothesis.

**TABLE 6 |** Results of the GLMs testing the effects of occurrence area reduction and of species loss on the ES index values after the incorporation of natural area suppression for the most speciose guilds.

Guild		Biomes					
Insectivory		Amazon	Cerrado	Caatinga	Atlantic forest	Pantanal	Pampa
ES_INS_DIFF	INS_Large_R_DIFF	<i>n.s.</i>	2.183*	<i>n.s.</i>	<i>n.s.</i>	4.283***	<i>n.s.</i>
	INS_Medium_R_DIFF	<i>n.s.</i>	−5.990***	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
	INS_Small_R_DIFF	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	−3.535*	−4.094***	<i>n.s.</i>
	INS_Large_REM_AREA	8.747e + 15***	<i>n.s.</i>	2.398e + 15***	<i>n.s.</i>	7.709e + 14***	2.265e + 14***
	INS_Medium_REM_AREA	3.765e + 15***	<i>n.s.</i>	1.024e + 15***	7.572*	2.862e + 14***	4.296e + 14***
	INS_Small_REM_AREA	3.355e + 15***	3.019**	1.042e + 15***	<i>n.s.</i>	3.959e + 14***	3.517e + 14***
ES_FRU_DIFF	FRU_Large_R_DIFF	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
	FRU_Medium_R_DIFF	<i>n.s.</i>	−4.808***	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
	FRU_Small_R_DIFF	<i>n.s.</i>	5.933***	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
	FRU_Large_REM_AREA	4.364e + 15***	3.375***	3.051e + 15***	9.621*	9.704e + 14***	4.013e + 15***
	FRU_Medium_REM_AREA	1.992e + 15***	7.674***	1.874e + 15***	<i>n.s.</i>	7.683e + 14***	1.928e + 15***
	FRU_Small_REM_AREA	2.689e + 15***	−4.040***	1.760e + 15***	<i>n.s.</i>	4.535e + 14***	1.820e + 15***
ES_NEC_DIFF	NEC_Medium_R_DIFF	<i>n.s.</i>	5.923***	<i>n.s.</i>	<i>n.s.</i>	—	—
	NEC_Small_R_DIFF	<i>n.s.</i>	−4.919***	<i>n.s.</i>	2.494*	<i>n.s.</i>	<i>n.s.</i>
	NEC_Medium_REM_AREA	2.638e + 15***	2.862**	3.665e + 15***	−1.968*	—	—
	NEC_Small_REM_AREA	8.463e + 15***	9.135***	3.958e + 15***	7.121*	7.004e + 15***	6.937e + 16***

INS, Insectivores; FRU, Frugivores; NEC, Nectarivores. ES\_guild\_DIFF variables represent the change in ES index values before and after natural habitat suppression. R\_DIFF variables represent the species richness differences before and after natural habitat suppression. REM\_AREA variables represent the remnant area available post natural area suppression. All variables were measured for all size groups within Insectivores, Frugivores, and Nectarivores. *n.s.*, stands for non-significant relations. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

statistical difference between carnivores, frugivores, and insectivores, but these three categories were more impacted than nectarivores (Table 4). The Pampa was the unique biome where the devegetation impact affected equally all guild categories (Table 4).

## Responses of Different Body Size Classes to Land Conversion

Considering all feeding guilds, the loss of ES provided by large species was significantly higher than the other two size categories (Yemeni test,  $p < 0.05$ ), but there was no statistical difference between medium and small size species (Yemeni test,  $p > 0.05$ ) (Table 5). This result partially corroborated our working hypothesis and was regionally observed in Amazon and Cerrado. We observed, as expected, the loss of bat ecosystem services in the Atlantic Forest, higher in large species than in medium and smaller-size species (Table 5). Furthermore, we did not detect a significant loss of size groups ES for the Pantanal and Pampa biomes (Table 5).

Considering each feeding guild separately, we observed different responses for each biome. For carnivores, the loss of ES per size group was not significantly different for Brazil, Amazon, Pantanal, and Pampa. We observed the expected trend for Caatinga and Atlantic Forest (Table 5). For the Cerrado, we observed the expected trend for all groups except for carnivores and nectarivores (Table 5). For Brazil, Cerrado, and Atlantic Forest, we observed the loss of ES per size group according to expectations for frugivores. The expected trend was observed only for insectivores in the Atlantic Forest and for most

other biomes, we found only a partial corroboration. Finally, nectarivores were the only group with a consistent response but presented the opposite pattern than expected (i.e., small species being more impacted than medium-size species).

## Species Richness, Redundancy, and Ecosystem Service Maintenance

Our results indicated that reducing area of occurrence and loss of species impacted the provision of ES by bats in Brazil. However, such changes vary among biomes (Table 6). For Atlantic Forest and Cerrado, both factors significantly reduced the ES index values for multiple groups. For instance, for frugivores and nectarivores, the reduction of species richness and occurrence area had significant relationship with the loss of ES in Cerrado (Medium frugivores species loss:  $t = -4.808$ ,  $p < 0.001$ ; Medium frugivores occurrence area reduction:  $t = 7.674$ ,  $p < 0.001$ ) (Table 6). A similar pattern was found for the Atlantic Forest, where loss of species and occurrence area reduction were relevant, but only for small nectarivores (Small nectarivores species loss:  $t = 2.494$ ,  $p < 0.05$ ; Small nectarivores area reduction:  $t = 7.121$ ,  $p < 0.05$ ). For the other bat groups only one of the factors significantly reduced the ES index values. For example, small insectivores associated services were affected only by the loss of species, whereas medium insectivores, only by the reduction of occurrence area (Small insectivores:  $t = -3.535$ ,  $p < 0.05$ ; Medium insectivores:  $t = 7.572$ ,  $p < 0.05$ ). For the biomes of Amazon, Caatinga, and Pampa only the reduction of occurrence area was significantly associated with the loss of ES index values for all guilds and sizes (Table 6).

## DISCUSSION

Our results reflect distributional patterns of ES provisioning potential and overall functional impacts of natural area suppression on regional bat assemblages across Brazil. We observed that ES index values vary between biomes, indicating regional differences in the composition of species available for service provision. Furthermore, guilds are differently impacted by land conversion with no apparent pattern. This indicates that different functional groups should be the focus of conservation actions in different regions. However, we did find a general relationship between the magnitude of loss and species body size. Except for nectarivores, in all other guilds and guilds combined, larger bats were generally more impacted by natural habitat conversion than the other size classes. Thus, larger bats have lost a greater extension of environmentally adequate area within their distribution and are disappearing at a faster rate than their smaller counterparts. By our assumptions, these species hold greater ES provisioning importance, and such pattern of losses should come with greater ecological impact. This general pattern of downsizing and its functional consequences have been documented for other taxonomical groups (Dirzo et al., 2014; Galetti et al., 2015; Donoso et al., 2020).

Generally, biomes held an above average potential for ES provisioning for about half of their territories. This means that about half of each biome is represented by essential areas for ES provision due to their predicted high provider richness (Isbell et al., 2011). Consequently, these regions should be safeguarded from further degradation if we aim to keep historical levels of ES potential in our biomes. However, the natural area suppression culminated in expressive loss of ES index values for large extensions across biomes. Considering a habitat threshold of 50% remaining area, biomes such as Atlantic Forest, Cerrado and Pampa have over half of their territories below this limit. This is a worrisome scenario since bat communities were shown to be sensitive to habitat loss, presenting a higher-than-average habitat threshold before abundances and diversity start to accentually drop (Muyllaert et al., 2016). This means that these extensive areas likely hold impoverished communities despite their potentials to hold above area average diversity and provide above average levels of ES.

### How Are We Losing Services?

ES provisioning potential is being lost across Brazil through two main processes. First, by guild occurrence area reduction where land conversion shrinks the available suitable area for species within a guild. This habitat area reduction likely culminates in population declines, negatively impacting ES provision numerically (Kremen, 2005; Watling et al., 2020). Second, by the loss of species. Some species may lose all their previously available area to land conversion and be considered locally extinct. This reduces the number of provider species present and adds yet another layer of ES vulnerability, the loss of redundancy within guilds (Elmqvist et al., 2003). One can imagine that ES can be sustained in low provider richness situations if the populations of the few species present

are healthy enough to maintain a stable provision (Kremen, 2005). However, habitat loss affects both species population and communities' composition, likely affecting ES provision and stability synergistically (Oliver et al., 2015).

Both processes (i.e., occurrence area reduction and species loss) were not always relevant for all groups within all biomes. Meaning that some groups' associated services were more impacted by area reduction, species loss or both. This is to be expected since guilds are differently distributed across biomes and biomes have different histories of occupation (Lapola et al., 2014). For example, for biomes where anthropogenic occupation is advanced (e.g., Cerrado and Mata Atlântica), both processes seem relevant, although not for all size groups within guilds. This means that beyond occurrence area reduction, species are being lost and this is also significantly impacting the ES potential of the region. Consequently, these regions are experiencing a strong enough loss of provider richness that outweighs the compensational effects of the remaining species within the assemblage. On the other hand, biomes where anthropogenic occupation is not yet as drastic or follows different spatial patterns (e.g., Amazon and Caatinga), reduction of occurrence area is the main driver of ES index values differences. Thus, area reduction is driving the observed differences in ES values, meaning that the functional impact of species losses is being buffered by the functional effect of remaining species. In the scenario, ES should be better safeguarded through mechanisms of redundancy. Are we losing ecosystem services?

Studies on bat's provision of ecosystem services have mainly focused on the aggregate function (i.e., the service resulting from the ensemble of providers present, Kremen, 2005). For example, a common practice for the studies on pest suppression is enclosure experiments (Maas et al., 2016). While these studies offer essential insights on local diversity impacts on crop yield and quality (Williams-Guillén et al., 2008; Maas et al., 2013; Maine and Boyles, 2015), little light is shed on the dynamics of provision. Even with the aggregate service measure at hand (e.g., number of fruit sets, plant damage), questions of how much diversity is needed for the desired outcome or which species/traits are associated with the effectiveness of service delivery remain unanswered. As such, these results offer evidence for service existence while making good cases for conservation of bat diversity, accounting for the importance of maintaining multiple species contributions to a service (Elmqvist et al., 2003; Aguiar et al., 2021). In other words, the importance of maintaining high provider richness (Isbell et al., 2011).

Thus, conservation of guild diversity is an essential precautionary approach to ecosystem services persistence in front of uncertainties in the dynamics of provision since it aims to secure function stability (Walker, 1992). As we assumed, function stability implies redundancy, which implies replacement among species (Luck et al., 2009). Through our classification, the potential for redundancy (i.e., the number of species for replacement) decreases as body size increases. This is a pattern observed on mutualistic networks (Zamora, 2000). It means that the local loss of larger species with relatively greater functional

importance should come with greater functional consequences due to reduced stability and the trait-limited possibility of compensatory responses from other species. Consequently, this may result in rapid function loss (Kremen, 2005). As reported, we observed such general pattern, but our results cannot ascertain that this is happening because we are not actually measuring ES provision, we calculated a proxy theoretically associated with the potential for ES provision.

Furthermore, in the case of redundancy, the very own capacity of the bat population to respond in a compensatory way should be experimentally investigated. Neotropical bat communities are not consistently structured by competitive interactions (Stevens and Willig, 2000), and bat species are long-lived organisms with low fecundity (Findley, 1993). Thus, bats are likely not responsive to population fluctuations and not capable of the rapid growth such compensatory responses require. Instead, due to their high mobility, function stability might depend on a rescue effect from surrounding populations, which suggests the importance of biodiversity conservation on a landscape scale and the preservation of diversity sources (Tscharntke et al., 2005; Farneda et al., 2018). We argue that areas with above average ES index values should be considered diversity sources for regional ES provision and, as such, should be of conservational focus and restoration actions.

Despite the uncertain role of redundancy in bat function stability, guild diversity can enhance aggregate function through mechanisms of species complementarity (Gaston and Spicer, 2004; Williams-Guillén et al., 2008; Aguiar et al., 2021). Bats exploring similar resources separate their uses in space and time (i.e., niche partitioning) (Arlettaz et al., 1997; Schnitzler and Kalko, 2001; Lopez and Vaughan, 2007; Amaral et al., 2016). Consequently, species performing similar functions at different spatial-temporal scales provide stability to ecosystem services provision (Peterson et al., 1998). This reiterates the importance of conserving the natural levels of diversity of regional bat assemblages. However, in the finer scale of ecological function, species likely differ in their potential contribution to ecosystem services provision, and body size, as we assumed, could be a trait dictating this in bats, as it is on other vertebrates (Luck et al., 2012). If such is proven, it is also a well-established response trait indicating vulnerability to disturbances like habitat fragmentation (Schulze et al., 2000; Farneda et al., 2015) and greater attention directed toward those species.

Identifying potential key provider species and their contributions to aggregate function and the stability of associated ES is crucial and urgent. The current trend of rapid destruction of native habitat may be leading to the disruption of ecosystem functioning and service provision with unknown consequences. The true state of the functional contribution of bat species and assemblages across Brazil to ecosystem service provision is yet to be described. As we stated, our results reflect general patterns, and any attempt to describe the effective distribution of ES provision by bats would be speculative. Many assumptions remain to be tested for our understanding of the dynamic ES provided by bats

to be consolidated. For now, we may be losing the benefits provided by these populations without even acknowledging their existence. Although Brazil is one of the countries with the most incredible diversity of bat species (181), this diversity could not be completely represented in our study for a couple of reasons. First, there are not enough records of good enough quality for all species to be modeled. In our study, seventy-eight species (42.6%) could not be modeled due to the lack of records. Secondly, Brazil is large country where only a few areas were well surveyed, remaining many areas with very few surveys. This causes an imbalance on the representation of the environmental space occupied by large ranged species that resulted in badly fit models even for species that had sufficient occurrence records (e.g., *Desmodus rotundus*, *Carollia perspicillata*, etc.).

If, on the one hand, the species that we modeled were sufficient to produce a scenario of the potential provision of ecosystem services in Brazil and its biomes, on the other, we detected that there is still a large gap to be filled concerning the occurrence of species in Brazil, as already pointed out by Bernard et al. (2011) and Aguiar et al. (2020). The search for records must be done optimally since the inclusion of new records in little-known regions can substantially alter the distribution modeling results (Aguiar et al., 2015). Furthermore, the study on bat's contribution should be done at the scale of the service, but country scale descriptions of species distribution must also continue in parallel. This way we can continue to improve our methods for large-scale descriptions of ecosystem service provision and better incorporate this aspect in future conservation plans.

## CONCLUDING REMARKS

Our results showed how the potential for ecosystem services provision associated with each bat guild is differentially distributed across Brazil, how each biogeographical region holds different species assemblages of providers, and how habitat conversion is affecting these groups. Our study is limited to descriptions and presents the many pros and cons of the SDM method (See Delgado-Jaramillo et al., 2020). Many questions about the role of bats in the provision of ecosystem services need to be further addressed. How much diversity is needed for the desired outcome of an ecosystem service? What is the relative role of abundance and species richness in ecosystem service provision? Which species are the key ecosystem service providers? Is aggregate function in high diversity areas different from those found in less diverse areas? How land use affects aggregate function? The answer to those questions will deepen our understanding of the underlying role of bat species as ecosystem services providers in Brazil and how our interventions on the landscape have been affecting such contributions. Nevertheless, we believe our results can substantiate public policies for the identification of degraded areas where redundancy is not yet completely lost and historical levels of ecosystem service provision can be regained by restoration. We suggest that



degraded area restoration should be promoted in areas with high ES values and areas near cities and croplands and that a precautionary approach of promoting the conservation of high provider richness should be applied to protect the continuation of bat's ES.

## DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: Species data available at: doi:10.5061/dryad.c59zw3r5.

## AUTHOR CONTRIBUTIONS

LA and LB contributed to conceptualization of the study. LA organized the database. RM and LB performed the analysis. LB wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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# Aerial insectivorous bats in the Brazilian-Uruguayan savanna: Modelling the occupancy through acoustic detection

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The Pampa is the least protected and one of the least sampled for bats among the Brazilian domains. This leads to significant Linnean and Wallacean shortfalls for bats in the Brazilian-Uruguayan savanna ecoregion. Here, we aimed to model the occupancy of aerial insectivorous bats in response to landscape structure at different scales, considering the influence of microclimate on bat detection. We acoustically monitored 68 locations during the spring and summer of 2019/2020, gathering data on temperature and humidity associated with each acoustic record using data loggers. We detected at least 11 species of the Molossidae and the Vespertilionidae families, of which 9 were used in the model. The response to landscape structure was species-specific: the occupancy probability of *Eptesicus brasiliensis* and *Molossus* cf. *currentium* increased with landscape connectivity at the 500 m scale while *Eptesicus furinalis* and *Histiotus* cf. *velatus* were negatively affected by landscape connectivity at the 5.0 km scale. *Molossus* occupancy probability responded negatively to landscape heterogeneity at the 3.0 km scale, while *Promops centralis* responded positively to landscape heterogeneity at the 5.0 km scale. *Molossus rufus* responded negatively to native vegetation cover and positively to landscape heterogeneity at the 5.0 km scale. *Myotis albescens* and *Molossops temminckii* did not respond significantly to any of the evaluated landscape metrics. Our results show that different bat species perceive the landscape differently, regardless of the guild of use of space – edge- or open-space forager. Our estimate of projected occupancy for the areas contiguous to those sampled ranged from 0.45 to 0.70 for the whole of the bat taxa, suggesting that the landscape, particularly where it still maintains its native elements, is reasonably favourable to aerial insectivores.

## KEYWORDS

acoustic monitoring, Chiroptera, landscape structure, microclimate, site occupancy



## Introduction

Habitat loss, fragmentation, and degradation are the most cited causes of species extinction and biodiversity decline globally (Taubert et al., 2018). Intensive land use changes alter the structure of the landscape and limit the potential occurrence, dispersal, and colonisation by different species (Fahrig, 2003; Jetz et al., 2007; Crooks and Sanjayan, 2010). The conversion of open habitats into monoculture plantations of fast-growing trees or their degradation through intensive use for agriculture and livestock production has changed the dynamics and structure of the landscape (Ellis et al., 2010; de Oliveira et al., 2017; Souza et al., 2020). Such landscape changes are of particular concern in tropical countries (Phalan et al., 2013), like Brazil, which despite being a megadiverse, is also one of the world's largest producers of agricultural commodities (Myers et al., 2000; de Sousa-Neto et al., 2018).

The main consequence of intense land use change is habitat homogenisation. This is of particular concern as heterogeneous and complex environments are drivers of diversification, governing species turnover (Tews et al., 2004). Indeed, patches and networks of distinct natural elements provide increased resource availability, including food, roosts and shelters, and niche space for other activities throughout the animals' life histories, favouring increased coexistence, persistence, and species diversification (Stein et al., 2014). The diversity of natural elements between different habitats is also paramount for landscape connectivity (Bennett et al., 2006). Indeed, connectivity is a key element in landscape structure and can be defined as the degree to which the landscape facilitates or restricts the movement of organisms between fragments (Calabrese and Fagan, 2004; Taylor et al., 2010). The smaller the distance between patches of similar habitat, the more connected they are. Patches that are more connected to each other facilitate exchanges between subpopulations, reducing the risk of population decline and local extinction (Bennett et al., 2006).

In addition to connectivity and heterogeneity, the amount of available habitat is another factor explaining species richness and diversity across landscapes and is usually a better predictor of these biodiversity dimensions than the size or isolation of a given fragment, as proposed in the habitat amount hypothesis (Fahrig, 2013). Furthermore, different animal species respond differently to landscape structure and this response may be affected both by spatial and temporal scales (Wiens, 1989; Chave, 2013). However, our understanding is still poor of how changes in the landscape, especially those resulting from anthropogenic action, affect the components of biodiversity, including different taxa, different diversity facets, and different environmental and landscape scenarios.

Brazil harbours a rich bat fauna, with 182 species recognised to date (Garbino et al., 2020, 2022). Insectivorous species constitute half of this diversity and are, in general, poorly

sampled throughout Brazil, since most studies on neotropical bats have been carried out on species more easily captured by mist nets (but see Arias-Aguilar et al., 2018; Hintze et al., 2020; Falcão et al., 2021). Species of this guild have great potential as bioindicators of environmental quality (Jones et al., 2009), playing an important role as biological control agents in altered landscapes, acting in the suppression of insect populations, including pests of agricultural crops (Cleveland et al., 2006; Rodríguez-San Pedro et al., 2018; Cohen et al., 2020; Kolkert et al., 2020; Aguiar et al., 2021). Despite this, bats may have different sensitivities to changes in landscape composition and structure. Such sensitivity depends on intrinsic factors that include body size, diet, flight, and dispersal abilities (Schnitzler et al., 2003; Lino et al., 2019). Undeniably, species with greater ability to fly and disperse are more likely to persist in altered landscapes, because they can search for favourable habitats within a less favorable matrix, while less vagile species may not be able to do the same, becoming restricted to suboptimal habitat conditions, with potentially severe consequences for their genetic diversity (Lino et al., 2019) and, ultimately, for their persistence.

Climate, habitat, and biotic interactions seem to be the factors most contributing to differences in bat composition, activity, and diversity (Estrada-Villegas et al., 2012; Appel et al., 2021; da Costa et al., 2021; Smith et al., 2021; Ramos Pereira et al., 2022). Climatic conditions are responsible for determining the temporal and spatial availability of resources at large scales and, at small scales may impose activity restrictions associated with metabolic costs, for instance, those associated with maintaining high and stable body temperatures when the ambient temperature is low. Moreover, the effects of temperature and relative humidity influence, in a complex and non-linear way, the propagation and attenuation of sounds emitted by echolocating bat species (Snell-Rood, 2012; Mutumi et al., 2016; Chaverri and Quirós, 2017). In terms of spatial resolution, different bat guilds perceive their habitat in different ways, both in terms of scale and landscape pattern (Bellamy et al., 2013; Ducci et al., 2015; Mendes et al., 2017; Falcão et al., 2021). So, due to the specificity of bat responses to the landscape, it is important to understand how different species and guilds respond to different habitat changes and configurations, considering the matrix and its quality.

The Uruguayan savanna ecoregion extends from the extreme south of Brazil, throughout Uruguay and a small section of the Argentinean province of Entre Ríos. In Brazil, this ecoregion is represented by the Pampa, characterised by extensive natural grasslands with shrubs and rocky outcrops (Pillar et al., 2009). In recent decades, the Pampean landscape has suffered with the conversion of natural areas into monocultures and the introduction of exotic species in silviculture (Roesch et al., 2009). Recent estimates indicate that the Pampa lost 21.4% of the remaining native vegetation cover between 1985 and 2020, remaining only 46% of the

original landscape (Souza et al., 2020). Although the Pampa is widely studied from the floristic point of view and in what concerns past and present human occupation (Guido et al., 2016; Leidinger et al., 2017), it remains largely understudied about the geographic distribution and patterns of occupancy of many animals (Konze, 2015; Queirolo, 2016; Tirelli et al., 2018). Bats are no exception to this pattern (Bernard et al., 2011), while it is known that most species occurring here are aerial insectivores, either open-space or edge-space foragers (Noronha, 2016).

Here, we use the history of acoustic detection and non-detection of bats to investigate the influence of landscape structure and microclimate on the occupancy and detection of aerial insectivores in the Brazilian Pampa. We hypothesise that the detection of all species should be influenced by microclimatic variables, and we predict that bat activity and, consequently bat detection, will increase positively with temperature, due to increased activity of their ectothermic prey, flying arthropods, and humidity, due to increased airborne sound propagation. Extremely low or high temperatures or humidity levels should negatively influence bat detection due to increased costs with thermal balance and reduced sound propagation or unpredictable echo behaviour in the lower and upper extremes of the humidity, respectively. We also hypothesise that species occupancy is influenced by the structure of the landscape, and we predict that (i) connectivity between patches of the same habitat positively affects the occupancy of edge-space foraging bats, as this guild should be favoured by forest patches offering extra roosts, perches, and food resources; (ii) heterogeneity should affect positively the occupancy of open-space bats, by favouring a more diverse and abundant prey community at different times of the night; and (iii) a greater amount of native vegetation cover should positively affect all species occurrences, as it offers greater carrying capacity, but potentially influencing, even more, the occupation of edge foragers.

## Materials and methods

### Study area

We sampled five areas in the Brazilian Pampa (within the Brazilian-Uruguayan savanna ecoregion; Figure 1) in the municipalities of Alegrete, Cacequi, and Quaraí, spanning a wide range of pristine habitats, including native grasslands, meadows, gallery forests, shrub formations, and rock outcrops, as well as areas that harbour different levels of cattle raising on natural grasslands and agriculture performed in converted areas. Sampling sites were classified into one of the two main physiognomies occurring in the region: (i) shallow soil fields, mostly composed of undergrowth vegetation, with a predominance of grasses, legumes, and composite plants that

grow from basalt formations with low moisture retention and (ii) mixed stands of andropogon grass, where most of the area has already been transformed into rice and soybean crops; in pastures with overgrazing, the proportion of bare soil increases, benefiting the development of composite vegetation, such as plants of the genera *Soliva*, *Vernonia*, and *Senecio* (Boldrini, 2009).

The climate is sub-tropical, with average annual temperatures ranging from 16 to 22°C and annual rainfall varying from 1,200 to 1,600 mm (Pillar and Lange, 2015). The geological formation is complex, including recent marine sedimentary deposits to ancient pre-Cambrian formations, in some areas of the South-Rio-Grandense Shield (Chernicoff and Zappettini, 2004). The relief is relatively homogeneous and flat, varying from sea level up to about 400 m elevation (Pillar and Lange, 2015). Currently, only 46% of Brazilian Pampa remains covered by native vegetation and only 2% is legally protected by conservation units; this makes the Pampa the least protected domain in Brazil (Souza et al., 2020). Still, many landowners subscribed the Alianza del Pastizal's initiative, aiming for the conservation of natural grasslands through the production of certified environmentally sustainable meat, an initiative led by BirdLife International and developed through local partners in Brazil, Uruguay, Argentina, and Paraguay (Save Brasil, Aves Uruguay, Aves Argentina, and Guyra Paraguay).

### Acoustic monitoring and analysis

We monitored 68 sites located at least 1.5 km apart, during the spring and summer of 2019 and 2020 (Figure 1). Autumn and winter are rainy, windy, and cold, which deemed acoustic bat monitoring inefficient. We sampled bats using automated sound detectors – AudioMoths (Silicon Labs) – set at a sampling rate of 256 kHz, 16 bits, programmed to record cuts of 15 s every 2 min from sunset to sunrise, for at least five nights in each site. We also coupled automated temperature and humidity sensors to each active AudioMoth to obtain detailed information on the microclimatic conditions associated with each bat record.

Species identification was done through manual analysis of recordings in Raven Pro 1.6 Software (K. Lisa Yang Center for Conservation Bioacoustics, 2022) selecting a Hamming window with 1,024 Fast Fourier Transformation (FFT; overlap 93%) to minimise the effect of spectral dispersion. We evaluated the following parameters: the overall shape of the pulse (constant frequency, CF; modulated frequency, FM; quasi-constant frequency, qCF; and variations therein), frequency modulation (FM), number of harmonics (nH), peak frequency (PF), duration (D), inter-pulse interval (IPI), frequency of maximum energy (FME), maximum frequency (Fmax), minimum frequency (Fmin), and bandwidth (BW = Fmax – Fmin). Whenever possible, we identified bat recordings to the species level, following acoustic identification keys for

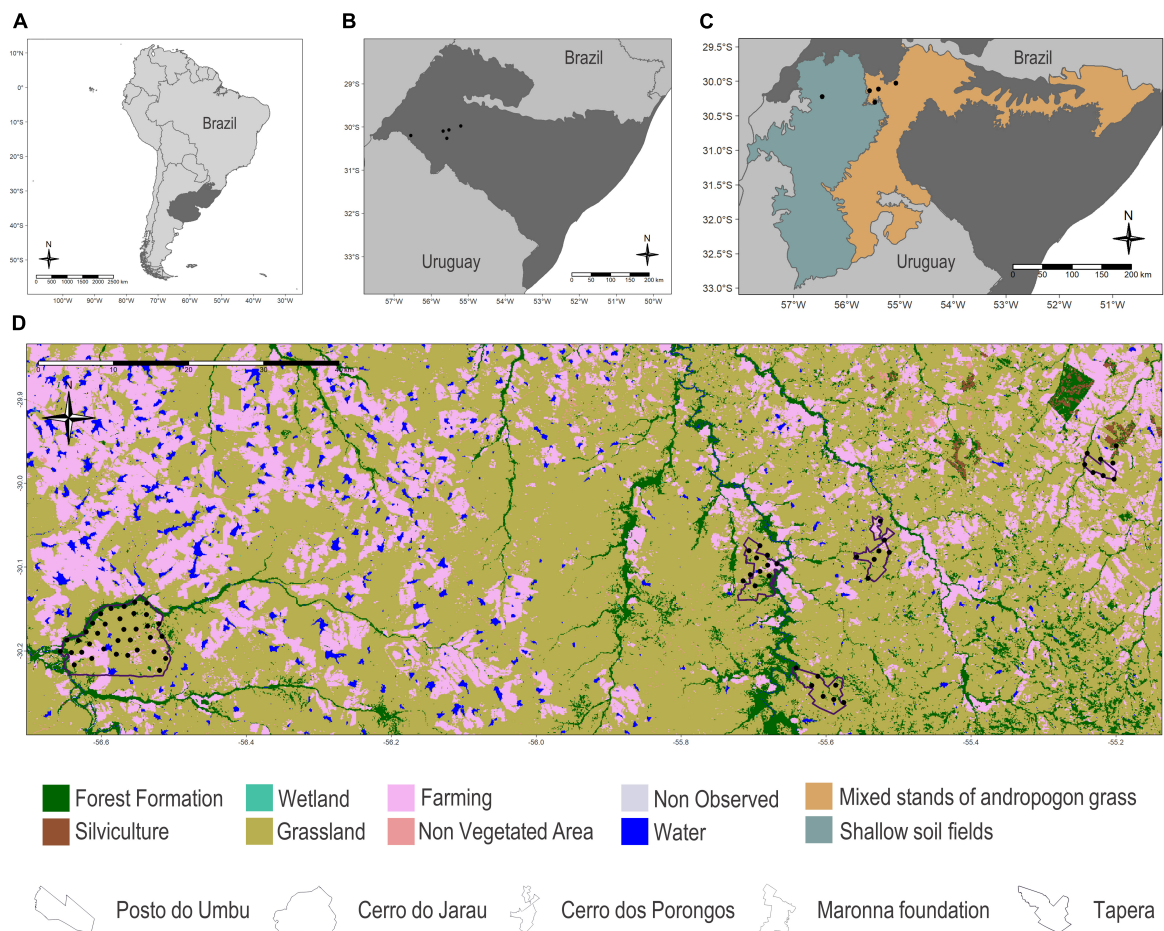


FIGURE 1

(A) Location of the Brazilian-Uruguayan savanna ecoregion within South America in dark grey. (B) Location of the five areas in the municipalities of Alegrete, Cacequi, and Quaraí, Brazilian Pampa, for bat acoustic sampling during the spring and summer of 2019 and 2020. (C) The two main physiognomies occurring in the Brazilian and Uruguayan grasslands: in turquoise the shallow soil fields and in orange the mixed stands of andropogon grass. (D) Land use and land cover map (MapBiomas Pampa Sudamericano Project, 2021) for the five sampled areas (Posto do Umbu, Tapera, Cerro do Jarau, Maronna foundation, and Cerro dos Porongos).

Neotropical and Brazilian bats (Barataud et al., 2013; López-Baucells et al., 2016; Arias-Aguilar et al., 2018). We quantified bat activity using sequences with at least three consecutive good quality (signal to noise ratio  $\geq 12$  dB; Jung et al., 2014) echolocation calls in a recording; each sequence that met this criterion was considered a “bat pass.” Species were classified as edge-space or open-space foragers according to Denzinger and Schnitzler (2013).

## Landscape metrics

To test for spatial autocorrelation in our dataset, we calculated Moran’s I index (Supplementary Table 1) for each sampled area, using the “Moran.I” function from the R package *ape* (Paradis et al., 2019). We obtained the landscape metrics from a categorical land use raster of the Brazilian-Uruguayan

savanna ecoregion for 2019 (MapBiomas Pampa Sudamericano Project, 2021). We created circular buffers of seven sizes (500 m, 1.0 km, 1.5 km, 2.0 km, 3.0 km, 4.0 km, and 5.0 km in radius) using the location of the AudioMoth as a centroid in each sampling site to extract the landscape metrics. Smaller buffers do not reflect the nightly dispersal ability of most of the species that potentially occur in the area. We calculated six structural landscape metrics for all buffers sizes at Landscape and Class levels (Table 1), using a classification raster of eight categories: forest formation, silviculture, wetland, grassland, farming, non-vegetated area, non-observed, and water. For class-level metrics, we used eight directions (queen’s case) that correspond to the number of directions in which patches may be connected, as recommended in McGarigal et al. (2012). All metrics were extracted using the *landscapemetrics* package (Hesselbarth et al., 2019) in R Program version 4.0.4 (R Core Team, 2021).

**TABLE 1** Selected landscape metrics and respective level, code and raster reclassification, for bat acoustic sampled during the spring and summer of 2019 and 2020 in the Brazilian Pampa.

Landscape metric	Level	Code	Raster reclassification
Connectivity – mean euclidean nearest-neighbour distance	Class	Enn_mn	1 = Forest formation, wetland, and water; 0 = all other classes
Favourable landscape (percentage)	Class	Pland	1 = Forest formation, wetland, and water; 0 = all other classes
Native vegetation (percentage)	Class	Pland_nvc	1 = Forest formation, grassland, and wetland; 0 = all other classes
Landscape altered by anthropogenic action (percentage)	Class	Pland_antro	1 = Forest plantation, farming and non-vegetated area; 0 = all other classes
Native grassland (percentage)	Class	Pland_ng	1 = Grasslands; 0 = all other classes
Heterogeneity – Shannon's evenness index	Landscape	Shei	None

## Single-season occupancy models and extrapolations

We used detection/non-detection records to build single-season occupancy models (MacKenzie et al., 2002, 2017). We treated each survey location as a sample unit and each night was halved to represent a survey occasion, resulting in two occasions per night per site. We used mean temperature and mean air relative humidity as detection covariates ( $p$ ). We used the abovementioned landscape metrics as occupancy covariates ( $\Psi$ ). All covariates were standardised by subtracting the mean and dividing by the standard deviation, resulting in mean  $\mu = 0$  and standard deviation  $\sigma = 1$ . Multicollinearity was evaluated using the variance inflation factor (VIF), using the “vifstep” function from R package *usdm* (Naimi, 2017), and only variables with  $VIF < 3$  were used for the modelling (Zuur et al., 2010). After the VIF analysis, our model included three landscape metrics at all selected scales (Enn\_mn, Shei, and Pland\_nvc), all showing a VIF value below 3 (Supplementary Table 2).

We fitted all models using the “occu” function in the *unmarked* R package (Fiske and Chandler, 2011). Detectability was modelled using the covariates mean relative humidity (humi) and mean temperature (temp), including the null model. Occupancy probability was modelled using the best detection model combined with landscape variables at each of the seven scales analysed, totalling 4 models for detection (Supplementary Table 3) and 21 models for occupancy by species (Supplementary Table 4). We ranked the models using the second-order Akaike Information Criterion (AICc) and the determination coefficient ( $r^2$ ), and considered as the best-supported models for those with  $\Delta AICc < 2$  (Burnham and Anderson, 2002). To evaluate models' goodness-of-fit (GoF), we used three discrepancy measures: sum of squared errors, Pearson's Chi-squared, and Freeman-Tukey Chi-squared, with at least 1,000 bootstraps. Additionally, to evaluate the model's fit based on the frequencies of the detection histories, we used the goodness-of-fit test recommended by MacKenzie and Bailey (2004), where well-fitted models should return a  $p$ -value  $> 0.05$ . As a measure of dispersion, we used the  $c$ -hat value as follows:  $c$ -hat  $< 1$  indicates underdispersion, we keep the value of  $c$ -hat at 1;  $1 < c$ -hat  $< 3$  indicates moderate

overdispersion, so we multiply the variance-covariance matrix of the estimates by  $c$ -hat, and as result, the SEs of the estimates are inflated, according to Burnham and Anderson (2002). This was done using the R package *AICcmodavg* (Mazerolle, 2020). To predict the probability of occupancy at each location, we used the “modavgPred” function in the *AICcmodavg* R package (Mazerolle, 2020), while considering the uncertainty of defining the best model using the averaged parameters across the best-ranked models ( $AICc < 2$ ; Burnham and Anderson, 2002). In addition, we also used the average of the best models to see how occupancy changes with the covariates.

To spatially extrapolate our results, we used a raster of the MapBiomass at a scale of 1:250,000 (MapBiomass Pampa Sudamericano Project, 2021) and cropped it with the adapted shapefile of ecological systems from the Uruguayan Savanna Ecoregion at a scale of 1:500,000 (Hasenack et al., 2010). With the final raster on the scale of 1:250,000, we extracted the polygons representing the two main sampled phytophysiognomies (shallow soil fields and mixed stands of andropogon grass), covering areas of the Brazilian and Uruguayan Pampa for each modelled scale. We created a square grid for each scale modelled on the entire polygon, extracted the coordinates of each cell, and extracted the same landscape metrics used as occupancy covariates, creating a new data frame to predict and extrapolate species occurrence across the region, using the model-averaged parameters. We standardised this data, by the mean and standard deviation, and used this information to extrapolate our predictions and to create occurrence maps for each species for the region using *raster* (Hijmans, 2012), *rgdal* (Bivand et al., 2015), *sp* (Pebesma and Bivand, 2005), and *tmap* R package (Tennekes, 2018).

## Results

We detected bat-passes in 8,111 (8.15%) out of 99,526 recordings. We recognised the occurrence of at least 23 taxa in the studied area, and we were able to identify 11 species of the Molossidae and the Vespertilionidae families. Four species were categorised as open-space foragers – *Molossus* cf.



**TABLE 2** Total number of bat passes in each of the five sampled areas, and information on species, family, and foraging guild, regarding bat acoustic sampling during spring and summer 2019 and 2020 in the Brazilian Pampa.

Family	Species	Foraging guild	TA	CP	MA	PU	CJ	Total
Molossidae	<i>Molossus cf. currentium</i>	Open-space	0	3	13	184	312	512
	<i>Molossus molossus</i>	Open-space	0	0	1	11	69	81
	<i>Molossus rufus</i>	Open-space	2	10	48	347	75	482
	<i>Promops centralis</i>	Open-space	2	17	124	126	156	425
	<i>Molossops temminckii</i>	Edge-space	8	29	139	39	203	418
Vespertilionidae	<i>Eptesicus brasiliensis</i>	Edge-Space	0	2	4	36	175	217
	<i>Eptesicus furinalis</i>	Edge-Space	0	22	12	291	1234	1559
	<i>Histiotus cf. velatus</i>	Edge-Space	2	9	11	148	478	648
	<i>Lasiurus blosevillii</i>	Edge-Space	1	0	3	5	15	24
	<i>Myotis albescens</i>	Edge-Space	2	1	42	8	30	83
	<i>Myotis ruber</i>	Edge-Space	0	1	0	0	8	9
			17	94	397	1.195	2.755	4.458

Area's abbreviations: TA (Tapera), CP (Cerro dos Porongos), MA (Maronna), PU (Posto do Umbu), and CJ (Cerro do Jarau).

*currentium*, *Molossus*, *Molossus rufus*, and *Promops centralis*. Seven species were categorised as edge-space foragers, including one molossid – *Molossops temminckii* – and six vespertilionids – *Eptesicus brasiliensis*, *Eptesicus furinalis*, *Lasiurus blosevillii*, *Myotis albescens*, *Myotis ruber*, and *Histiotus cf. velatus* (Table 2).

## Site occupancy models

*Lasiurus blosevillii* and *Myotis ruber* were excluded from occupancy modelling because they accounted for less than 1% of the total bat passes. Of the nine bat species included in the occupancy modelling, *E. furinalis* presented the highest finite-sample occupancy ( $\psi_{FS} = 55.97$ ), followed by *M. cf. currentium* ( $\psi_{FS} = 55.81$ ), *H. cf. velatus* ( $\psi_{FS} = 54.47$ ), *P. centralis* ( $\psi_{FS} = 51.83$ ), *M. temminckii* ( $\psi_{FS} = 47.98$ ), *E. brasiliensis* ( $\psi_{FS} = 44.78$ ), *M. rufus* ( $\psi_{FS} = 44.69$ ), *M. albescens* ( $\psi_{FS} = 36.33$ ) and, finally, *M. molossus* ( $\psi_{FS} = 34.33$ ). Most species were registered in over half the sites; however, the highest number of bat passes does not necessarily reflect occurrence in more sites (Table 2 and Figure 2).

The models of occupancy converged and showed good fits for the nine species, with discrepancy values ranging from 0.01 to 0.93 and c-hat ranging from 0.55 to 2.88. Detection estimates ranged from 0.10 to 0.55, while occupancy estimates ranged from 0.51 to 0.99 (Figure 3).

## Effect of microclimate on bat detection probability

Among the sampled sites, the mean temperature ranged from 8.03 to 31.99°C while the mean relative humidity varied

from 37.1 to 99.88%. Best supported models ( $\Delta AIC_c < 2$  and  $\beta$   $p$ -value  $< 0.05$ ) for the probability of detection varied by species, guild, and scale. Considering the highest weighted models, mean temperature and mean relative humidity positively affected the detection probability of the edge-space forager *E. brasiliensis* and the open-space forager *M. cf. currentium* at the 500 m scale and of the edge-space forager *H. cf. velatus* at the 5.0 km scale (Table 3). The detection probability of the edge-space forager *M. temminckii* increased with mean temperature at the 500 m scale, the open-space forager *M. molossus* responded positively to the temperature at the intermediate scale of 3.0 km, and the edge-space forager *E. furinalis* and the open-space forager *M. rufus* had a similar response, but at the larger scale of 5.0 km. The detection of *M. albescens* and *P. centralis* did not respond to any of the microclimatic variables.

## Effect of landscape structure on bat site-occupancy probability

Considering the highest weighted models, connectivity is increased, that is, the closer the fragments of favourable habitat are, the greater the chances of occupancy by *E. brasiliensis* and *M. cf. currentium* at the 500 m scale. The open-space forager *M. molossus* was the only species whose probability of occupancy responded to landscape heterogeneity, and negatively, at the 3.0 km scale. The probability of occupancy of the edge-space foragers *E. furinalis* and *H. cf. velatus* was negatively affected by connectivity at the 5.0 km scale, while the open-space forager *P. centralis* responded positively to landscape heterogeneity at the same scale. *M. rufus* responded negatively to native vegetation cover and positively to landscape heterogeneity at the 5.0 km scale. Meanwhile, the occupancy of the

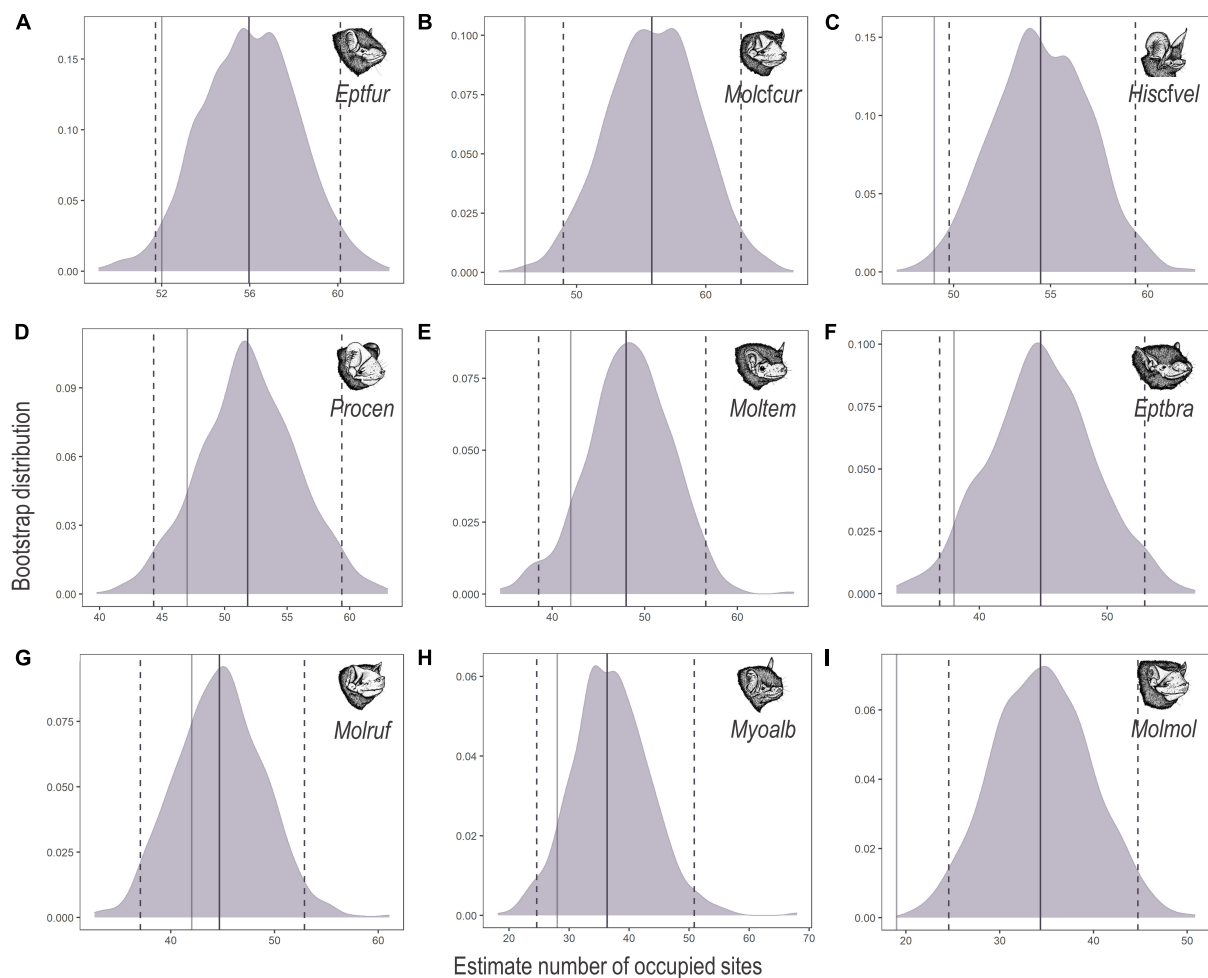


FIGURE 2

Bootstrap distributions of the estimated number of sites occupied ( $\psi_{FS}$ ) by (A) *Eptesicus furinalis* (Eptfur), (B) *Molossus cf. currentium* (Molcfur), (C) *Histiotus cf. velatus* (Hiscfel), (D) *Promops centralis* (Procen), (E) *Molossops temminckii* (Moltem), (F) *Eptesicus brasiliensis* (Eptbra), (G) *Molossus rufus* (Molruf), (H) *Myotis albescens* (Myoalb), and (I) *Molossus molossus* (Molmol) across 68 acoustic survey sites in the Brazilian Pampa during spring and summer 2019 and 2020. Mean occupancy estimates (solid purple lines) and 95% confidence intervals (dashed purple lines) are shown, along with the total number of survey sites at which each species was detected (solid grey lines). Panels are in order of decreasing probability of occupancy.

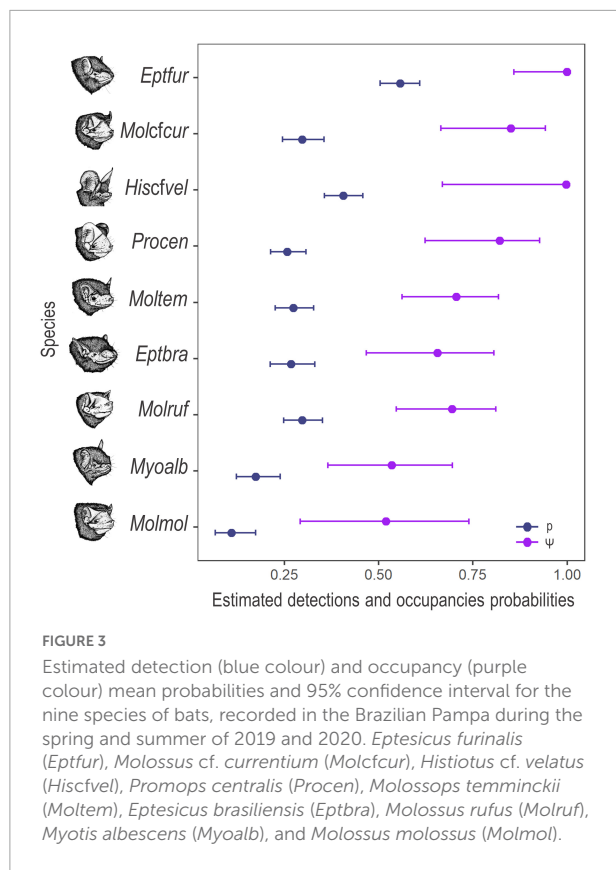
edge-space foragers *M. albescens* and *M. temminckii* did not significantly respond to any of the evaluated landscape metrics (Table 3).

## Spatial extrapolation of the species' occupancy

Species showing the highest estimated occupancy probabilities (values ranging from  $\beta\psi$  0.55 to 1.00) in the two main phytophysionomies – shallow soil fields and mixed stands of andropogon grass – present in the Brazilian and Uruguayan portion of the Uruguayan Savanna were *E. furinalis* and *H. cf. velatus*. Those were followed by *M. rufus* and *P. centralis* (values ranging from  $\beta\psi$  0.34 to 0.99), and finally,

*E. brasiliensis*, *M. cf. currentium*, and *M. molossus* with moderate occupancy probabilities (values ranging from  $\beta\psi$  0.04 to 0.89; Figure 4).

The projected occupancy of the edge-space foragers, *H. cf. velatus*, *E. brasiliensis*, *E. furinalis*, and the open-space forager, *M. cf. currentium*, was higher in areas characterised by native forests including the *espinilho* tree, riparian forests, and water bodies, but was still moderate in areas characterised by monoculture plantations of fast-growing exotic trees and agriculture. On the other hand, the projected occupancy of the open-space forager *M. molossus* was higher in large open areas of native grasslands, with patches of native forest formations and small and medium water bodies, with considerable restriction of potential occurrence in environments with an excess of silviculture and



agriculture. On the other hand, the projected occupancy of *M. rufus* and *P. centralis* was more related to heterogeneous elements of the landscape, floodplains, and large bodies of water, but still moderate in matrices of silviculture and agriculture.

## Discussion

### Different bats perceive the landscape differently

We predicted that species occupancy should be influenced by landscape structure, with structural connectivity as the most important factor affecting the occupancy of edge-space foraging bats. This prediction assumed that, in altered landscapes, well-connected woodland patches should provide increased availability of roosts, temporary perches, and foraging resources, determining the occupancy of edge-space aerial insectivorous bats. Indeed, the occupancy of three of the five edge-space foragers detected, *E. brasiliensis*, *E. furinalis*, and *H. cf. velatus* responded to the structural landscape connectivity, although the first positively and the two latter negatively. Also, the occupancy of the open-space

forager *M. cf. currentium* was positively affected by this landscape trait.

*Molossus cf. currentium* and *Eptesicus brasiliensis* are seldom captured by mist nets and, therefore, we do not have basic information about these species in the Brazilian-Uruguayan savanna ecoregion (Reis et al., 2017; Barquez and Díaz, 2020). Our results indicate that these bats prefer well-connected natural landscape elements rather than extensive open areas or anthropogenic elements at local scales. Similar results were found for aerial insectivorous bat assemblages in modified landscapes of the Brazilian Atlantic Forest, where bat activity and composition responded to landscape structure at small scales (Falcão et al., 2021). Landscape elements, particularly trees, especially in open areas, may provide roosting and foraging sites with potentially greater insect availability and protection from wind (Russ et al., 2003). Open-space foragers, despite their general increased dispersal ability, may also avoid flying in completely open areas to minimise predation risks (Jones and Rydell, 1994) or because they use linear elements of the landscape, such as forest patches, perhaps for increased spatial orientation (Verboom and Huitema, 1997).

The occupancy of *E. furinalis* and *H. cf. velatus* was negatively affected by structural landscape connectivity at a larger scale. Previous studies have shown that the connectivity between forest patches is directly related to the quality and permeability of the surrounding matrix (Kupfer et al., 2006; Watling et al., 2011). In modified landscapes, the matrix can positively influence the occurrence and persistence of many species, for example, by providing greater diversity of prey, corridors, and stepping stones, or negatively, for instance, acting as a dispersal barrier (Ricketts, 2001; Bernard and Fenton, 2007; Watling et al., 2011; Brändel et al., 2020; Farneda et al., 2020; Mendes and Srbek-Araújo, 2021). *E. furinalis* and *H. cf. velatus* seem to avoid areas composed of large extensions of exotic trees and monocultures. Possibly, such a matrix reduces the possibility of acquiring resources, such as food, protection, and roosts even for bats able to fly long distances, making it difficult for them to move between the favourable neighbouring fragments of native vegetation. Occupancy should thus be higher in areas showing small patches of native or riparian vegetation, or even other isolated elements in the landscape, such as scattered trees. Our results are consistent with those found for aerial insectivorous bats in rural landscapes in southeastern Australia (Lumsden and Bennett, 2005) and for fruit bats in the northernmost portion of Mexico (Galindo-González and Sosa, 2008), where in both cases, trees dispersed in rural land mosaics showed high value as foraging or roosting habitat for bats.

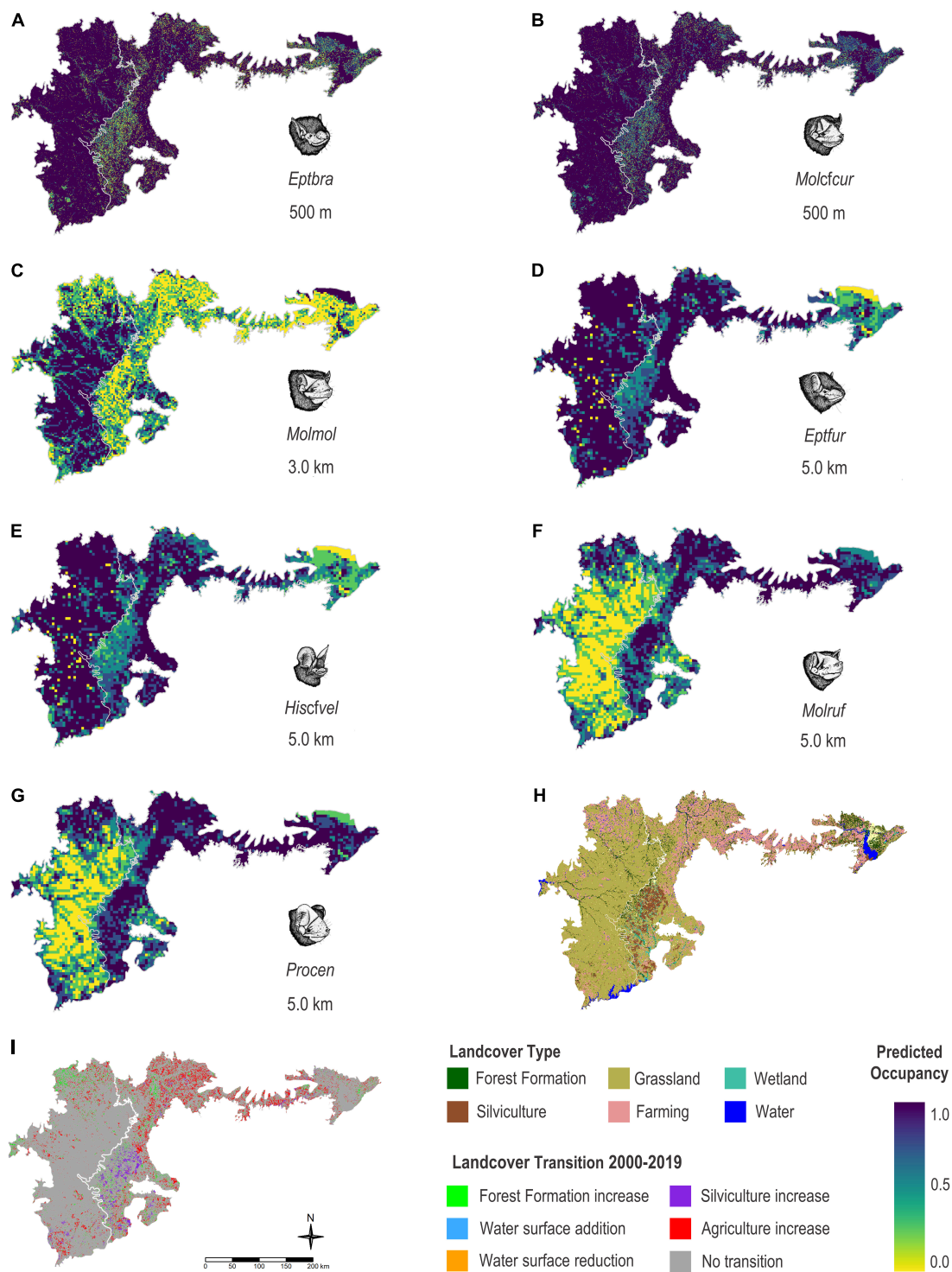
We also predicted that landscape heterogeneity would positively affect the occupancy of open-space bats. Still, only the occupancy probabilities of *P. centralis* increased with

TABLE 3 Summary of the best-fit models and the significant variables for detection ( $p$ ) and occupancy ( $\Psi$ ) for nine species of bats recorded in the Brazilian Pampa during spring and summer 2019 and 2020.

Species	Scale	Model	Intercept	Detection	Intercept	Occupancy	AIC	$\Delta$ AIC	AICwt
			( $\beta$ p; SE)	( $\beta$ p; SE)	( $\beta$ $\Psi$ ; SE)	( $\beta$ $\Psi$ ; SE)			
<i>Eptesicus furinalis</i>	5.0 km	p(temp) $\Psi$ (enn_mn)	(0.23; 0.11)	(1.21; 0.14)	(7.58; 3.95)	(8.34; 3.25)	551.31	0.00	1.00
<i>Molossus cf. currentium</i>	500 m	p(temp + humi) $\Psi$ (enn_mn)	(−0.86; 0.13)	(0.98; 0.15) + (0.23; 0.11)	(1.74; 0.54)	(−1.12; 0.54)	570.57	0.00	0.44
	5.0 km	p(temp + humi) $\Psi$ (pland_nvc)	(−0.83; 0.14)	(0.94; 0.16) + (0.22; 0.11)	(1.78; 0.57)	(−1.43; 0.70)	570.93	0.44	0.36
	4.0 km	p(temp + humi) $\Psi$ (shei)	(−0.88; 0.13)	(0.97; 0.16) + (0.23; 0.11)	(2.05; 0.70)	(1.45; 0.70)	572.11	1.54	0.20
<i>Histiotus cf. velatus</i>	5.0 km	p(temp + humi) $\Psi$ (enn_mn)	(−0.38; 0.11)	(0.64; 0.13) + (0.36; 0.11)	(5.83; 2.62)	(6.75; 2.90)	621.04	0.00	1.00
<i>Promops centralis</i>	5.0 km	p(null) $\Psi$ (shei)	(−1.06; 0.13)		(1.52; 0.52)	(1.33; 0.49)	536.13	0.00	0.70
	5.0 km	p(null) $\Psi$ (l5000 m. pland_nvc)	(−1.04; 0.13)		(1.46; 0.47)	(−1.24; 0.50)	537.84	1.71	0.30
<i>Molossops temminckii</i>	Null	p(temp) $\Psi$ (null)	(−0.97; 0.13)	(0.60; 0.13)	(0.87; 0.32)		508.65	0.00	0.63
<i>Eptesicus brasiliensis</i>	500 m	p(temp + humi) $\Psi$ (enn_mn)	(−1.01; 0.15)	(0.70; 0.17) + (0.27; 0.12)	(0.64; 0.40)	(−1.59; 0.58)	496.31	0.00	1.00
<i>Molossus rufus</i>	5.0 km	p(temp) $\Psi$ (pland_nvc)	(−0.86; 0.13)	(0.38; 0.13)	(0.82; 0.32)	(−1.07; 0.41)	516.38	0.00	0.31
	5.0 km	p(temp) $\Psi$ (shei)	(−0.86; 0.13)	(0.39; 0.13)	(0.75; 0.31)	(0.95; 0.35)	516.70	0.32	0.26
	4.0 km	p(temp) $\Psi$ (pland_nvc)	(−0.86; 0.13)	(0.39; 0.13)	(0.82; 0.32)	(−0.96; 0.38)	517.03	0.65	0.22
<i>Myotis albescens</i>	Null	p(null) $\Psi$ (null)	(−1.56; 0.21)		(0.14; 0.35)		328.91	0.00	1.00
<i>Molossus molossus</i>	3.0 km	p(temp) $\Psi$ (shei)	(−2.10; 0.27)	(1.27; 0.28)	(0.07; 0.49)	(−1.43; 0.64)	242.27	0.00	0.64
	2.0 km	p(temp) $\Psi$ (shei)	(−2.08; 0.28)	(1.24; 0.29)	(−0.06; 0.45)	(−1.11; 0.52)	243.94	1.66	0.28

temp (temperature), humi (relative humidity), enn\_mn (Connectivity), shei (Heterogeneity), and pland\_nvc (Native vegetation).





**FIGURE 4**  
Estimated occupancy for nine species of bats for the area occupied by two main phytophysiognomies present in the Brazilian and Uruguayan portion of the Uruguayan Savanna – shallow soil fields and mixed stands of andropogon grass, based on the modelling results using the bat acoustic data gathered in the Brazilian Pampa during spring and summer 2019 and 2020. (A) *Eptesicus brasiliensis* (Eptbra), (B) *Molossus cf. currentium* (Molcfur), (C) *Molossus molossus* (Molmol), (D) *Eptesicus furinalis* (Eptfur), (E) *Histiotus cf. velatus* (Hiscfel), (F) *Molossus rufus* (Molruf), (G) *Promops centralis* (Procen), (H) map showing landcover types, and (I) map showing the land use and land cover transition between the years 2000 and 2019.

landscape heterogeneity at the largest scale. The occupancy by *P. centralis* seems to be favoured by the combination of suitable habitat patches immersed in a complex mosaic of other land use cover types in the surrounding matrix. Positive relationships between heterogeneous habitats and bat species diversity are well-documented at local and regional scales (Ramos Pereira et al., 2009; Frey-Ehrenbold et al., 2013; Mendes et al., 2017; Monck-Whipp et al., 2018). Artificial elements dispersed in the landscape, such as artificial ponds, created for irrigation in agricultural landscapes, perhaps provide greater variability and availability of foraging resources and drinking opportunities for bats (Korine et al., 2015; Ancillotto et al., 2019). The presence of ponds and even artificial lighting can change the dynamics of competitive exclusion by food disputes between bats with different sensitivities (Arlettaz et al., 2000; Russo and Ancillotto, 2015), promoting more diverse and abundant prey assemblages at different times of the night. Like most molossids, *P. centralis* presents great plasticity in its echolocation calls, probably allowing individuals of this species to explore a wide range of habitats, including urban areas (Hintze et al., 2020).

Contrary to our expectations, the occurrence of *M. molossus* seems to follow an opposite trend – this species preferred less heterogeneous habitats at medium scales (2.0 – 3.0 km). *M. molossus* is considered relatively common in urban areas and usually uses artificial roosts (Pacheco et al., 2010). Despite this, our models suggest that this species avoids areas with excess silviculture, preferring homogeneous areas in large open landscapes characterised by native grasslands and scattered native trees. *M. molossus* seems to take advantage of linear landscape elements, which is in line with previous findings, where linear elements in agricultural landscapes appear to be more attractive for some aerial insectivorous bats (Verboom and Huitema, 1997; Boughey et al., 2011; Toffoli, 2016; Rodríguez-San Pedro et al., 2018; Finch et al., 2020), probably because they are used as orientation landmarks and reference points during flight (Schnitzler et al., 2003; Schaub and Schnitzler, 2007), creating corridors for daily commute routes or occasional regional dispersal (Gelling et al., 2007).

Increased native vegetation cover does not favour the probability of occupancy of the black mastiff bat, *M. rufus*, contradicting our hypothesis that this landscape feature would favour the occupation of all species, especially the edge-space foragers. *M. rufus* is the largest species of this genus in the Brazilian territory and presents gregarious and synanthropic habits (Barquez et al., 1999; Esbérard et al., 1999). Our results suggest that, as for *P. centralis*, *M. rufus* presents higher occupancy in areas with greater heterogeneity and environmental complexity. This is especially concerning as areas, where the occupancy of the two species is maximum, are being rapidly converted by

humans, through intensive livestock production in natural grasslands, and silviculture and agriculture in otherwise converted fields.

Finally, edge-space foragers *M. temminckii* and *M. albescens* did not respond to any landscape metrics at the different scales evaluated. *M. temminckii* is the only species of the Molossidae capable of exploring background-cluttered environments while remaining able to exploit clearings and overall open environments, by changing from short downward frequency-modulated calls with short pulse intervals in cluttered environments to long upward frequency-modulated calls with longer intervals and shorter bandwidth in uncluttered sites (Oliveira et al., 2018). *M. albescens* is one of the most widely distributed species of its genus, occurring from southern Mexico to Brazil (Braun et al., 2009), this may be mirrored by a wide dietary plasticity, favoured by the changes in the activity of different species of prey at different thermal niches during the night. *M. albescens* is known for its trawler-style foraging and is therefore often captured in wetlands, using its high-frequency echolocation calls to detect its prey and capture it with its feet (Fenton and Bogdanowicz, 2002). Perhaps the phenotypic plasticity of *M. temminckii* and the foraging style of *M. albescens* make them less sensitive to connectivity, heterogeneity, or the amount of native vegetation cover in open grasslands at the analysed scales or they perceive the landscape at even larger scales. Due to the high specificity of bat responses to landscape configuration, the multiple-scale approach proved to be crucial to understand how bats respond to different changes in the composition and configuration of the landscape, considering the matrix and its quality (Meyer and Kalko, 2008; Martins, 2016).

## Microclimate and bat detection: Finding species optimum detection interval

Temperature and relative humidity had, overall, positive effects on the detection of most bat species. However, nightly temperatures probably did not get high enough (maximum temperature recorded 33°C, but in 95% of the nights below 20°C) to test the prediction that, above a given limit, bats would decrease their activity in response to the increased cost of overheating. However, our data suggest that the optimum temperature range is between 19°C and 24°C, the interval within which we recorded most bat passes (Supplementary Figure 1). Generally, the feeding activity of aerial insectivores tends to increase on warmer nights due to the greater activity of their prey, flying arthropods (Racey and Swift, 1985; Aldridge and Rautenbach, 1987; Schowalter, 2006). Thus, we can assume that if bats are more active, they will soon be more detected, as has been effectively

observed in temperate environments (Kaiser and O’Keefe, 2015; Blakey et al., 2019). Still, above certain temperatures, the cost of endothermy, specifically cooling may become too high for animals with such increased metabolism. Indeed, despite the advantages and efficiency of air transport, the flight is a metabolically expensive mode of locomotion: the metabolic rates of flying bats can be as high as 3 to 5 times those of terrestrial mammals of the same size, with heart rates going over 1,000 beats per minute (Thomas and Suthers, 1972; Maina, 2000). Bats have several metabolic adaptations and perhaps they also show behavioural adaptations, avoiding too high temperatures even if their preys are still available, particularly if the gain by ingestion does not compensate for the physiological risk of overheating. However, nightly temperatures above 25°C seem to be rare even in the Pampean summer, so a scenario where bats trade-off hunting for inactivity because of potential overheating seems unlikely.

## Reducing the Wallacean shortfall through acoustic monitoring

Here, we present the first comprehensive study of aerial insectivorous bats in the Brazilian Pampa using acoustic monitoring. Previous records resulted almost exclusively from mist-net sampling and roost searches (but see Barros, 2012), and represented less than 20% of the species occurring in Brazil (Garbino et al., 2020, 2022). With acoustic monitoring we added to the Pampa biome, records for two new species – *P. centralis* and *M. cf. currentium* – and records for at least six species from the genera *Cynomops*, *Eumops*, *Nyctinomops*, *Eptesicus*, *Histiotus*, and *Molossus* were to be identified in the future, when we can unambiguously identify the species of those complexes through their echolocation calls. Therefore, we estimate that the bat fauna of the Brazilian Pampa may easily exceed 40 species. Through acoustic monitoring, it is evident that the bat fauna of the Pampa is far more diverse than previously thought, deserving more attention, both from researchers and government agencies.

Most detected species are categorised as least concern, although *E. brasiliensis* and *P. centralis* are also still lacking basic ecological information, including distribution ranges, population sizes, and regional threats to their conservation, which is certainly preventing an adequate assessment of their conservation status; *M. cf. currentium* is classified as data deficient in Brazil (ICMBio, 2018). Indeed, it was recently shown that the distribution of *P. centralis* is much broader in South America than previously predicted, adding over 3.8 million km<sup>2</sup> to its former known area (Hintze et al., 2020). Our work has shown that the distribution

of this species goes even further south in the Neotropic and that its occupancy is far from low in the Pampean landscapes. Also, if confirmed, the detection of *M. cf. currentium* would represent the southernmost record of the species in Brazil, and the first for the Brazilian portion of the Uruguayan Savanna; this species also shows a high probability of occupancy in the region, potentially suggesting that this is not its distribution limit and that, perhaps, it has a much wider distribution range than previously thought.

The occupancy estimates projected for the regions neighbouring those sampled suggest that the landscape is reasonably favourable for the overall assemblage of aerial insectivorous bats, particularly the areas with native elements including the *espinilho* tree, *Vachellia caven*, wetlands, water, and riparian forests. This remains to be validated by further field data and for the remaining regions of the Uruguayan Savanna, but sites with those landscape elements are potentially the ones with higher probabilities of detection of aerial insectivore bats. Our results significantly add to the knowledge of Pampean bats and are alarming: environments characterised by native vegetation, highly suitable for the occupancy of a wide range of diversity of aerial insectivorous bat species, are rapidly disappearing by intense anthropogenic activities. In the last two decades, silviculture and agriculture have increased their areas by 34 and 44%, respectively, replacing native grasslands, particularly in mixed stands of the native andropogon grass. In shallow soil fields, intensive agriculture is almost impracticable and is here replaced by intensive livestock production. Such economic activities, when carried out inappropriately and at such excessive levels, often cause direct contamination of water resources by the release of pesticides and herbicides, leading to soil depletion and unproductivity, while facilitating the establishment of invasive plant species that generate not only loss of biodiversity, but also the de-characterisation of the gaucho cultural identity.

For all these reasons, future acoustic monitoring is paramount in areas of the Brazilian Pampa undergoing more intense anthropogenic changes, where acoustic monitoring will be key to increasing the knowledge of the distribution and occupancy of aerial insectivores, and how the ecosystem services provided by these bats, particularly in the context of the traditional agricultural systems, are being affected.

## Data availability statement

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

## Author contributions

CC and MR contributed equally to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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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.2022.937139/full#supplementary-material>



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# Global systematic map of research on bats in agricultural systems

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**Introduction:** The conversion of natural habitats to agricultural systems is one of the main global threats to bats. Here, we aimed to develop a systematic mapping to identify publication trends and research gaps in studying bats and agricultural systems.

**Methods:** We reviewed 309 studies published between 1990 and 2021 that sampled bats in agricultural systems or evaluated the effect of these systems on these animals.

**Results:** We found that most studies were conducted in the Palearctic and Neotropical regions (55.3%) and forest biomes (66.0%). Grassland-cropland systems (50.2%) and forest plantations that do not require cutting during the extraction of their products (47.9%) were more studied than forest plantations that require cutting (19.7%). Additionally, acoustic recordings (41.1%) and mist nets (34.3%) were the primary sampling methods used, with few studies combining these methods (7.1%). Also, most studies were conducted on a local scale (77.7%). The number of landscape-scale studies was smaller (34.3%) and concentrated in the Palearctic region (39.6%). Most studies assessed how agricultural systems affect biodiversity (62.1%). However, the phylogenetic and functional dimensions and b-diversity were little explored, with 2.5% and 23.3% of the biodiversity studies, respectively. Of the proposed mitigation measures, the most cited was including natural/semi-natural/potential bat habitats in cultivated landscapes (59.5%).

**Discussion:** In summary, our findings highlight the need for attention to the Afrotropic and Indo-Malaysia regions; predominantly non-forested biomes; plantations that require cutting during the extraction of their products; combined use of different sampling methods, as well as other methods as telemetry; use of multiple biodiversity descriptors and others biological descriptors, such as ecological services; landscape-scale studies and the role of conservation policies in promoting their conservation and raising awareness of their importance among producers and local communities. Filling these knowledge gaps is necessary to understand the factors influencing bat survival in cultivated landscapes. This is the only way to develop management and conservation strategies in these landscapes.

## KEYWORDS

bat sampling, Chiroptera, communities, ecological indices, guilds, global regions, mitigations, scale



# 1 Introduction

Agricultural systems have already replaced millions of hectares of native vegetation in the world (Food and Agriculture Organization, 2020a; Potapov et al., 2022). This conversion changed the structure (e.g., canopy cover) and composition (e.g., plant species present) of local vegetation, and transformed the landscape into a patchy mosaic where the original habitat has become fragmented or reduced (Wiegand et al., 2005; Fischer and Lindenmayer, 2007; May et al., 2019). These changes decrease the availability of shelter and food resources, thus affecting animals' presence, abundance, and behavior (Gibson et al., 2011; Tuck et al., 2014; Newbold et al., 2020; Outhwaite et al., 2022). For bats, for example, the conversion of natural habitats to agricultural systems represent one of the main global threats to their conservation (Frick et al., 2019).

Bats provide several ecological services which are beneficial in both natural and anthropogenic habitats (Boyles et al., 2013; Castillo-Figueroa, 2020; Regolin et al., 2020). Some of these services are directly related to the productivity of agricultural systems (e.g., pollination, pest control), while others are related with the restoration of degraded habitats (e.g., seed dispersal) that appear as a consequence of the establishment of plantations, grasslands or croplands (Frick et al., 2019; Castillo-Figueroa, 2020). Previous studies show that bats' responses to habitat conversion can vary according to the type of the original habitat replaced (Carballo-Morales et al., 2021), type of agricultural systems that replaces it (Law et al., 2016; Farneda et al., 2020; Carballo-Morales et al., 2021) and the intensity of management (Park, 2015; Williams-Guillén et al., 2016). Furthermore, bat responses are influenced by their traits such as their diet, wing shape, body mass, and echolocation type (García-Morales et al., 2013; Farneda et al., 2020; Loeb, 2020; Mendes and Srbek-Araujo, 2021). Due to this variability, it is necessary to understand the consequences of replacing natural environments with agricultural systems, filling existing knowledge gaps. This represents a crucial initial step in the development of effective mitigation strategies to ensure the preservation of the ecosystem services provided by these animals (Aizpuru et al., 2018; Ongole et al., 2018; Costa et al., 2020; Charbonnier et al., 2021).

Bat responses to the presence of plantation or the conversion of their habitats to agricultural systems have been partially reviewed in previous studies (e.g., Park, 2015; Williams-Guillén et al., 2016; Frick et al., 2019). However, most of these reviews are focused on a particular group of bats (e.g., Aziz et al., 2016; Law et al., 2016; Carballo-Morales et al., 2021), country or geographical region (e.g., Maas et al., 2016; Meyer et al., 2016; Farneda et al., 2020; Carballo-Morales et al., 2021). Therefore, such studies do not provide a clear overall picture of current research publication trends and potential knowledge gaps, nor identify general future research venues. Here, we employ a systematic mapping approach which aims to describe the publication trends and find potential gaps in existing literature, allowing to identify aspects of a particular research question that are still missing additional empirical research (James et al., 2016). Particularly, we focus on the research performed on bats and agricultural systems, evaluating the geographic regions that have

been studied, the methods used, the research objectives, and the proposed mitigation strategies for.

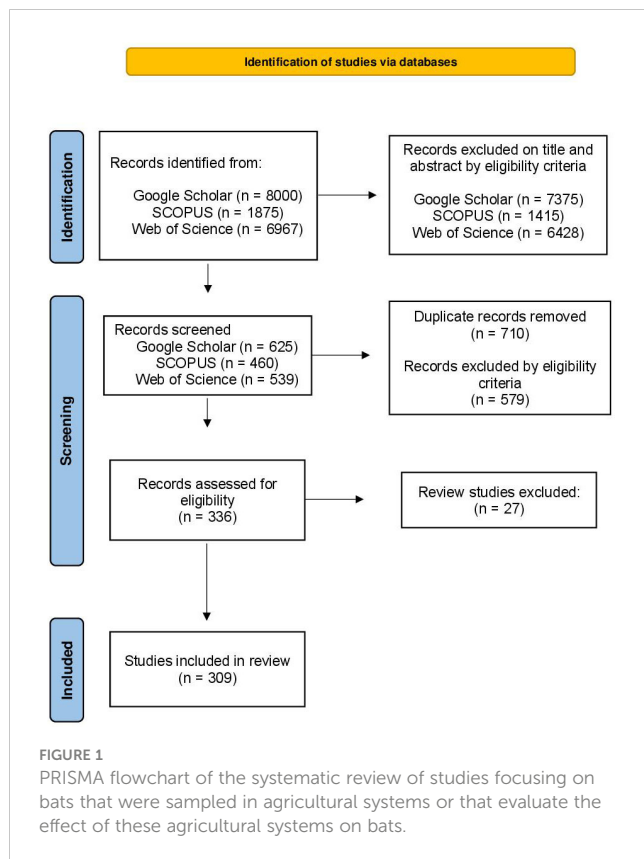
# 2 Materials and methods

## 2.1 Systematic search

We systematically reviewed in three databases (Google Scholar, Web of Science and SCOPUS). Data collection was carried out in June 2020 and updated in August 2021. We did not add year of publication restriction to searches. We search for the following keywords and their variations in all studies fields: "bat", "Chiroptera", "farming", "farm", "farmland", "plantation", "planting", "silviculture", "silviculture", "agriculture", "forestry", "crop", "agroforestry" (Supplementary Table 1). This initial search resulted in 16,842 records. We screened the title and abstract of each study, and retained those studies that followed these eligibility criteria: 1) were written in English; 2) were peer-reviewed scientific articles; and 3) included sampling of bats in agricultural systems or considered the effect of agricultural systems on bats. Here we define agricultural systems as areas cultivated by humans for the purpose of commercial production and subsequent sale and which encompass areas cultivated with crops, forestry, groves, and grassland (for more details see Curveira-Santos et al., 2021). Thus, we also included cultivated pastures (grassland) used locally to feed livestock, analyzing this type of agriculture system together with croplands (hereinafter simply grassland-cropland system), since both systems do not present vertical/arboreal strata. Finally, review studies and studies that mixed the effects of the agricultural system considered by us with other land uses, so that it was not possible to know which disturbance the bats were responding to, or mixed the response of bats with other organisms, so that it was not possible to know what was the response of the bats to the analyzed variables, were excluded. In a second stage, we excluded duplicates and assessed the eligibility of studies by screening the entire text, using the same criteria described above. The flowchart in Figure 1 illustrates the procedure applied for article screening, that was built according to the PRISMA (Preferred Reported Items for Systematic Reviews and Meta-Analyses statement; Moher et al., 2009). After following these steps, we retained a total of 309 publications, which are listed in Supplementary Table 2.

## 2.2 Data analysis

We extracted the following information from the selected studies: 1) publication year; 2) region where the study was conducted, namely: Australasia, Afrotropic, Indo-Malaysia, Nearctic, Neotropics, and Palearctic (following the Ecoregions2017<sup>®</sup> Resolve, available in [ecoregions2017.appspot.com](http://ecoregions2017.appspot.com)); 3) structure type of the original biome, as defined by Dinerstein et al. (2017): predominantly forested, and predominantly non-forested; 4) type of agricultural systems sampled: grassland-cropland (agricultural systems that do not present vertical/arboreal strata; i.e., are herbaceous or shrubby),



forest plantation that require cutting during the extraction of its products (tree-dominated plantations where product extraction leads to the cutting of trees), forest plantation that does not require cutting during the extraction of its products (tree-dominated plantations where product extraction does not lead to the cutting of trees); 5) focal taxa (species or group of bats studied); 6) sampling method; 7) spatial scale of the study (local: studies conducted within of the agricultural systems and studies comparing habitats; landscape: studies related to an area and studies comparing landscapes); 8) predictors used to assess the effect of agricultural systems (e.g., comparison between types of agricultural systems, comparison between agricultural systems and natural/semi-natural area, use of agrochemicals, percentage of cultivated area in the landscape); 9) biological descriptors used in the study (e.g., biodiversity, ecological services, mortality); 10) biodiversity descriptor of the groups of bats studied (e.g., species richness, taxonomic diversity, total abundance) and; 11) proposals for mitigating the impact of agricultural systems on bats. For more details see the [Supplementary Table 3](#). We quantified studies (n) in each of these categories; however, when a study fell into more than one category, it was counted in all categories to which it belonged. Also, in some situations we refer to cases, which were different situations evaluated within the studies. For example, the same study that compares abundance and richness between two different types of agricultural systems and between agricultural systems and other land uses, has four cases (one comparing abundance between different types of agricultural systems, one comparing abundance between agricultural systems and another land use, one comparing richness between different types of

agricultural systems, and lastly, one comparing richness between agricultural system and another land use). Likewise, four different studies comparing abundance between different types of agricultural systems also constituted four different cases.

### 3 General characteristics of studies in agricultural systems

The systematic review resulted in 309 studies ([Figures 1, 2; Supplementary Table 2](#)) that either used empirical data of bat collected from agricultural systems or that considered the effect of these agricultural systems on bats. These studies were published between 1990 and 2021 and showed an increasing publication rate over the years ( $r^2 = 0.78$ ;  $p < 0.001$ ; [Figure 2](#)). However, our data revealed an unequal geographic distribution of knowledge across the globe ([Figure 3A](#)). The Palearctic (n = 89) and Neotropical (n = 82) regions concentrated most of the studies (55.3% of total), followed by Indo-Malaysia (n = 43, 13.9%), Nearctic (n = 38, 12.3%), Afrotropic (n = 35, 11.3%), and Australasia (n = 22, 7.1%; [Figure 3A](#)). Each region has unique characteristics, such as climate, species diversity, and economic development, which can impact how bat communities are affected by agricultural systems ([Williams-Guillén et al., 2016; Frick et al., 2019; Outhwaite et al., 2022](#)). For example, in cases comparing abundance, richness, and taxonomic diversity between natural/semi-natural habitats and agricultural systems or assessing the effect of the presence/amount of the cultivated area on these descriptors, most communities and individuals across all regions did not respond to the presence/amount of the agricultural systems (66.3% of 1779 cases). However, cases that respond significantly revealing that communities and individuals were negatively affected by the presence of agricultural systems, are best represented in the Australasia, Indo-Malaysia, Nearctic and Palearctic regions (88.5% of 61 cases, 79.6% of 49 cases, 58.6% of 29 cases, and 52.4% of 206 cases, respectively). In the Afrotropics and Neotropics, most studies show positive responses to the agriculture systems (81.4% of 43 cases and 58.3% of 211 cases, respectively). This means that knowledge acquired in one region may not apply to other areas, so is it is essential to study all regions. However, some regions (Neotropics, Afrotropic and Indo-Malaysia) are considered a priority for bat conservation due to their high bat diversity and prevalence of endemic, threatened, or poorly studied species ([Frick et al., 2019](#)). Despite this, our analysis found that only the Neotropics received significant attention. Therefore, it is crucial to increase efforts to understand the impact of agricultural systems on bat populations in the less studied regions of Afrotropic and Indo-Malaysia.

Most studies (n = 204, 66.0%) were carried out in predominantly forested biomes, while only 31.7% (n = 98) were carried out in predominantly non-forested biomes ([Figure 3B, Supplementary Table 3](#)). Additionally, among the 128 studies that examined the impact of the presence of natural/semi-natural habitats on bats in agricultural systems or compared bats in agricultural systems with those in natural/semi-natural habitats, only 27 studies investigated non-forested habitats (e.g., flooded and

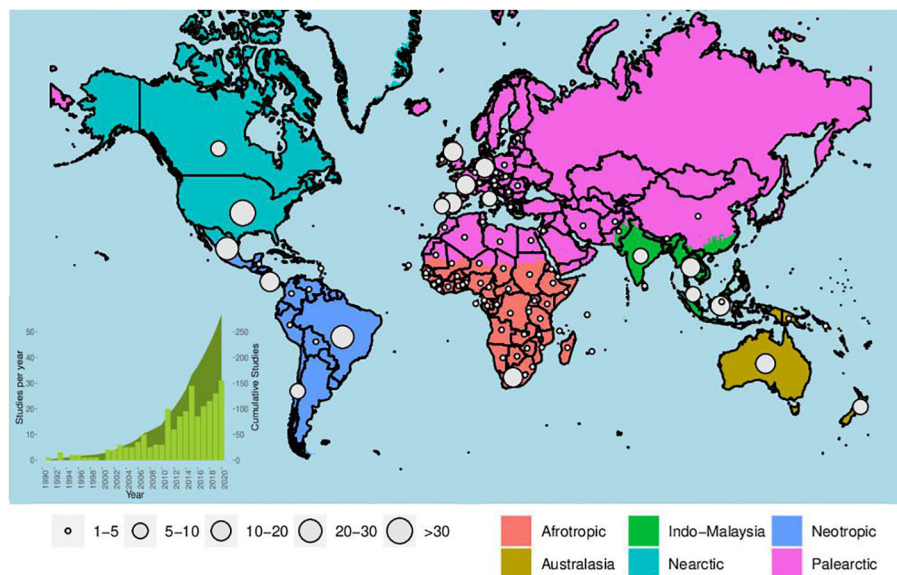


FIGURE 2

Worldwide distribution of studies published in which bats were sampled in agricultural systems or that assess the effect of these agricultural systems on bats. The circles on the map indicate the number of studies per country and the colors demarcate the global regions, according to Ecoregions2017<sup>®</sup>Resolve (available in [ecoregions2017.appspot.com](https://ecoregions2017.appspot.com)). The green bars in the graph (lower left side of the map) represent the number of studies published per year and the curve shaded in green represents the cumulative number of published studies.

natural fields), while 118 studies focused on forested habitats. Bats are often forest dependent organisms (Meyer et al., 2016; Williams-Guillén et al., 2016; Mendes and Srbek-Araujo, 2021), which may explain the bias in the type of habitats and biomes that have been studied more often. However, the presence of non-forested habitats in the landscape can also influence bat communities, acting as

complementary habitats for resource and movement (Lentini et al., 2012; Weier et al., 2018; Muñoz et al., 2019; Carvalho et al., 2021). Indeed, of the 27 studies that considered non-forested natural/semi-natural habitats, 20 showed the effect of these natural areas on bats present in agricultural ecosystems, with 13 of these indicate positive effects (e.g., Taylor et al., 2011; Rodríguez-San Pedro et al., 2019;

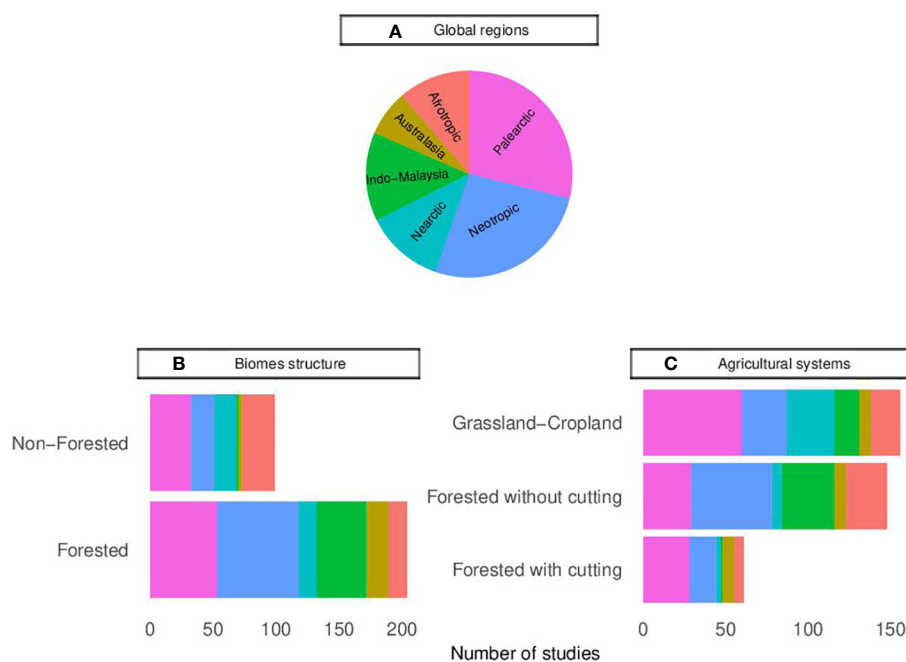


FIGURE 3

Distribution of studies published worldwide in which bats were sampled in agricultural systems or that evaluate the effect of these agricultural systems on bats, according to the (A) global regions, (B) type of structure of the original biomes, and (C) types of agricultural systems.

Carvalho et al., 2020). Replacing non-forested habitats with agricultural systems can change the dynamics of these landscapes, which in turn might have a negative on bat diversity and activity (see Weier et al., 2018; Muñoz et al., 2019; Rodríguez-San Pedro et al., 2019; Carvalho et al., 2020). Thus, further studies investigating the replacement of these habitats with agricultural systems are needed.

Not all types of agricultural systems have been equally studied (Figure 3C; Supplementary Table 3). Grassland-cropland systems (e.g., soybean, rice, cultivated pasture) have been studied more often than others ( $n = 155$ , 50.2%). Most of the studies on this type of agricultural system took place in vineyards ( $n = 25$ , 16.1%), corn fields ( $n = 22$ , 14.2%) and rice ( $n = 21$ , 13.5%). Globally, cultivated areas are mainly represented by this type of agricultural systems (Food and Agriculture Organization, 2020a), which may explain our result. However, despite forest plantations representing a small percentage of the world's cultivated area, the number of studies conducted in forest plantations that do not require cutting (e.g., agroforestry, orchards, oil palm;  $n = 148$ , 47.9%) is comparable to the number of studies in grassland-cropland systems. Most of the studies on this type of agricultural system took place in banana plantations ( $n = 32$ , 21.6%), shaded cafe ( $n = 27$ , 18.2%) and cacao ( $n = 22$ , 14.9%). Forest plantations may represent permeable matrices for bats or even work as complementary habitat for these organisms, while grassland-cropland systems may represent the opposite (Kunz and Lumsden, 2003; Law et al., 2016; Meyer et al., 2016; Williams-Guillén et al., 2016). Of the cases that compared abundance, richness, and taxonomic diversity between natural/semi-natural habitats and agricultural systems, most of those who responded significantly found negative effects of grassland-cropland systems and forest plantations on these descriptors. However, the percentage of studies that responded negatively to grassland-cropland systems (81.1% of 106 cases) is higher than those that responded to forest plantations (57.3% of 293 cases). In addition, even within forest plantations, the differences between plantations that require cutting for the extraction of their products (e.g., acacia, eucalyptus, heart of palm) and those that do not require cutting can be relevant. This occurs because in the latter case, the forest structure is generally maintained all the time, while in plantations that require cutting, mainly in a short-time rotation system, the matrix or habitat can change from a permeable matrix and/or suitable habitat to a matrix that can even be very limiting to bat movements (Stephens and Wagner, 2007; Zhang and Stanturf, 2008; Law et al., 2016). We also found that negative relationships between abundance, richness, or taxonomic diversity were reported more often in forest plantations that require cutting (87.9% of 78 cases) than on those that do not require cutting (48.5% of 204 cases). However, forest plantations that require cutting was the least studied ( $n = 61$ , 19.7%), with most studies focusing on pine ( $n = 29$ , 47.5%) and eucalyptus ( $n = 23$ , 37.7%) plantations. With the representation of these plantations in the world's cultivated area increasing in recent years (Food and Agriculture Organization, 2020b), there is a growing need for a better understanding of the potential impact this type of agricultural systems can have on bats.

The Neotropical region had the highest number of studies in predominantly forest biomes ( $n = 65$ , 31.9%; Supplementary Table 3)

and in forest plantations that do not require cutting ( $n = 48$ , 33.1%; Supplementary Table 3) when compared to other global regions. This region has a larger area covered originally by forested biomes than by non-forested biomes (Ecoregions2017<sup>©</sup>Resolve; [ecoregions2017.appspot.com](https://ecoregions2017.appspot.com)), which may explain this difference. Furthermore, it has already been found in other reviews (e.g., Meyer et al., 2016; Williams-Guillén et al., 2016), that the Neotropics have many studies on agroforestry, included here as forest plantations that do not require cutting, which may be driving this pattern. Agroforestry, which can maintain the structural complexity of native forests, has been found to mitigate the negative effects of agricultural systems (Williams-Guillén et al., 2016). Therefore, it is important to conduct studies on this type of plantation in other regions as well. The Palearctic leads in studies in predominantly non-forest biomes ( $n = 32$ , 32.7%; Supplementary Table 3), in grassland-cropland systems ( $n = 57$ , 37.3%; Supplementary Table 3) and forest plantations that require cutting ( $n = 28$ , 43.8%; Supplementary Table 3) compared to other global regions. In addition to being the region with more studies, the Palearctic has the largest area of originally non-forested biome (Ecoregions2017<sup>©</sup>Resolve; [ecoregions2017.appspot.com](https://ecoregions2017.appspot.com)), and of grassland-cropland cultivated areas (Food and Agriculture Organization, 2020a).

## 4 Methodologies of collecting data

Twenty data collection methods were used in the studies reviewed (Figure 4; Supplementary Table 3). Most studies sampled bats with either acoustic recorders ( $n = 127$ , 41.1%) or mist nets ( $n = 106$ , 34.3%). Acoustics were mainly used in the Palearctic region ( $n = 61$ , 48.0%) while mist nets were used mainly in the Neotropics ( $n = 55$ , 51.9%). Using exclusively one of these methods can lead to sampling bias, as acoustic recordings perform better at recording insectivorous bats that echolocate, while mist nets are a more effective method for capturing bats that are unable to avoid interception traps (MacSwiney-G et al., 2008; Yoh et al.,

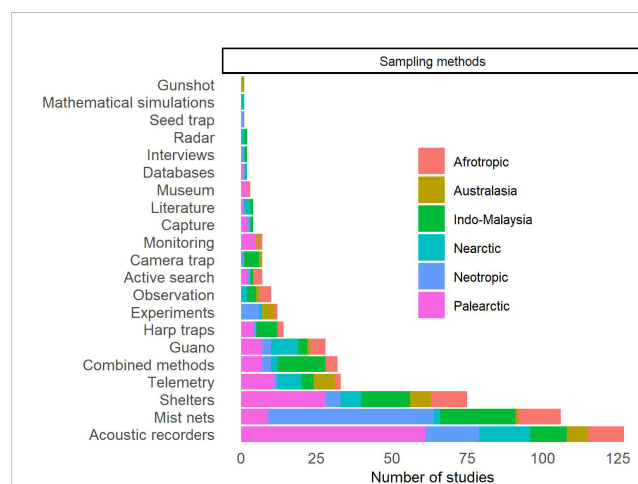


FIGURE 4  
Distribution of studies published worldwide in which bats were sampled in agricultural systems or that evaluate the effect of these agricultural systems on bats, according to the sampling methods.



2020; Appel et al., 2021; Carvalho et al., 2023). Ultimately, this can lead to an incorrect interpretation of the results found. For example, Heer et al. (2015) compared forest fragments with rubber-cacao plantations and found that the species richness recorded with acoustics did not differ between these habitats, while the number of species was higher in forest fragments when considering only the species sampled with mist nets. Thus, an approach combining several sampling methods, such as mist nets and acoustic recorders, would be ideal to reduce the risk of sampling bias for certain bat groups and, thus, gain a better understanding of their response to replacement of natural areas with agricultural systems (MacSwiney-G et al., 2008; Appel et al., 2021; Carvalho et al., 2023). Another option would be to combine mist nets with harp-traps or with captures in roost (e.g., Flaquer et al., 2007; Pech-Canche et al., 2011; Xavier et al., 2018; Appel et al., 2021). Among the selected studies, 33 (10.7%) combine various bat sampling methods, with 24 of them using one of the aforementioned combinations.

Bat roosts were used in 75 studies (24.3%), of which 27 were intended to study the roosts themselves and 48 studies used roosts to capture bats or collect information about them (e.g., ectoparasites, guano for food diet studies). Roost captures facilitate sampling of high-flying bats, that are not often caught in interception traps (e.g., mist nets, harp traps). This is very important to enrich acoustic databases that can help understand the consequences of agricultural systems on bats (Taylor et al., 2013). The fourth most used method was telemetry ( $n = 33$ , 10.7%). Telemetry is crucial for understanding bat behavior and ecology, including their habitat selection and home range (Clerc et al., 2021). New technologies that make telemetry less costly and more suitable for different bat species may increase its general use in research (O'Mara et al., 2014). The fifth most used method was the collection of guano of bats ( $n = 28$ , 9.1%), a method mainly associated with foraging studies (diet composition, diversity, richness and selection) and ecological services and disservices. Harp traps were used only in 14 studies (4.5%). Studies that used an experimental approach ( $n = 12$ , 3.9%) had the main objective of evaluating ecological services. Capture by gunshot was mentioned in one study; however, it is important to note that this approach raises ethical concerns, and we strongly advise against its use. Other methods, such as seed traps, camera traps, mathematical simulations, and interviews, were also rarely used. Studies based on information obtained from databases, literature and museum collections were used to complement the collected data or for macroecological studies.

## 5 Studied groups of bats

Certain bat groups (e.g., guilds and taxa) and species may have different responses to landscape changes (Farneda et al., 2020; Loeb, 2020; Carballo-Morales et al., 2021; Mendes and Srbeek-Araujo, 2021). Thus, the choice of bat group will influence the results of the studies, being important consider the communities and subgroups or functional characteristics of these communities when evaluating the effects of agricultural systems on bats to plan conservation strategies in cultivated areas. Most studies are described as being developed at the community level ( $n = 167$ , 54.0%; Supplementary

Table 3). However, although these studies claim to assess the whole community, some of these focused on a particular taxon. This is mainly due to the methods used which are often selective and bias sampling towards some species. Some of these studies ( $n = 79$ ), for example, are focused on insectivores by using acoustic recording as the only methods sampling, including in the Neotropics where insectivorous bats are not predominant.

Single species are the second most common focal taxa studied ( $n = 157$ , 50.8%). This type of study tend to focus on behavior, hunting, abundance, contamination, populations, ecological services and disservices and, in nine of these studies, a single species was used to represent a guild (based on body mass and use of space). The third most common focal taxa was the trophic guilds ( $n = 66$ , 21.4%), with studies of this type being conducted mainly in the Neotropics ( $n = 30$ , 45.5%). Diet or trophic level are recurrently evaluated in the Neotropics, as bats have a diverse diet in this region (Kalko et al., 1996; Kalko, 1998; Kalka et al., 2008; Kunz et al., 2011). In addition, diet reflects other important characteristics in bats, such as taxonomic group, morphological characteristics and type of echolocation (Jones et al., 2013; Castillo-Figueroa and Pérez-Torres, 2021; Potter et al., 2021). Other types of guilds were also studied ( $n = 36$ , 10.7%), mainly those based on the use of space (bats classified as open, closed or edge foragers;  $n = 20$ ). In addition, six studies classified bats by their foraging strategy (aerial or gleaners), two by echolocation parameters, four by specialization in habitat use (foraging, general use and roost), two differentiated bats as rare and dominant, two used size and body mass and one used maneuverability.

## 6 Scales and predictors used

Most studies were carried out on a local scale, comparing two distinct habitats ( $n = 135$ , 43.7%; Supplementary Table 3). The analyzes carried out on this scale show significant responses in 39.4% of cases. The second most common type was the studies on a local scale carried out only within of some agricultural systems ( $n = 128$ , 41.4%), with the analyzes made in this scale presenting significant responses in 36.4% of the cases. Landscape studies relating to an area were the third most common ( $n = 94$ , 30.4%), with few analyzes made on this scale showing significant responses (14.1%). Lastly, a few studies compared landscapes ( $n = 14$ , 4.5%) and found significant responses in 41.8% of cases. The scale at which bat populations are being studied is crucial, since some variables may affect bats on one scale but not on another. For example, Pina et al. (2013) found that bat composition changes with the amount of eucalyptus plantation in the landscape, but it is similar when locally comparing eucalyptus plantations with forest patches in Cerrado (Brazilian savanna) landscapes. Furthermore, bat responses on one scale may be influenced by variables acting at another scale (e.g., Herrera et al., 2016; Mendes et al., 2017; Schoeman and Monadjem, 2018; Luz et al., 2020). For example, in studies that consider the local scale and compare natural habitats with agricultural systems, bat responses to agriculture systems may vary according to the proximity to natural forest habitats or the amount of these habitats in the landscape (Park, 2015; Meyer et al.,

2016). Despite this, only 38 studies (12.3%) evaluated both local and landscape scales simultaneously. Therefore, to better understand how agricultural systems affect bats, further studies are needed incorporating multiple scales of analysis, when possible.

In addition to the importance of carrying out more studies on more than one scale, using an appropriate size scale for these studies is also essential. When examining the most used scale size, specifically the circular buffer with a radius of 1000 m (842 cases), bats exhibited a significant response to the variable in question in 9.4% of cases. The other scale sizes used in more than ten studies (500, 2000, 3000, and 5000 m radius circular buffer, 422 to 486 cases) had similar percentages (from 7.1% to 13.6%). Studies that use scales size relative to the home range of bats (126 cases) are the exception, as bats responded significantly to the analyzed variables in 75.4% of cases. Based on our findings, it is plausible that the ideal size of a study area is relative to the home range of the bats under investigation. However, determining the home range of all species in a community can be challenging. Furthermore, it is essential to consider factors such as seasonality that can impact bat home range size (Meyer et al., 2016; Peixoto et al., 2018). Thus, we consider that studies using multiple scale sizes are of higher value to understand how variables in cultivated landscapes will affect bat communities (Gonthier et al., 2014). An alternative would be to compare landscapes. For example, Rodríguez-San Pedro et al. (2021) compared vineyard farms adjacent to natural habitats with vineyard farms neighboring cultivated habitats and showed that taxonomic diversity and total insectivore foraging activity were similar between these landscapes. Still, the foraging activity of *Lasiurus varius*, *Lasiurus villosissimus*, and *Myotis chiloensis* was higher in vineyard farms adjacent to cultivated habitats (Rodríguez-San Pedro et al., 2021). Shapiro and Bordignon (2014) found higher richness, evenness, and taxonomic diversity and lower abundance in fragmented Cerrado surrounded by small agricultural matrix fields when compared to fragmented Cerrado surrounded by urban matrix. Also, Faria et al. (2006) and Faria and Baumgarten (2007) found greater taxonomic richness of bats in shade cocoa plantations within well-preserved landscapes with a higher amount of forest compared to isolated shade cocoa plantations within less conserved landscapes. These studies aimed to compare cultivated landscapes with matrices of different cover qualities or to compare more preserved landscapes (e.g., with a higher amount of natural habitat) with less preserved landscapes. These studies constitute a qualitative way of evaluating patch and matrix contrast in the first case and the amount of land use in the second case. They may be helpful ways to assess the effects of agricultural systems on bat communities at the landscape scale.

Our analysis found a relatively even distribution of studies conducted at various scales, except for those comparing landscapes, which were fewer in number (Supplementary Table 3). However, when considering global regions, notable biases in research efforts emerged (Supplementary Table 3). The Afrotropic and Australasia regions had limited studies across all scales, highlighting the need for more comprehensive studies in these regions. The Nearctic region would benefit from additional studies incorporating reference habitats. In the Indo-Malaysia region, studies should focus on enhancing our understanding of plantation landscapes

and studies incorporating reference habitats. Similarly, the Neotropics would benefit from more comprehensive studies examining the impacts of cultivated landscapes on bats.

## 6.1 Predictors used in local scale

Most studies carried out on a local scale and comparing two distinct habitats, compared agricultural systems with natural/semi-natural habitats ( $n = 106$ , 78.5%; Supplementary Table 3). These studies were mostly performed in the Neotropics ( $n = 50$ , 47.2%; Supplementary Table 3), region where the high availability of natural environments facilitate this type of comparisons (Food and Agriculture Organization, 2020b). Although the Palearctic region had the highest number of total studies, the highly urbanized and developed landscape limits the number of comparisons that can be made between natural habitats and agricultural systems (Park, 2015; Food and Agriculture Organization, 2020b). In addition to comparisons between agricultural systems and natural/semi-natural habitats, comparisons were also made between two types of agricultural systems ( $n = 63$ , 46.7%) and between other land uses (e.g., urban area, pasture) and agricultural systems ( $n = 29$ , 21.5%). Comparing different types of agricultural systems can provide valuable insights into the effects of different management practices on bats and, thus, help create strategies to balance biodiversity conservation and crop production (e.g., Barré et al., 2017; Froidevaux et al., 2017; McFadden and Dirzo, 2018; Chaiyarat et al., 2020). For example, we found that among the selected studies, there are more cases (81.1% of 106 cases) reporting significant negative effects of grassland-cropland systems on abundance, species richness, and diversity compared to forest plantations (57.3% of 293 cases). This indicates that forest plantations maintain a higher structural complexity that is less detrimental to bat communities. On the other hand, comparing different land uses can provide valuable insights into the specific anthropogenic changes that pose the greatest threat to bats, thereby enabling targeted efforts to mitigate these impacts (Frick et al., 2019). Here, we found a higher percentage (65.2% of 92 cases) of significant negative responses in terms of abundance, species richness, and diversity to agricultural systems when compared to other land uses, such as urban areas and pastures. This suggests that agricultural systems may have a more pronounced impact on bat communities, highlighting the need for specific attention to mitigate their effects.

We identified 10 different types of predictors used in studies in local scale carried out within the agricultural systems (Supplementary Table 3). Most these studies ( $n = 37$ , 28.9%) assessed structure and/or composition of the agricultural systems (e.g., basal area, canopy cover, vegetation height, presence of water) and abiotic variables (e.g., rain, seasonality, humidity) appear as the second most used type of predictors ( $n = 25$ , 19.5%). Bats were also used as predictors of ecological services and disservices ( $n = 25$ , 19.5%). The direct effect of agricultural pests on bats was also evaluated ( $n = 6$ , 4.7%), and a few studies have also evaluated how the vegetative/reproductive stage of the plantation affects bats ( $n = 5$ , 3.9%). Despite the importance of knowing how these parameters

of agricultural systems affect bats, the analysis of some variables, such as structural complexity and vegetation composition, are only meaningful when compared to reference habitats (Park, 2015; Meyer et al., 2016). In addition, 34 studies (26.6%) carried out within agricultural systems were only descriptive and did not test descriptors such as biodiversity, foraging, and home range with any predictors of the agriculture systems (e.g., abiotic variables, composition of the plantation). These studies represent 23.3% ( $n = 10$ ) and 21.1% ( $n = 8$ ) of the studies on bats and croplands published in Indo-Malaysia and Nearctic, respectively. Thus, it is necessary, mainly in these regions, to test hypotheses and use control habitats, especially natural ones, to enhance our understanding and conservation efforts for bats in agricultural systems.

## 6.2 Predictors used in landscape scale

Landscape studies are of crucial importance for this highly mobile taxon, as they provide valuable insights on how the surrounding composition and configuration influence these species in their habitats (Meyer et al., 2016; Peixoto et al., 2018; Schoeman and Monadjem, 2018; Outhwaite et al., 2022). We identified 15 different predictors at this scale, most these studies have examined the presence/amount of agricultural systems on bat populations within a particular landscape ( $n = 79$ , 84.0%; Supplementary Table 3). In contrast, only 26 studies (27.7%) have examined the presence/amount of natural/semi-natural habitat, and 22 studies (23.4%) have examined the presence/amount of other land uses in the landscape (Supplementary Table 3). Therefore, even in the Palearctic, where the number of landscape studies is the largest (43.7%) compared to other regions, there is still a scarcity of research on how the presence/amount of natural/semi-natural habitats and other land uses (e.g., urban areas, roads, managed forests) in landscapes with some agricultural systems impact bat populations. We also found studies that took into consideration the landscape configuration (e.g., distance to some landscape elements, such as linear elements, water, buildings; landscape complexity; isolation/connectivity/fragmentation). These studies were scarcer ( $n = 27$ , 28.7%) and more concentrated in the Palearctic ( $n = 11$ , 40.7%). To effectively conserve bat populations in cultivated landscapes, it is crucial to comprehend how these respond to the composition and arrangement of the surrounding landscape (Park, 2015; Williams-Guillén et al., 2016; McFadden and Dirzo, 2018). However, our knowledge about bat responses to landscape variables may be region-specific and not broadly applicable to other regions. Lastly, studies that compare landscapes include comparisons (i) between some agricultural systems and natural/semi-natural area ( $n = 5$ , 35.7%) or (ii) other land uses ( $n = 4$ , 28.6%), (iii) between types of agricultural systems ( $n = 3$ , 21.4%), (iv) presence or amount of area natural/semi-natural ( $n = 3$ , 21.4%), and (v) landscape management ( $n = 1$ , 7.1%).

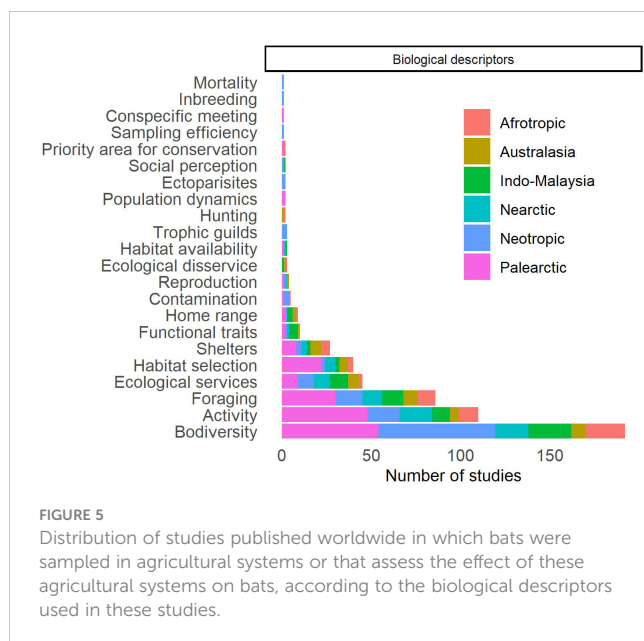
## 6.3 Predictors on more than one scale

Predictors such as abiotic variables ( $n = 26$ , 8.4%), presence/number of insects ( $n = 12$ , 3.9%) and agricultural system

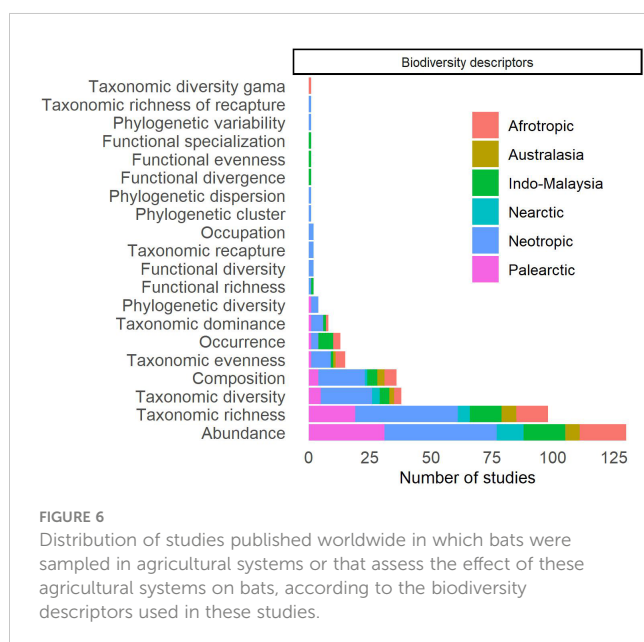
management approaches ( $n = 47$ , 15.2%) were occasionally studied in more than one scale (Supplementary Table 3). Abiotic variables can affect bat responses to agricultural systems (Cisneros et al., 2015; Heim et al., 2016; Shapiro et al., 2020). In cultivated landscapes in the Neotropics, for example, bats may respond positively to forest patch size in the dry season and have no relationship with this variable in the wet season (Cisneros et al., 2015). In the Afrotropic, insectivores respond more strongly to landscape metrics in the dry season, while in the wet season they respond more strongly to local metrics (Shapiro et al., 2020). To better understand the response of bats to agricultural systems, it is important to analyse how abiotic variables interact with other factors in both the agriculture system and the surrounding landscape. Of the few studies that have evaluated the effect of insect abundance or availability on bats, all have done so at the local scale ( $n = 12$ ), with only one study also evaluating it at the landscape level. Understanding food availability is of utmost importance in agricultural systems and cultivated landscapes, as it plays a vital role in determining the presence of bats in these areas. This includes investigating whether the required food resources are found within the agricultural system itself or in nearby habitats (Park, 2015; Meyer et al., 2016; Williams-Guillén et al., 2016). In addition to these studies, three others evaluated food availability as a response variable (descriptors). In all cases, the amount of fruit or plants potentially consumed by bats was estimated. Another predictor assessed at more than one scale was management. Management is essential to mitigate the impacts of agricultural systems on bats (Park, 2015; Williams-Guillén et al., 2016; McFadden and Dirzo, 2018), and can be evaluated and cultivated at different scales. For instance, both plantations with less intensive uses and landscapes that preserve potential habitats for bats while maintaining connectivity between them, hold the potential to conserve bat populations, even in the presence of agricultural systems (Park, 2015; Meyer et al., 2016). However, these studies were concentrated in the Palearctic ( $n = 23$ , 48.9%) and Neotropical ( $n = 15$ , 31.9%) regions.

## 7 Biological descriptors

The biological descriptors used in the selected studies were grouped into 22 categories (Figure 5; Supplementary Table 3). The most used descriptor was biodiversity ( $n = 192$ , 62.1%), with most studies being carried out in the Neotropical ( $n = 65$ , 33.9%) and Palearctic ( $n = 54$ , 28.1%). Of these studies that assess biodiversity, 82.8% ( $n = 159$ ) assessed the biodiversity of bat communities and guilds (Figure 6), with the other studies assessing the abundance of a species. All studies that used biodiversity to describe guilds and communities explored the taxonomic dimension, while the phylogenetic and functional dimensions of biodiversity were addressed in four studies (2.5%) each. However, among the studies that use taxonomic descriptors, 35.2% ( $n = 56$ ) estimated these descriptors for a guild and 5.7% ( $n = 9$ ) aimed to study one or more families of Chiroptera. Thus, 135 studies (84.9%) aimed to assess the taxonomic biodiversity of all bats recorded in the studied area. The indices used to assess biodiversity are important tools for



comparing habitats and, thus, assessing the effect of disturbances, such as the replacement of natural habitat by agricultural systems. However, it is important to note that these indices may only capture part of the changes occurring in communities, particularly when solely relying on taxonomic approaches (Pellens and Grandcolas, 2016; Moreno et al., 2018; Peixoto et al., 2018; Presley et al., 2018). Species will play different ecological functions in a habitat, but when there is some redundancy, the loss of a species may not necessarily lead to the loss of a function (Fonseca and Ganade, 2001; Blakey et al., 2019). Furthermore, species' responses to environmental factors may be driven by their functional traits and/or evolutionary histories (Pellens and Grandcolas, 2016; Presley et al., 2018; Blakey et al., 2019). Thus, functional and phylogenetic studies can add valuable information about the consequences of converting a natural habitat to an agricultural



systems or about the presence of these agricultural systems in landscapes. For example, Carvalho et al. (2020) described that while taxonomic and functional diversity is lower in acacia plantations than in forest patches, phylogenetic diversity is similar. In Olivier et al. (2020), phylogenetic diversity was found to respond negatively to the amount of agriculture in the landscape, but taxonomic diversity is unaffected. Additionally, most studies that used biodiversity to describe guilds and communities, employed  $\alpha$ -diversity descriptors ( $n = 157$ , 98.7%), whereas  $\beta$ -diversity was less frequently utilized ( $n = 37$ , 23.3%). While  $\alpha$ -diversity measures are crucial for understanding local biodiversity patterns, it is equally important to investigate how species composition, as described by  $\beta$ -diversity and its components (turnover or species replacement and nestedness or richness difference), is affected by agricultural ecosystems. For example, Alpizar et al. (2019) showed that taxonomic diversity was similar between pineapple cultivation and forests, but community composition differed between these habitats. The same pattern was observed by Olimpi and Philpott (2018) when comparing forest fragments with organic and conventional agriculture. We highlight that such investigations are essential for identifying conservation strategies for fauna in cultivated landscapes (Cardoso et al., 2014; Socolar et al., 2016).

We found that 20 biodiversity descriptors were used to describe bat communities and guilds (Figure 6). Of these, abundance was the most used ( $n = 130$ , 81.8%), followed by taxonomic richness ( $n = 98$ , 61.6%). Thus, many quantitative reviews use only these descriptors to assess disturbance effects on bat communities, at best, evaluating guilds separately (e.g., Cunto and Bernard, 2012; García-Morales et al., 2013; Williams-Guillén et al., 2016; Carballo-Morales et al., 2021). Abundance and taxonomic richness may show opposite trends when compared to other biodiversity indices. For example, Dawson et al. (2012) did not find a difference in abundance and taxonomic richness when comparing primary forests to plantations but found a decrease in taxonomic diversity in plantations. The scarcity of studies using other indices limits our understanding of how plantations affect bats. This gap in knowledge includes large-scale comparisons and meta-analyses, due to the limited information provided by existing studies.

The second most used biological descriptor was bats activity ( $n = 110$ , 35.6%; Figure 5; Supplementary Table 3). However, most studies ( $n = 105$ , 94.5%) used activity as a proxy for abundance. Thus, analyzes such as changes in the duration and peak of activity and social activity received less attention ( $n = 5$ , 8.2%). In addition to these few behavioral studies on bat activity, bat behavior has been evaluated in foraging studies ( $n = 86$ , 27.8%), habitat selection ( $n = 40$ , 12.9%), roosts selection ( $n = 27$ , 8.7%) and home range ( $n = 9$ , 2.9%), of which only the last was little represented. While we found several aspects of bat behavior to be well-studied, it is important to note that most of these studies were conducted in the Palearctic region (Supplementary Table 3). Therefore, future studies focusing on these topics should be conducted in regions other than the Palearctic, to gain a comprehensive understanding of bat behavior in different environments.

Out of the 45 studies (14.6%; Supplementary Table 3) that investigated the ecological services provided by bats, 33 focused on



pest control/suppression, nine on pollination, three on seed dispersal, and one on litter decomposition. However, it is possible that our review was not able to locate all studies on this topic, as some may not mention the agricultural systems themselves. For example, despite the fact that seed dispersal is often cited as one of the most important and more studied ecosystem services provided by bats, according to recent studies that do not focus on agricultural systems (Castillo-Figueroa, 2020; Regolin et al., 2020), our analysis revealed that it was one of the least studied services among the studies reviewed. However, other comprehensive reviews, such as Ramírez-Francel et al. (2022), found that most ecosystem services studies aim to study pest suppression, and other ecosystem services, such as seed dispersal, are less studied. Eight studies assigned monetary value to the service provided, of which six of them dealt with pest control and two with pollination. Although challenging, it is essential to value the benefits of bats to ecosystem functioning, and ultimately to humans, in order to raise awareness about their importance and ensure their protection and conservation (Kunz et al., 2011; Boyles et al., 2013). We recommend further efforts to investigate the impact of agricultural systems on ecological services beyond agricultural pest control/suppression, as well as to improve the quantification of the monetary value of these services.

Few studies used trophic guilds ( $n = 3$ ) or other guilds ( $n = 10$ ) as biological descriptors (Supplementary Table 3). Those which did, evaluated the changes in composition or proportion of functional ( $n = 3$ ) and trophic guild ( $n = 10$ ) characteristics. The functional traits used in these cases were: morphological aspects ( $n = 8$ ), mainly from the bat wings ( $n = 7$ ); echolocation parameters ( $n = 4$ ); body mass ( $n = 3$ ); fertility ( $n = 2$ ); growth rate ( $n = 2$ ); specialization in habitat use ( $n = 1$ ); and diet specialization ( $n = 1$ ). However, as already discussed, many studies used these guilds as focal taxa, analyzing them with abundance and taxonomic descriptors, and, thus, the guilds ended up being extensively explored in the studies selected here.

Contamination of bats by pesticides has received little attention ( $n = 5$ , 1.6%; Supplementary Table 3). However, it is possible that our review was not able to locate all studies on this topic, as some may not mention the agricultural systems themselves. Oliveira et al. (2021), identified 28 recent studies on the contamination of bats by pesticides, indicating a higher number compared to our study, although the total number of studies remains small considering the importance of this topic. Contamination studies were the only ones to consider physiological responses. These studies, along with those the assessment of the presence and prevalence of ectoparasites ( $n = 2$ , 0.6%), were the sole investigations that encompassed the assessment of potential diseases affecting bats within agricultural systems or cultivated landscapes. No other diseases or cases of zoonoses were evaluated in the studies selected. Sex ratio or other issues related to reproduction were also little studied ( $n = 4$ , 1.3%). In addition to these, four other studies (on home range, diet composition and diversity, and roost characteristics) considered the gender of the studied individuals. Apart from studies that assess the abundance of a single species, populations were analyzed in only a few studies (two studies on population dynamics, one on inbreeding, one on conspecific encounter, one on differentiation

and genetic diversity, and one on allelic richness). Apart from these few population studies, none other used genetic descriptors (Supplementary Table 3).

## 8 Mitigation proposals

Mitigation proposals were made in 205 studies (66.3%), and these were categorized into 16 types (Figure 7; Supplementary Table 3). The measure proposed more often in the selected studies was the conservation or restoration of natural, semi-natural, or potential areas for bats in cultivated landscapes ( $n = 122$ , 59.5%). These studies refer mainly to forested habitats, but wetlands, karstic areas and savannas are also cited. Natural forested habitats vary from continuous and well-preserved forests, with the potential to maintain the original bat community, to riparian forests and forest fragments that can function as corridors and promote connectivity (Yoshikura et al., 2011; Akasaka et al., 2012; Toffoli and Rugghetti, 2020). The preservation or restoration of secondary forests have also been suggested to provide resources for some less sensitive bat species (Louzada et al., 2010; Ervis et al., 2021). The second most cited measure was less intensive management ( $n = 85$ , 41.5%). These studies mention “friendly” agriculture, agroforestry, organic agriculture, traditional agriculture, polyculture, fallow practices, shaded plantations, presence of trees, presence of forest characteristics, maintenance or clearance of the understory in forest plantations, decrease and regulation of pesticide use, and increased heterogeneity and structural complexity of plantations (e.g., Fuller et al., 2005; Faria et al., 2006; Dietz et al., 2013). These measures are intended to make these environments less hostile for bats, increasing their roosting and foraging potential and facilitating displacement between adjacent habitats (Law and Chidel, 2006; Cortes-Delgado and Sosa, 2014; Rodríguez-San Pedro and Simonetti, 2015; Fill et al., 2021). In third place, studies propose that increasing or maintaining connectivity is an important measure to mitigate the presence of agricultural systems in landscapes ( $n = 60$ , 29.3%). These studies propose that the presence of riparian forests, forest fragments, trees in plantations,

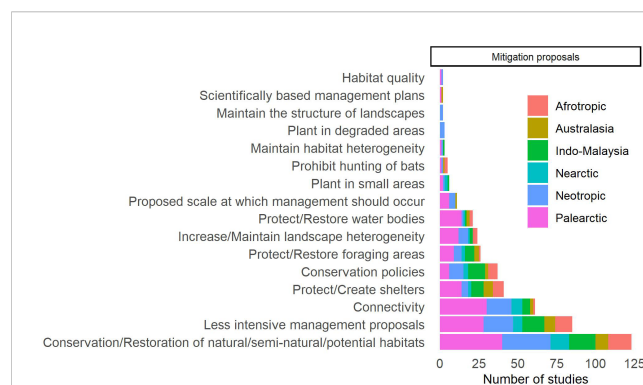


FIGURE 7

Distribution of studies published worldwide in which bats were sampled in agricultural systems or that assess the effect of these agricultural systems on bats, according to the proposals for mitigating the consequences of agricultural systems for bats.

networks of water bodies and the presence of linear elements (e.g., living fences) can promote connectivity (Davy et al., 2007; Akasaka et al., 2012; Heer et al., 2015; Heim et al., 2016). In addition to the aforementioned recommendations, several studies emphasize the importance of increasing roost availability ( $n = 41$ , 20.0%), both artificial and natural, as well as protecting and restoring foraging areas ( $n = 26$ , 12.7%). To achieve this, it may be necessary to maintain natural or semi-natural areas that have the potential to support bat populations, promote less intensive land management practices, utilize artificial roosts, and increase connectivity to ensure that bats can access roosts and food resources within cultivated landscapes (Koschnicke et al., 2010; Wordley et al., 2017). Restoration of water bodies ( $n = 21$ , 10.2%) to maintain connectivity and foraging areas, and other landscape-scale management, such as preserving heterogeneity ( $n = 24$ , 11.7%) and original landscape structure ( $n = 2$ , 1.0%) were also mentioned. Some studies also proposed other mitigations, such as preserving the quality of remaining natural habitats ( $n = 2$ , 1.0%), using degraded areas for planting ( $n = 3$ , 1.5%), prohibiting bat hunting ( $n = 4$ , 2.0%), and avoiding large-scale planting ( $n = 6$ , 2.9%).

Some studies also mentioned the importance of implementing policies and regulations ( $n = 36$ , 17.6%). In most cases, the measures aim to create actions that satisfy both producers and bat conservation efforts simultaneously. Among these, include the promotion of environmental education to highlight the importance of bats in providing ecological services, incorporating local and ecological scientific knowledge in mitigation measures, and fostering collaboration between scientists, legislators, and producers. Furthermore, financial incentives were also proposed that add value to sustainable products pollinated or dispersed by bats, which can benefit everyone, including small producers. Additionally, other actions were suggested, like involving local residents in inspections, promoting ecotourism, and exploring technologies to reduce conflicts between humans and bats (e.g., using protection nets in fruit production). Finally, some studies recommended funding research focused on developing effective mitigation measures (MacDonald et al., 2018; Sheherazade et al., 2019; Sow et al., 2020; Oleksy et al., 2021).

## 9 Summary and conclusion

Our review resulted in a considerable number of studies ( $n = 309$ ) related with bats and agricultural systems. These studies revealed an uneven distribution of knowledge across global regions, with a predominant focus on the Palearctic and Neotropical regions. This highlights the need to direct more resources on other geographical regions. Specifically, we recommend prioritizing the Indo-Malaysia and Afrotropic regions. These areas have received limited attention in previous studies, and they are critical regions for bat conservation. To understand how bats are affected by agricultural systems, we need filling this and others knowledge gaps that we identified here, such as the groups of bats studied, and the methods applied for data collection. For example, although most studies aimed to assess the bat community, few have combined sampling methods that allows knowing the whole community, which has biased results towards

certain groups (e.g., insectivorous bats, phyllostomid bats). Combining sampling methods is important for a more comprehensive sampling of these bat communities. Complementary methods are more often needed in regions where bats that fly high and/or have efficient echolocation to perceive interception traps (e.g., mist nets) coexist with bats that do not echolocate or do not have enough variation in echolocation to be identified by acoustic recordings. Another critical aspect that can impact our comprehension of the effects of commercial plantations is the type of descriptors used. Most studies rely on taxonomic biodiversity as the primary descriptor, with a particular emphasis on abundance and taxonomic richness. However, there is a need to explore other biodiversity dimensions, such as phylogenetic and functional diversity, and  $\beta$ -diversity. Furthermore, it is worth noting that relying solely on abundance and taxonomic richness can lead to incomplete interpretations, as these indices can show opposing trends when compared to other biodiversity indices. Therefore, we highly recommend utilizing multiple biodiversity indices to gain a more holistic understanding of the effects of agricultural systems on bat populations.

Our analysis uncovered several other significant gaps in current research on the effects of agricultural systems on bat populations. For instance, few studies have examined how the presence or number of trophic resources, or the influence of abiotic factors, impact bats in agricultural systems. We recommend evaluating these variables, particularly outside the Palearctic region, where these studies are most often performed. Additionally, we found that studies that investigated contamination, disease, and other physiological responses, as well as those that assessed sex ratio, reproduction, and genetic diversity, were severely lacking. Only less than 10 studies have focused on these crucial factors. While many studies focused on a single bat species, most primarily aimed to understand bat abundance response, other critical population parameters such as population dynamics, inbreeding, and conspecific encounter have often been overlooked. Therefore, we urge researchers to broaden their focus and explore these important population parameters. Furthermore, although there is a balanced number of studies using different scales (except for those that make comparisons between landscapes), studies at the landscape scale are concentrated in the Palearctic region. Thus, in addition to the need for more studies at all scales outside the Palearctic and Neotropical regions, it is necessary to concentrate efforts on landscape-scale studies in the Neotropical region. Our analysis suggests that the optimal scale size in landscape studies depends on the home range of the bats under investigation. As such, we recommend that greater efforts be made to understand this parameter, for instance, by using telemetry studies. In the absence of such data, we believe that studies that utilize multiple scale sizes or make comparisons between different landscapes can provide a more comprehensive understanding of bats in cultivated landscapes.

We also found gaps in the type of agricultural systems studied. There are still few studies that assess the consequences that forest plantations that require the cutting of trees have on bats, in all regions. These type of plantations may have different impacts from other agricultural systems (grassland-cropland systems and forest that do not require cutting) on bat communities, as they are subject to cyclical changes in their structure; we recommend further studies in these type of agricultural systems. Furthermore, predominantly non-

forested biomes (e.g., African and South American savannas), as well as non-forested habitats (e.g., flooded and natural fields), have been understudied compared to forested ones. The most frequently proposed mitigation measure in the selected studies was the conservation or restoration of natural, semi-natural, or potential bat habitats in cultivated landscapes. Therefore, understanding what these potential habitats are and how they benefit bats in agricultural systems will help to outline strategies for the conservation of these organisms. This reinforces the importance of studies that evaluate natural non-forest habitats as well as forest ones. Non-forest habitats can influence bat communities by functioning as complementary habitats for resource and promote movement and their replacement by agricultural systems can change the dynamics of these landscapes. In addition, studies of bat behavior, such as those using telemetry, were more common in the Palearctic region and are extremely relevant to understand what these potential areas are. These studies can provide information on home range size, roosting and foraging habitat selection, dispersal patterns and, in addition, can help determine the ideal scale size for landscape studies. The relevance of the conservation or restoration of natural, semi-natural or potential areas for bats also reinforces the importance of focusing on studies that considered natural/semi-natural areas (as the amount and presence of natural/semi-natural areas affects bats in cultivated landscapes) in regions where these studies are scarce (outside the Neotropical region). In addition to this landscape composition variable, studies evaluating the configuration variables of cultivated landscapes were scarce in all regions. Connectivity and other landscape configuration variables, such as heterogeneity, were cited in many studies as mitigating measures. Thus, we reinforce the importance of studying this landscape parameter. In addition to conservation or restoration of natural bat habitats, many studies also proposed less intensive agricultural system management as a mitigation measure. Therefore, a better understanding of how bats respond to different types of management, particularly outside the Palearctic and Neotropics, where these studies are most often performed, is essential in creating effective strategies for improving connectivity in these landscapes. This understanding will also enable the identification of ways to increase roost and food availability within plantations, thereby making them complementary habitats for bats.

Raising awareness of the importance of bats is crucial for their conservation. However, few studies have investigated producers' perception of bats. Furthermore, the ecological service studies included in this analysis have predominantly focused on agricultural pest control/suppression, with limited research exploring the impact of agricultural systems on other ecological services provided by bats. Moreover, only a few studies have attributed a monetary value to these services. Therefore, we recommend increased efforts to understand the impact of agricultural systems on ecological services other than pest control/suppression and to assign economic value to these services. Finally, conservation policies are vital for the success of these strategies, as they can promote environmental education, raise awareness among local populations and producers about the importance of bats, provide financial incentives to producers for their conservation efforts, and fund research to fill knowledge gaps.

In summary, our findings highlight the urgent need for a more comprehensive understanding of the impact of agricultural systems on bat conservation, particularly in the Afrotropic and Indo-Malaysia regions. In addition, future studies should focus on forest plantations that require cutting, predominantly non-forested biomes (e.g., African and South American savannas), and non-forested habitats (e.g., flooded and natural fields). Also, studies should use a combination of different sampling methods (e.g., mist net and acoustic recorders), telemetry, and multiple biodiversity descriptors. Further research is essential to gain a comprehensive understanding of the impact of trophic resources and abiotic factors, contamination, disease prevalence, physiological responses, landscape-scale effects, population ecology, and the ecological services provided by bats. Additionally, there is a need to enhance the role of conservation policies in promoting bat conservation, as well as raise awareness of their importance among producers and local communities. Only by filling these gaps and understanding all the factors that influence bat occurrence and survival in these human impacted habitats, it becomes possible to develop science-supported and effective management and conservation strategies, in areas affected by agricultural systems.

## 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

BSX, WC, and MV originally formulated the idea. BSX conducted the review and compilation of data. BSX performed the qualitative analysis of this review. BSX wrote the drafts of the main manuscript and the online resources. All authors contributed article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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