Trait-mediated filtering predicts phyllostomid bat responses to habitat disturbance in the Orinoco Llanos

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Abstract

Which functional traits allow a bat species to survive habitat disturbance? Empirical evidence regarding this question remains limited for many tropical regions despite their importance for conservation. Here, we used body mass, wing morphology, trophic level, and diet to identify which traits make phyllostomid bat species more vulnerable to human impacts in the Colombian Orinoco Llanos. Bats were sampled using mist nets in riparian forests, unflooded forests, flooded savannahs, and conventional rice crops on traditional farmlands with high-intensity agriculture and in private reserves with greater ecosystem protection. We tested the associations between species traits and landscape-structure variables (habitat cover and type, number of habitat patches, shortest distance to water) using RLQ and fourth-corner analyses, accounting for both spatial and phylogenetic autocorrelation. Trophic level and diet were the most important traits linked to disturbance sensitivity. Our results indicated that rice crop cover, savannah patches, and altered unflooded forest act as a filter, benefiting disturbance-adapted frugivorous genera in farmlands (e.g., *Artibeus* spp., *Carollia* spp., *Platyrrhinus* spp., *Uroderma* spp.). Conversely, animalivorous species were strongly associated with savannah cover and riparian forests within reserves (e.g., *Lampronycteris brachyotis*, *Lophostoma brasiliense*, *Micronycteris minuta*, *Trachops cirrhosus*). Encouraging the creation of more wildlife-friendly landscapes through payments for ecosystem services across the Colombian Llanos will ensure the long-term persistence of disturbance-sensitive species and sustain a complete set of ecological functions and ecosystem services that these bats provide.

Keywords: Chiroptera, environmental filters, functional traits, land-use change, landscape composition and configuration, Llanos Orientales

Introduction

The conversion of natural vegetation into an agricultural-livestock matrix is increasing substantially across tropical savannahs (Buchadas et al. 2022), and recent evidence suggests that < 3% of their ecosystems remain highly intact (Williams et al. 2022). This highlights the enormous importance of savannahs for effective conservation targets to address the global decline in biodiversity and ecosystem services. The second-largest Neotropical savannah, the Orinoco Llanos, has been severely affected by multiple and deleterious anthropogenic pressures since the 1970s (Romero-Ruiz et al. 2012). The Llanos account for ~15% (170,000 km^2) of the total area of Colombia and ~25% (240,000 km^2) of Venezuela (Borghetti et al. 2019). Its ecosystems are highly biodiverse, threatened, ecologically understudied, support the livelihoods of local human communities (Suárez-Castro et al. 2021), and harbour important carbon stocks (Grace et al. 2006). Over 85% of the original cover of the region falls outside of protected areas (Williams et al. 2022), and typically comprises a mosaic of savannahs and forests, with interspersed croplands, pastures varying in the degree of livestock grazing intensity, and urban settlements (Romero-Ruiz et al. 2012). Substitution of native vegetation by human-disturbed habitats is spatially complex and has contributed to the loss of species and ecosystem functions and services worldwide (Newbold et al. 2016). Making conventional agriculture sustainable is a central task for farmers and environmental scientists. To tackle this challenge, jointly considering human-modified landscapes (Pereira and Daily 2006) and functional information in the form of species traits (Cadotte et al. 2011) in ecological studies is critical to devising more effective conservation strategies.

Characteristics of an organism or species that potentially affect its survival, growth/reproduction, and ecological functions (functional trait *sensu* Weiss and Ray 2019) have been a focus of extensive research in the last decade across different spatiotemporal scales and levels of biological organization (Palacio et al. 2022). Trait-based ecology has broadly contributed to advancing our understanding of biodiversity patterns and responses to environmental shifts in complex natural systems in the Anthropocene (Green et al. 2022). This approach has provided an innovative conservation-planning tool to disentangle the mechanisms structuring communities, such as the relative role of environmental filtering and interspecific competition (Cadotte and Tucker 2017). Therefore, assessing how functional traits and environmental variables influence the ability of species to persist in small, isolated, and disturbed habitats is essential to understanding the processes underlying community assembly and minimizing local species loss (Jeliazkov et al. 2020).

Neotropical bats may evince different responses and extinction risks depending on land-use intensity and disturbance (reviewed in Meyer et al. 2016). Their selection as focal taxon for trait-based conservation is appropriate given their high diversity in the tropics and their crucial contribution to ecosystem functioning, as pollinators, seed dispersers, prey, and predators of arthropods and small vertebrates (Kunz et al. 2011). While trait-environment relationships have lately been assessed in some studies to predict anthropogenic effects on phyllostomid and aerial-hawking insectivorous bat species and ecosystem functioning across the Neotropics (e.g., Farneda et al. 2015; Gonçalves et al. 2017; Núñez et al. 2019; Carballo-Morales et al. 2021; Bobrowiec et al. 2022; Colombo et al. 2023) results differ across ecosystems, and studies are rare for many tropical ecoregions or countries such as Colombia (but see Ramírez-Mejía et al. 2020 and Díaz-B et al. 2023).

Multivariate trait-based research focusing on different ecological systems and geographic regions is pivotal for determining if traits identified as important in one ecosystem can be helpful as general predictors of local species decline (Chichorro et al. 2019). Here, we used a robust approach that accounts for phylogenetic and spatial autocorrelation (Braga et al. 2018) within an analytical framework that integrates RLQ (R = environmental variables, L = species distributions, Q = species traits) and fourth-corner methods (Dray et al. 2014) to evaluate how landscape-structure variables (composition and configuration) in the Colombian Llanos influence the vulnerability of phyllostomid bat species based on their functional traits. We anticipated that increasing land-use intensity and decreasing structural complexity of the vegetation would act as a filter, promoting the selective loss of species in more disturbed habitats (e.g., rice monocultures) through their functional traits (Wordley et al. 2017; Carvalho et al. 2021). Specifically, our study was guided by the following questions and associated predictions:

1. Which functional traits are the best predictors of bat sensitivity to habitat disturbance in the Orinoco Llanos?

Trophic level and diet will be the most important traits linked to species vulnerability. Phytophagous bats (those with mainly a fruit- or nectar-based diet) will be less affected by the conversion of natural habitat to rice paddies, as they often forage and commonly roost in human-disturbed habitats compared to animalivorous bats (Castro-Luna and Galindo-González 2012; Farneda et al. 2015).

2. Which bat species are most vulnerable to habitat disturbance based on the traits identified in (1)?

Animalivorous species (those with mainly a vertebrate- or arthropod-based diet), such as *Lampronycteris brachyotis*, *Lophostoma brasiliense*, and *Trachops cirrhosus*, will be more vulnerable to disturbance and thus be absent or considerably less abundant in rice fields. As secondary consumers these species are commonly considered habitat specialists which are more dependent on preserved forests compared to phytophagous phyllostomids (Gonçalves et al. 2017; Carballo-Morales et al. 2021).

3. Which landscape-structure variables are the most important in determining bat functional trait composition?

Landscapes with small, irregular, or narrow habitat patches generally exhibit a high number of patches (Fahrig et al. 2011). Therefore, a high number of patches is more representative of traditional farmlands in our study area. This would be reflected in a significant positive relationship between number of patches of unflooded forests with phytophagous bats due to a greater supply of roosts and fruits, while forest cover and the shortest distance to water would benefit animalivorous bats due to their more significant association with riparian forest (Arroyo-Rodríguez et al. 2016; Chambers et al. 2016).

Material and methods

Study area

The study was carried out in two Civil Society Nature Reserves (La Esperanza 5°42’N-71°14’W and El Boral 5°19’N-71°47’W) and four traditional farmlands (Hato California 5°39’N-71°17’W, Sinaloa 5°46’N-71°27’W, Las Acacias 5°25’N-71°46’W, and Finca Bella Vista 5°25’N-71°45’W), in Casanare state, Colombian Orinoco Llanos (Fig. 1). The climate in the region is characterized by a unimodal seasonality pattern: a dry season between December and March (monthly accumulated rainfall < 100 mm) and a rainy season from April to November (monthly variation of 150 to 600 mm) – total annual rainfall varies from 1500 to 3000 mm (IDEAM 2015). Temperatures vary from 27 to 30 °C during dry and 23 to 26 °C during rainy seasons (Etter 1997).

La Esperanza and El Boral (~137 m a.s.l.) are private reserves that constitute a mix of flooded savannahs with native grass and others used for cattle grazing, and mature and secondary riparian forests (gallery forest) that vary in size and experience seasonal inundation. On farmlands, the understory of unflooded forest patches (California, Las Acacias, and Bella Vista, ~164 m a.s.l.) and riparian forest (Sinaloa, 159 m a.s.l.) has been partially removed and is often used as a passageway for cattle. Naturally flooded savannahs were replaced mainly by conventional rice crop monocultures (Fig. 1), which were subjected to synthetic pesticides and fertilizers between three and ten years (mean of 8 years) before this study.

In all farmlands and reserves, there is selective non-commercial logging of larger trees, and some exotic trees (e.g., *Mangifera* spp., Anacardiaceae) are present in riparian (La Esperanza) and unflooded forests (California). The canopy in riparian and unflooded forests is ca. 15 m high, with occasional emergent trees reaching 20 m, and closed due to the high vegetation density. Forest pioneer species that produce fruits consumed by many frugivorous bat species, such as *Cecropia* spp. (Urticaceae), *Ficus* spp. (Moraceae), and *Vismia* spp. (Hypericaceae) were observed in riparian and mainly unflooded forests. The savannah has an open canopy composed primarily of a grassy vegetation stratum interspersed with some shrubs and trees of small diameter and stature (between 2 to 6 m in height) (A. Otálora-Ardila, unpublished data). See Supporting Information Plate S1 for differences in vegetation structure among habitats.

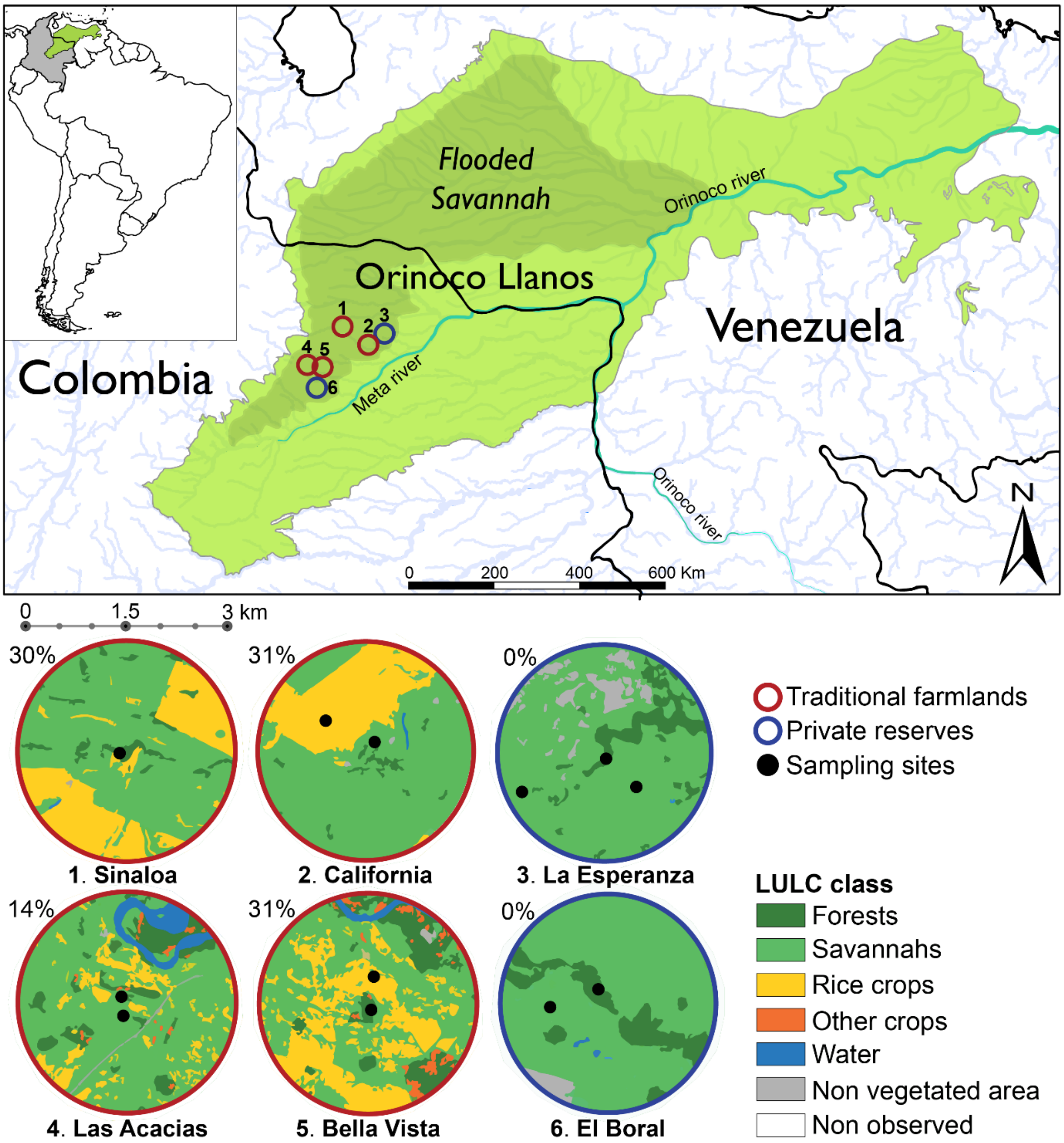


Fig. 1 Spatial distribution of the six Colombian landscapes overlaid on a hydrographic mesh of the Orinoquia region and the respective "Land Use Land Cover" (LULC) class quantified within a focal landscape buffer of 1.5 km radius. The darkest area highlights the flooded (hyperseasonal) savannah, Northern South America. The rice crop cover percentage is given in each landscape's upper left corner.

Bat sampling

Each habitat was sampled for a total of 23 to 26 nights, evenly distributed among four replicate surveys (one per season and rice production stage): land preparation (transition dry-wet season), vegetative growth (wet), grain maturation (transition wet-dry), and post-harvest (dry). Bat sampling covered three sampling units in riparian forests (La Esperanza, El Boral, Sinaloa), three in unflooded forests (California, Las Acacias, Bella Vista), three in flooded savannahs (La Esperanza [two units], El Boral), and three in conventional rice crops (California, Las Acacias, Bella Vista). Sampling sites in savannahs and rice crops were located at least 150-400 m from the edge of riparian and unflooded forests. These distances are generally greater than those of other Neotropical bat studies (e.g., at least 50 m was used in the Brazilian Amazon by Carvalho et al. 2021 and 75 m in Colombian Andes by Otálora-Ardila and López-Arévalo 2021) and were delimited according to the total area of each habitat in each sampling site to maximize spatial independence.

Phyllostomid bats were sampled using five ground-level mist nets (12 × 2.5 m, ECOTONE Inc., Poland, intercalating nylon/polyester and monofilament nets) in each of the 12 sampling sites distributed in the four habitats. The nets were opened for two to three consecutive nights per site from dusk (~18:00 h) until 5 to 7 h after exposure (except during torrential rains) and revised at intervals of ~25 minutes. Bias in capture rates due to the ability of bats to detect the location of nets (Marques et al. 2013) was avoided by moving nets on the third night across the same site and spacing visits to the same habitat more than three months apart. Sampling effort was roughly similar among habitats: riparian forests = 24,678 m^2.h (m^2.h = net area multiplied by the number of nets, exposition time, and sampling repetitions; Straube and Bianconi 2002), unflooded forests = 22,590 m^2.h, flooded savannahs = 26,901 m^2.h, conventional rice crops = 23,310 m^2.h, total = 97,479 m^2.h.

Bat sampling was conducted in each habitat in all seasons: wet season (July-August 2022), transition wet-dry season (November-December 2020), dry season (January-February 2022), and transition dry-wet season (March 2021). Phyllostomid bats were individually marked with tattoos on the right wing at the lower part of the plagiopatagium (project phase 1 funded by the "Neotropical Grassland Conservancy") or with small, coloured plastic rings on a plastic cable tie necklace (project phase 2 funded by "The Rufford Foundation") (Sikes 2016) and released at the capture site on the same night. This study was approved by the Institutional Committee for the Care and Use of Animals (CICUA-060-21, National University of Colombia at Medellín), and bat sampling was conducted under a Colombian government permit (ANLA, resolution 0255/2014).

Species traits and phylogenetic relatedness

The functional traits used as predictors of species' sensitivity to habitat disturbance reflect a variety of ecological roles and indicate potential vulnerability to human-modified ecosystems in Neotropical bats (Castillo-Figueroa and Pérez-Torres 2021): (i) body mass, (ii) wing morphology, (iii) trophic level, and (iv) diet (Table 1). See Appendix S1 for a description of the wing morphology traits, and Table S1 for individual species values of each functional trait. We preferred not to include the "vertical stratification" trait due to high variation in vertical vegetation structure across the different habitats in our study area (Plate S1). This trait could make our results more difficult to interpret given that it can create a pattern of indifferentiable use of the vertical stratum with capture height probably not designating foraging height (Rex et al. 2011).

Table 1 List and description of the four functional traits used as predictors of bat species vulnerability to habitat disturbance in the Orinoco Llanos, Colombia. Literature sources are provided in Table S1.

Trait	**Description**	**Source**
Body mass	Average body mass of each species (adults only but excluding pregnant females)	Our capture data
Wing morphology	Aspect ratio and relative wing loading	Our capture data
Trophic level	Phytophagous or animalivorous	Literature
Diet	Based on the main food item consumed by each species: nectar or pollen, fruits or leaves, blood, invertebrates, vertebrates	Literature

To account for phylogenetic autocorrelation, we used the phyllostomid species-level phylogeny proposed by Rojas et al. (2016) as it avoids a known mislabelling error for *Phyllostomus discolor* present in other phylogenies that renders the genus *Phyllostomus* paraphyletic based on RAG2 in GenBank (Dávalos et al. 2012). One of the 20 phyllostomid species (*Platyrrhinus angustirostris*) was not present in the phylogeny and was replaced by its closest congener (*P. incarum*) (Velazco and Lim 2014). The supertree was pruned to obtain the local phylogeny (R package 'picante', Kembel et al. 2010) and the pairwise phylogenetic distances ('cophenetic.phylo' function, R package 'ape', Paradis et al. 2004). See Fig. S1 for detailed information on the phylogenetic relationships between bat species in this study.

Landscape characteristics

We included only aspects of landscape composition and configuration in the analyses to equalize the representation of environmental variables between all habitat types and avoid bias from over-representation of local vegetation structure of riparian and unflooded forests

(Cushman et al. 2008). We used ESRI ArcMap 10.4.1 and ERDAS Imagine 2014 software based on 2021 Sentinel-2A satellite images (10 and 20 m resolution) to assess the proportional cover of forests, savannah, water, rice, and other crops in the landscape. We considered mature and secondary riparian forests and unflooded forests as "forests". This simplification reduces the probability of misclassification of the different habitats in our study area, increases statistical power for not adding more layers of complexity in a multivariate analysis framework, and is based on their influence on the distribution and abundance of Neotropical bats (e.g., Cleary et al. 2016; Falcão et al. 2021; Carvalho et al. 2021). The landscape metrics were based on their effect on tropical bat diversity (Meyer et al. 2016) and calculated for circular buffers of 1.5 km radius centered on the 12 sampling sites using the R package "landscapemetrics" (Hesselbarth et al. 2019): "habitat cover" (total area in hectares of forests, savannahs, and rice croplands) and "patch number" (number of patches of each habitat); and using Google Earth Pro 7.3.4: "water distance" (distance in meters between each sampling site and the nearest water body). We also considered "habitat type" as a qualitative variable: riparian forest, unflooded forest, flooded savannah, and conventional rice crop (see Table S2). We chose to quantify the landscape metrics within a circle of 1.5 km radius to reflect the home ranges of different-sized Neotropical bat species (Chambers et al. 2016), to reduce the probabilities of inflating type I errors due to multiple testing and, at the same time, minimize spatial overlap between sites.

Data analysis

We considered only phyllostomid species as they can be reliably sampled with mist nets (Kalko et al. 1996) and excluded same-site recaptures and rare species with fewer than three captures to increase explanatory power. This resulted in 20 species and 661 individuals for analysis (Table S3), but see Table S4 for a complete list of species captured. We also analyzed all rice production stages jointly because species richness and abundance did not differ significantly among them (Shapiro-Wilk test on residuals $P > 0.5$; Gaussian-GLM $P > 0.2$ for both response variables). All functional traits and environmental variables were standardized to a mean of zero and a standard deviation of one using the ‘scale’ function (R package ‘FD’, Laliberté and Legendre 2010) to facilitate comparison of their relative effects. Relative species abundance was calculated based on net sampling effort for each site. Inventory completeness was evaluated across the different habitats using a rarefaction/extrapolation approach (R package ‘iNEXT’, Hsieh et al. 2016).

To infer associations between bat functional traits and species vulnerability to habitat conversion, we employed a statistical framework that integrates RLQ and "fourth-corner" analyses (Dolédec et al. 1996; Dray et al. 2014). This multivariate approach provides a direct and appropriate way to test and estimate trait-environment relationships mediated by species abundances (Kleyer et al. 2012). The ordination-based RLQ analysis summarizes the link between three input datasets: R (site-environmental data), L (site-relative species abundances), and Q (species traits). We analyzed table L through a correspondence analysis (CA) and the R and Q tables through Hill-Smith principal components analysis (PCA) because they contained a mix of continuous and categorical traits (Hill and Smith 1976). The link between the three matrices is established by weighting the ordinations of the R and Q matrices with scores (eigenvalues) from the correspondence analysis.

While RLQ maximizes the covariance between the three matrices, "fourth-corner" allows to statistically test individual trait-environment relationships in the output of the RLQ. We conducted the fourth-corner analysis in a highly conservative way to provide total control over type I error rates. First, we used a combination of site-based permutation model 2, which tests if the distribution of species with site-independent traits is influenced by environmental conditions, with species-based model 4, which tests if the species composition of sites with fixed environmental conditions is influenced by the species traits. Second, due to spatial and phylogenetic effects that can be pervasive in trait-based ecological studies, we used a randomization approach based on Moran's spectral randomization (MSR; 999 random replicates) to account for spatial autocorrelation and phylogenetic relatedness between species (Braga et al. 2018). Third, due to multiple comparisons, the *P* values were controlled by the false discovery rate method (FDR; Benjamini and Hochberg 1995), and significance was assessed based on 49,999 permutations (Dray et al. 2014). Analyses were performed using the 'ade4' R package (Dray and Dufour 2007; R Development Core Team 2020).

Results

We captured 996 bats (excluding 29 same-site recaptures) belonging to five families and 39 species. Phyllostomidae was the dominant family (67% of the total captures, 25 species), followed by Molossidae (17%, 6), Vespertilionidae (6%, 5), Emballonuridae (2%, 2) and Noctilionidae (8%, 1). The species richness and abundance of phyllostomid bats was higher in riparian forests (22 species, 169 individuals) and unflooded forests (16, 427) than in savannahs

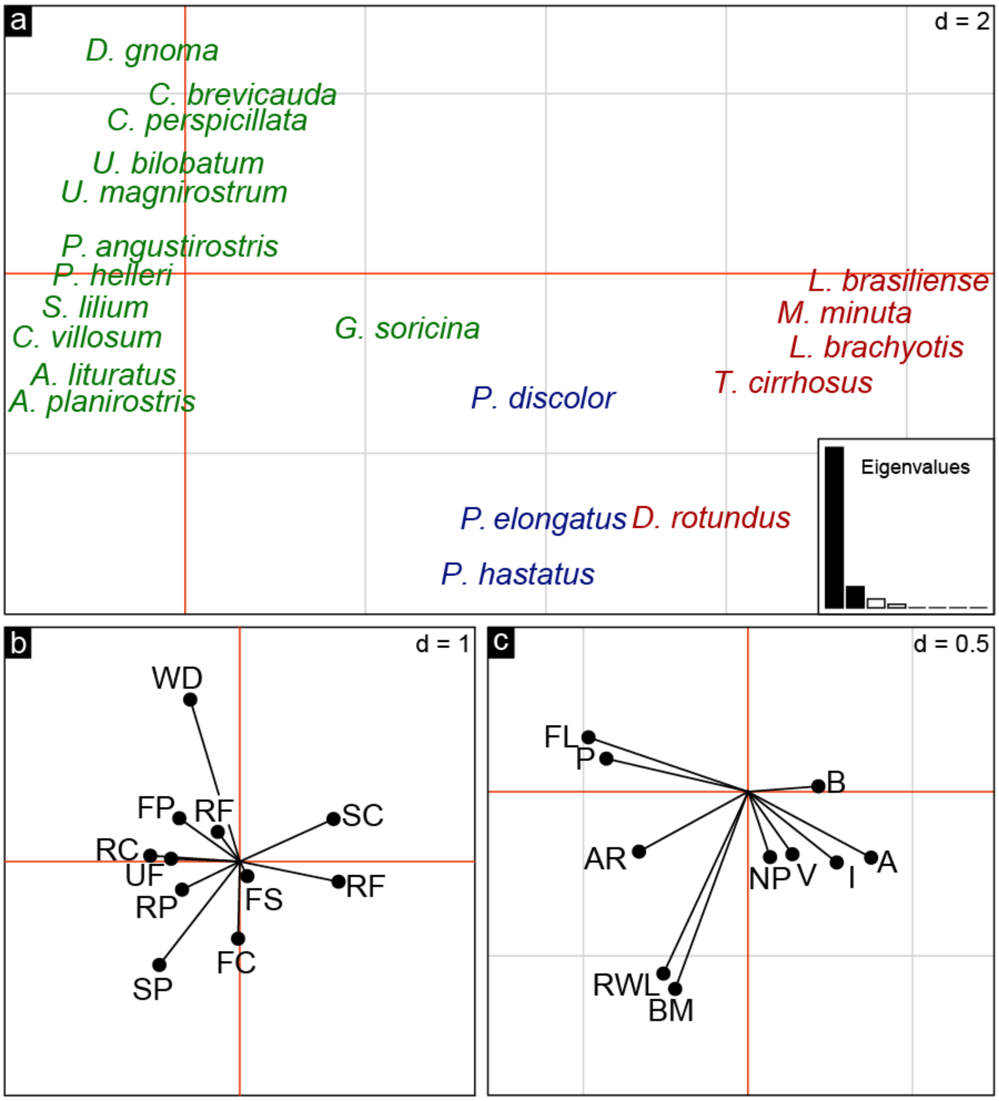
(9, 26) and rice fields (9, 46) (Table S4). Sample coverage values for phyllostomid species from all habitats were close to 1 (Fig. S2), indicating good sampling completeness.

The total variance between landscape characteristics and functional traits from the first two RLQ ordination axes was 84.8% for axis 1 and 11% for axis 2 (Table 2). The variance expressed for the first RLQ axis also indicated variability in trait values across the different habitats (R = 41.8%, L = 28.7%, Q = 44.8%) (Table 2).

Table 2 Summary of RLQ axes values for phyllostomid bats: eigenvalues and percentage of total co-inertia accounted for by the first two axes, covariance and correlation with the L matrix, projected variance with the R and Q matrices, and ordinations of tables L (CA), R and Q (Hill-Smith PCA).

	Axis 1 (%)	Axis 2 (%)
RLQ axis eigenvalues	3.36 (84.79)	0.43 (11)
Covariance	1.82	0.66
Correlation: L	0.42	0.43
Projected variance: R	4.49	6.23
Projected variance: Q	4.26	5.61
L table CA	0.49 (28.65)	0.34 (19.74)
R table PCA (Hill-Smith)	4.60 (41.78)	2.19 (19.95)
Q table PCA (Hill-Smith)	4.48 (44.82)	2.04 (20.38)

In the three-table RLQ ordination, trophic level and diet grouped according to habitat type (Fig. 2), i.e., unflooded forests and rice crops in farmland-dominated landscapes were separated from more pristine habitats such as riparian forests and savannahs at reserve sites (Fig. 3). While frugivorous bats (11 species, e.g. *Artibeus* spp., *Carollia* spp., *Platyrrhinus* spp., *Uroderma* spp.) were associated with rice cover, savannah patches, and unflooded forests, animalivorous bats (five species, e.g. *Lampronycteris brachyotis*, *Lophostoma brasiliense*, *Micronycteris minuta*) with a diet composed mainly of invertebrates were associated with more preserved habitats at private reserves such as riparian forests and savannah (Fig. 2 and Fig. 3).



315 **Fig. 2** Results of the first two axes of RLQ analysis: (a) species, (b) principal component analysis (PCA Hill-Smith) analyzing the covariation of environmental variables, and (c) functional traits. Abbreviations: (a) see Table S3 for full species names; green species names = trophic level phytophagous, red = trophic level animalivorous, blue = both; (b) FC = forest cover, SC = savannah cover, RC = rice cover, FP = forest patches, SP = savannah patches, RP = rice patches, WD = water distance, RF = riparian forest, UF = unflooded forest, FS = flooded savannah, RF = rice fields; (c) BM = body mass, AR = aspect ratio, RWL = relative wing loading, P = phytophagous, A = animalivorous, NP = nectar or pollen, FL = fruits or leaves, B = blood, I = invertebrates, V = vertebrates. See Table 1 and Appendix S1 for trait descriptions.

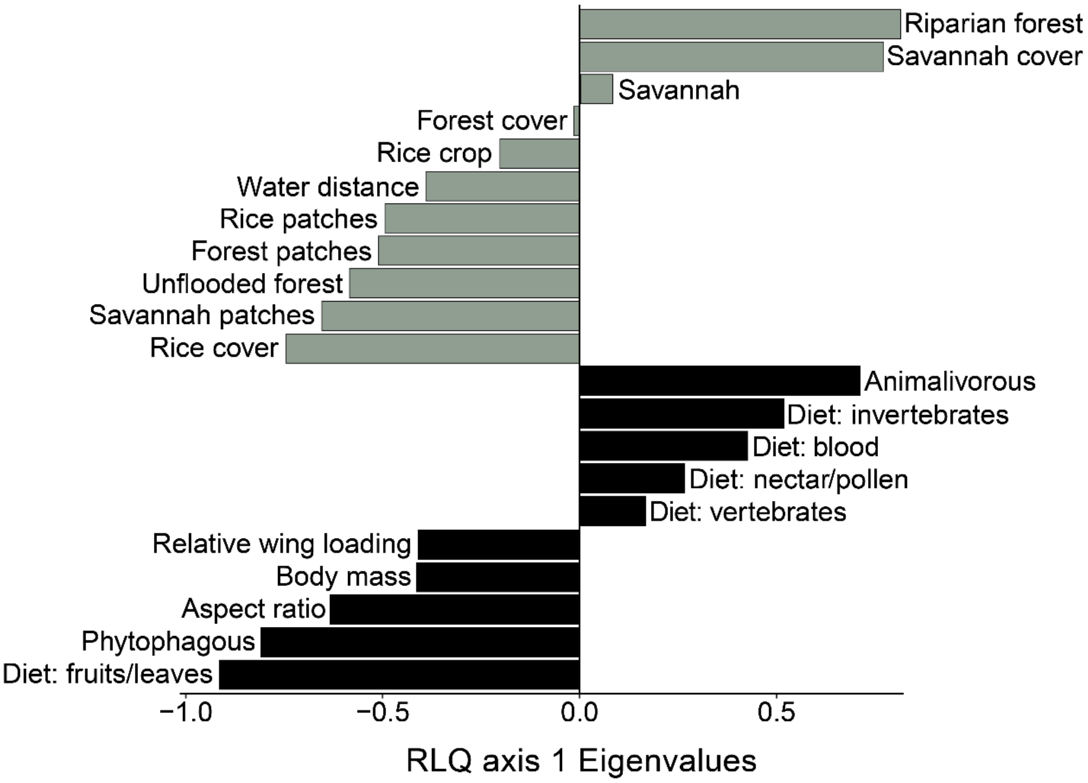
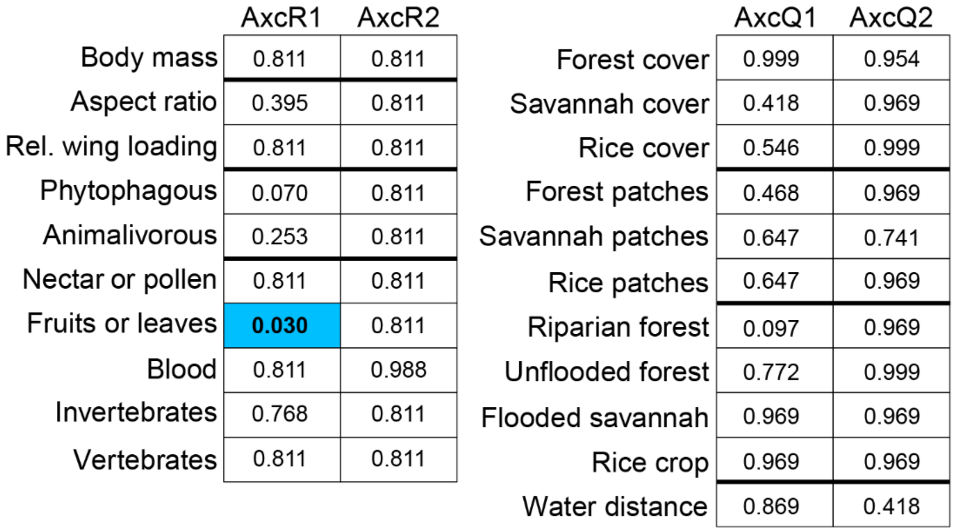


Fig. 3 Results of the RLQ analysis relating phyllostomid species traits (black bars) and environmental variables (grey) along RLQ axis 1.

The global test of the fourth-corner statistic indicated that species composition is more dependent on the environmental site conditions (model 2, *P* = 0.007) and not influenced by functional traits (model 4, *P* = 0.126). Bat species associated with a diet composed mainly of fruits or leaves revealed a significant relationship with the environment (*P* = 0.03), manifesting negatively with the first RLQ axis of the environmental variables (AxcR1) (Fig. 4).



	AxcR1	AxcR2
Body mass	0.811	0.811
Aspect ratio	0.395	0.811
Rel. wing loading	0.811	0.811
Phytophagous	0.070	0.811
Animalivorous	0.253	0.811
Nectar or pollen	0.811	0.811
Fruits or leaves	**0.030**	0.811
Blood	0.811	0.988
Invertebrates	0.768	0.811
Vertebrates	0.811	0.811

	AxcQ1	AxcQ2
Forest cover	0.999	0.954
Savannah cover	0.418	0.969
Rice cover	0.546	0.999
Forest patches	0.468	0.969
Savannah patches	0.647	0.741
Rice patches	0.647	0.969
Riparian forest	0.097	0.969
Unflooded forest	0.772	0.999
Flooded savannah	0.969	0.969
Rice crop	0.969	0.969
Water distance	0.869	0.418

Fig. 4 Results of fourth-corner tests with P-values controlled by FDR. Significant ($P < 0.05$) negative associations are represented by blue cells. Thick black lines separate different types of variables.

Discussion

Despite the importance for biodiversity conservation, studies addressing the link between species, functional traits, and environment are still rare across the tropics (Gonçalves-Souza et al. 2023). Here, we assessed how functional traits of phyllostomid bat species are correlated with environmental characteristics and species distributions in two landscapes in the Colombian Llanos with different levels of anthropogenic disturbance: traditional farmland-dominated sites and private reserves. In general, our study revealed that while high-intensity agriculture in farmlands benefited frugivorous species, habitat conversion towards conventional rice monocultures negatively affected animalivorous bat species. Our results support the importance of well-preserved riparian forests and savannahs in Civil Society Nature Reserves for safeguarding disturbance-sensitive species. However, the conservation of most phyllostomid species in the Orinoco Llanos is only possible with the protection of savannahs surrounding forest patches. This protection helps maintain the species pool within the riparian forests in private reserves compared to forests adjacent to intensive agricultural fields.

Trophic level and diet

A particularly interesting finding in line with our initial prediction is that phytophagous bats, represented mainly by frugivores, have shown a remarkable ability to tolerate habitat disturbance. More stable population dynamics make Neotropical bat species at the bottom of food chains less threatened than those at higher trophic levels (e.g., Farneda et al. 2015; Carvalho et al. 2021; Bobrowiec et al. 2022). The interpatch movements and habitat use by many frugivorous species across the farmland forest patches probably is facilitated due to the high abundance of fruits of successional plants, such as *Cecropia* spp., *Ficus* spp., and *Vismia* spp. (A. Otálora-Ardila and F. Z. Farneda, pers. obs.) (Giannini and Kalko 2004). On the other hand, the RLQ analysis suggested that animalivorous bats (mainly species which feed on arthropods) are more extinction-prone, highlighting the importance of native vegetation cover (landscape composition) and well-preserved forests for the conservation of this particular bat group, as found by numerous studies elsewhere (e.g., Klingbeil and Willig 2009; Voss et al. 2016; Wordley et al. 2017). Farmland habitats with a high percentage of rice crops act as a selective filter for many gleaning animalivorous bats (i.e., species that capture prey from the surface of the vegetation or ground; ter Hofstede and Faure 2023) due to their limited roost and prey availability compared to more conserved riparian forests and savannahs at private reserves. Specialist forest-dwelling gleaning animalivorous bats were also strongly and negatively affected by human disturbance in the Brazilian Amazon (Farneda et al. 2018) and Colombian Llanos (Morales-Martínez et al. 2018; Ramírez-Mejía et al. 2020).

Body mass

Studies generally point to a strong negative correlation between body size and land-use intensity, suggesting that larger mammals are demographically more fragile due to their lower reproductive potential and higher trophic levels (Colinvaux 1980), which requires vast areas of primary habitats for their conservation (Semper-Pascual et al. 2022). Fourth-corner analyses have suggested that habitat fragmentation and disturbance significantly and negatively affect larger phyllostomid bat species, both in the Amazon and on Panamanian land-bridge islands (Farneda et al. 2015). However, the lack of evidence of body mass as a predictor of bat vulnerability in our study may be explained by the similarities in species richness and abundances of farmlands and reserves, as the largest bat species (*Phyllostomus hastatus* [average 91.1 g] and *Artibeus lituratus* [66.4 g]) and one of the smallest species (*Dermanura gnoma* [9.7 g]) were recorded in both. Furthermore, we did not record heavier gleaning species, such as *Vampyrum spectrum* (average 169 g) and *Chrotopterus auritus* (77 g) (ecoregister.org, accessed on December 19, 2023), considered more vulnerable to habitat disturbance (Gonçalves et al. 2017). These species generally require vast areas of pristine forest (Farneda et al. 2015) that probably are absent in our study landscape due to multiple human activities.

Wing morphology

Wing morphology is an equally important and widely used trait to predict the sensitivity of bat species in human-modified landscapes (Marinello and Bernard 2014), which intricately correlates with diet, habitat use, home-range size (Crane et al. 2022), and echolocation characteristics (Zou et al. 2022). The fact that some phyllostomid generalist species with similar wing morphology values are present throughout the different habitats may have resulted in weak support for this trait as predictor of bat species vulnerability to habitat conversion in the Orinoco Llanos (see Table S1). For example, the haematophagous bat *Desmodus rotundus* was recorded in three habitats (riparian forests, unflooded forests, and savannahs) and had average values of aspect ratio and relative wing loading similar to some widespread frugivorous bats, such as *Chiroderma villosum* and *Platyrrhinus helleri*.

Caveats and guidelines for future research

Fieldwork in the Orinoco Llanos is challenging due to public safety situations and poor or absent road infrastructure, and our results might have been slightly biased due to the limited number of replicates of each habitat. Sampling more riparian forests could increase the power of the fourth-corner test (ter Braak et al. 2012), and may have resulted in a more evident relationship between riparian habitats and animalivorous bats. In a context of information loss, we had to convert categorical traits into a numerical factor (0 or 1, Table S1) to be able to perform the phylogenetic and spatial autocorrelation analyses (MSR; Braga et al. 2018). We also calculated the shortest distance to water between each sampling site and the nearest water body based on fixed values, which may have underestimated its effects on bat communities due to the high seasonal fluctuation of the Llanos, with dry and rainy extreme periods.

The type of trait considered can influence species' vulnerability, and some physiological traits (e.g., "thermal tolerance", "metabolic rate") could potentially be important for functional bat ecology (McKechnie and Wolf 2019). Nevertheless, the general lack of physiological data for most Neotropical bat species makes it impossible to understand how environmental temperature fluctuations and energy requirements affect the resilience of species to habitat disturbance. The paucity of ecological information for many bat species regarding other traits such as "mobility or home range" (Bernard and Fenton 2003), "roosting behaviour" (Marroquin et al. 2023), and "diet specialization" (Villalobos-Chaves and Santana 2022) further challenges our ability to make better-informed model predictions.

The exponential increase in trait-based studies in the last decade has led to a wide range of often disparate results due to different geographic locations, widespread use of certain species traits (Gonçalves-Souza et al. 2023), a proliferation of statistical procedures in functional ecology (Palacio et al. 2022), and the integration or not of phylogenetic and spatial information in the analyses (Chichorro et al. 2019). Therefore, we recommend extending this line of research through a global meta-analysis to determine under what ecological and methodological circumstances a specific trait is more important than others. Further, we suggest replicating the methodological approach of this study across the other habitat types in the Orinoco Llanos, such as aeolian and highplain savannahs (see Romero-Ruiz et al. 2010). Furthermore, we also highlight the urgency of evaluating how different scenarios of intensive monoculture, fire management, and climate change across the Orinoquia ecosystems affect bat functional composition and ecosystem services.

The importance of Civil Society Nature Reserves for conservation

The capacity of agricultural landscapes to support biodiversity will likely determine new pathways for conservation policy (Melo et al. 2013), especially in tropical savannahs currently characterized by high rates of habitat and species loss (Williams et al. 2022). Understanding which species traits are most closely correlated to different land-uses will enable us to identify which species are particularly vulnerable and ways to mitigate the harmful effects of habitat conversion on biodiversity (Jeliazkov et al. 2020). Our study showed that some animalivorous bat species (e.g., *Lampronycteris brachyotis*, *Lophostoma brasiliense*, *Micronycteris minuta*, *Trachops cirrhosus*) are lost with increasing land-use intensity (rice crops). In this regard, private reserves like La Esperanza and El Boral, are important strongholds for the conservation of many disturbance-sensitive bat species. The importance of private protected areas for conserving some threatened vertebrate species has also been documented in Colombia by López-Arévalo et al. (2021) and in the Brazilian Cerrado by De Marco et al. (2023).

The private reserves protect part of a natural ecosystem, and their owners have voluntarily committed to biodiversity conservation without receiving financial government assistance (Pasquini et al. 2011). Initiatives of the Colombian and Venezuelan government's environmental departments and agencies to support the creation of private reserves via payments for ecosystem services are scarce (Aldana and Mitchley 2013). Protecting ecosystems outside protected and indigenous areas is imperative and urgent, mainly in conservation units-scarce ecoregions such as the Orinoco Llanos (Williams et al. 2022), recognized for its high diversity of natural wetlands (Piraquive-Bermúdez and Behling 2022). Encouraging the creation of more wildlife-friendly farming practices and supporting private reserves in the long-term is key to ensuring the functional connectivity between forest and savannah patches in the Orinoco Llanos. This, in turn, would enable the conservation of a more complete set of bat species across these human-disturbed landscapes and the maintenance of their crucial ecosystem functions and services, such as insect suppression and pollination.

Supporting information

Additional supplementary material may be found online in the Supporting Information section.

Authors' contributions

AOA and FZF designed research; AOA and FZF performed the landscape/statistical analyses and FZF led the writing of the manuscript, supported mainly by AOA and CFJM; AOA and FZF collected data; AOA and FZF carried out the field expeditions, funding acquisition and project administration. CGP gave support from Instituto Alexander von Humboldt and HFLA and JP from Colombia National University as project supervisors. All authors contributed critically to the drafts, gave final approval for publication, and do not have any conflict of interest to declare.

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Availability of data and material

Data on species functional traits: uploaded as online supporting information (Table S1).

Environmental descriptors of the study sites: uploaded as online supporting information (Table S2).

Bat species occupancy and abundance change: uploaded as online supporting information (Table S3).

References

Aldana A, Mitchley J (2013) Protected areas legislation and the conservation of the Colombian Orinoco Basin natural ecosystems. Nat Conserv 4:15–28. https://doi.org/10.3897/natureconservation.4.3682

Arroyo-Rodríguez V, Rojas C, Saldaña-Vázquez RA, Stoner KE (2016) Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. Biol Conserv 198:84–92. https://doi.org/10.1016/j.biocon.2016.03.026

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B: Stat Methodol 57:289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bernard E, Fenton MB (2003) Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. Biotropica 35:262–277. https://doi.org/10.1111/j.1744-7429.2003.tb00285.x

Bobrowiec PED, Farneda FZ, Nobre CC, Tavares VC (2022) Taxonomic and functional responses of bats to habitat flooding by an Amazonian mega-dam. Biodivers Conserv 31:1359–1377. https://doi.org/10.1007/s10531-022-02396-8

Borghetti F, Barbosa E, Ribeiro L, et al (2019) South American Savannas. In: Scogings PF, Sankaran M (eds) Savanna Woody Plants and Large Herbivores. John Wiley & Sons, pp 77–122.

Braga J, ter Braak CJF, Thuiller W, Dray S (2018) Integrating spatial and phylogenetic information in the fourth-corner analysis to test trait–environment relationships. Ecology 99:2667–2674. https://doi.org/10.1002/ecy.2530

Buchadas A, Baumann M, Meyfroidt P, Kuemmerle T (2022) Uncovering major types of deforestation frontiers across the world’s tropical dry woodlands. Nat Sustain 5:619–627. https://doi.org/10.1038/s41893-022-00886-9

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. J Appl Ecol 48:1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Cadotte MW, Tucker CM (2017) Should environmental filtering be abandoned? Trends Ecol Evol 32:429–437. https://doi.org/10.1016/j.tree.2017.03.004

Carballo-Morales JD, Saldaña-Vázquez RA, Villalobos F (2021) Trophic guild and forest type explain phyllostomid bat abundance variation from human habitat disturbance. Glob Ecol Conserv 25:e01425. https://doi.org/10.1016/j.gecco.2020.e01425

Carvalho WD, Mustin K, Farneda FZ, et al (2021) Taxonomic, functional and phylogenetic bat diversity decrease from more to less complex natural habitats in the Amazon. Oecologia 197:223–239. https://doi.org/10.1007/s00442-021-05009-3

Castillo-Figueroa D, Pérez-Torres J (2021) On the development of a trait-based approach for studying Neotropical bats. Pap Avulsos Zool 61:e20216124. https://doi.org/10.11606/1807-0205/2021.61.24

Castro-Luna AA, Galindo-González J (2012) Enriching agroecosystems with fruit-producing tree species favors the abundance and richness of frugivorous and nectarivorous bats in Veracruz, Mexico. Mamm Biol 77:32–40. https://doi.org/10.1016/j.mambio.2011.06.009

Chambers CL, Cushman SA, Medina-Fitoria A, et al (2016) Influences of scale on bat habitat relationships in a forested landscape in Nicaragua. Landsc Ecol 31:1299–1318. https://doi.org/10.1007/s10980-016-0343-4

Chichorro F, Juslén A, Cardoso P (2019) A review of the relation between species traits and extinction risk. Biol Conserv 237:220–229. https://doi.org/10.1016/j.biocon.2019.07.001

Cleary KA, Waits LP, Finegan B (2016) Agricultural intensification alters bat assemblage composition and abundance in a dynamic Neotropical landscape. Biotropica 48:667–676. https://doi.org/10.1111/btp.12327

Colinvaux P (1980) Why big fierce animals are rare? An ecologist's perspective. Penguin Books, London, UK

Colombo GT, Di Ponzio R, Benchimol M, et al (2023) Functional diversity and trait filtering of insectivorous bats on forest islands created by an Amazonian mega dam. Funct Ecol 37:99–111. https://doi.org/10.1111/1365-2435.14118

Crane M, Silva I, Grainger MJ, Gale GA (2022) Limitations and gaps in global bat wing morphology trait data. Mamm Rev 52:165–176. https://doi.org/10.1111/mam.12270

Cushman SA, McGarigal K, Neel MC (2008) Parsimony in landscape metrics: strength, universality, and consistency. Ecol Indic 8:691–703. https://doi.org/10.1016/j.ecolind.2007.12.002

Dávalos LM, Cirranello AL, Geisler JH, Simmons NB (2012) Understanding phylogenetic incongruence: lessons from phyllostomid bats. Biol Rev 87:991–1024. https://doi.org/10.1111/j.1469-185X.2012.00240.x

De Marco P, De Souza RA, Andrade AFA, Villén-Pérez S, Nóbrega CC, Campello LM, Caldas M (2023) The value of private properties for the conservation of biodiversity in the Brazilian Cerrado. Science 380:298–301. https://doi.org/10.1126/science.abq7768

Díaz-B CA, Otálora-Ardila A, Valdés-Cardona MC, et al (2023) Bat functional traits associated with environmental, landscape, and conservation variables in Neotropical dry forests. Front For Glob Change 6:. https://doi.org/10.3389/ffgc.2023.1082427

Dolédec S, Chessel D, ter Braak CJF, Champely S (1996) Matching species traits to environmental variables: a new three-table ordination method. Environ Ecol Stat 3:143–166. https://doi.org/10.1007/BF02427859

Dray S, Choler P, Dolédec S, et al (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14–21. https://doi.org/10.1890/13-0196.1

Dray S, Dufour AB (2007) The *ade4* package: implementing the duality diagram for ecologists. J Stat Softw 22:1–20. https://doi.org/10.18637/jss.v022.i04

Etter A (1997) Sabanas. In: Chaves ME, Arango N (eds) Informe Nacional Sobre el Estado de la Biodiversidad en Colombia. Tomo I: Diversidad Biológica. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, pp 76–95

Falcão F, Dodonov P, Caselli CB, et al (2021) Landscape structure shapes activity levels and composition of aerial insectivorous bats at different spatial scales. Biodivers Conserv 30:2545–2564. https://doi.org/10.1007/s10531-021-02210-x

Fahrig L, Baudry J, Brotons L, et al (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14:101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Farneda FZ, Rocha R, López-Baucells A, et al (2015) Trait-related responses to habitat fragmentation in Amazonian bats. J Appl Ecol 52:1381–1391. https://doi.org/10.1111/1365-2664.12490

Farneda FZ, Rocha R, López-Baucells A, et al (2018) Functional recovery of Amazonian bat assemblages following secondary forest succession. Biol Conserv 218:192–199. https://doi.org/10.1016/j.biocon.2017.12.036

Giannini NP, Kalko EKV (2004) Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos 105:209–220. https://doi.org/10.1111/j.0030-1299.2004.12690.x

Gonçalves F, Fischer E, Dirzo R (2017) Forest conversion to cattle ranching differentially affects taxonomic and functional groups of Neotropical bats. Biol Conserv 210:343e348. https://doi.org/10.1016/j.biocon.2017.04.021

Gonçalves-Souza T, Chaves LS, Boldorini GX, et al (2023) Bringing light onto the Raunkiæran shortfall: a comprehensive review of traits used in functional animal ecology. Ecol Evol 13:e10016. https://doi.org/10.1002/ece3.10016

Grace J, José JS, Meir P, et al (2006) Productivity and carbon fluxes of tropical savannas. J Biogeogr 33:387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Green SJ, Brookson CB, Hardy NA, Crowder LB (2022) Trait-based approaches to global change ecology: moving from description to prediction. Proc R Soc B: Biol Sci 289:20220071. https://doi.org/10.1098/rspb.2022.0071

Hesselbarth MHK, Sciaini M, With KA, et al (2019) *landscapemetrics*: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657. https://doi.org/10.1111/ecog.04617

Hill MO, Smith AJE (1976) Principal component analysis of taxonomic data with multi-state discrete characters. Taxon 25:249–255. https://doi.org/10.2307/1219449

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

IDEAM (2015) Atlas climatológico de Colombia. atlas.ideam.gov.co/visorAtlasClimatologico.html. Accessed 19 Apr 2023.

Jeliazkov A, Mijatovic D, Chantepie S, et al (2020) A global database for metacommunity ecology, integrating species, traits, environment and space. Sci Data 7:6. https://doi.org/10.1038/s41597-019-0344-7

Kalko EKV, Handley CO, Handley D (1996) Organization, diversity, and long-term dynamics of a neotropical bat community. In: Cody M, Smallwood J (eds) Long-term studies in Vertebrate Communities. pp 503–553.

Kembel SW, Cowan PD, Helmus MR, et al (2010) *picante*: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kleyer M, Dray S, Bello F, et al (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? J Veg Sci 23:805–821. https://doi.org/10.1111/j.1654-1103.2012.01402.x

Klingbeil BT, Willig MR (2009) Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. J Appl Ecol 46:203–213. https://doi.org/10.1111/j.1365-2664.2008.01594.x

Kunz TH, Braun de Torrez E, Bauer D, et al (2011) Ecosystem services provided by bats. Trans N Y Acad Sci 1223:1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

López-Arévalo HF, Liévano-Latorre LF, Montenegro Díaz OL (2021) El papel de las pequeñas reservas en la conservación de mamíferos en Colombia. Caldasia 43:354–365.

Marinello MM, Bernard E (2014) Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. Can J Zool 92:141–147. https://doi.org/10.1139/cjz-2013-0127

Marques JT, Ramos Pereira MJ, Marques TA, et al (2013) Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. PLoS ONE 8:1–8. https://doi.org/10.1371/journal.pone.0074505

Marroquin C, Gerth T, Muñoz-Garcia A (2023) The influence of roost type and diet on energy expenditure in bats. Diversity 15:655. https://doi.org/10.3390/d15050655

McKechnie AE, Wolf BO (2019) The physiology of heat tolerance in small endotherms. Physiology 34:302–313. https://doi.org/10.1152/physiol.00011.2019

Melo FPL, Arroyo-Rodríguez V, Fahrig L, et al (2013) On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol 28:462–468. https://doi.org/10.1016/j.tree.2013.01.001

Meyer CFJ, Struebig MJ, Willig MR (2016) Responses of tropical bats to habitat fragmentation, logging and deforestation. In: Voigt C, Kingston T (eds) Bats in the Anthropocene: conservation of bats in a changing world. Springer, pp 63–105.

Morales-Martínez DM, Rodríguez-Posada ME, Fernández-Rodríguez C, et al (2018) Spatial variation of bat diversity between three floodplain-savanna ecosystems of the Colombian Llanos. Therya 9:1–9. https://doi.org/10.12933/therya-18-537

Newbold T, Hudson LN, Hill SLL, et al (2016) Global patterns of terrestrial assemblage turnover within and among land uses. Ecography 39:1151–1163. https://doi.org/10.1111/ecog.01932

Núñez SF, López-Baucells A, Rocha R, et al (2019) Echolocation and stratum preference: key trait correlates of vulnerability of insectivorous bats to tropical forest fragmentation. Front Ecol Evol 7:373. https://doi.org/10.3389/fevo.2019.00373

Otálora-Ardila A, López-Arévalo HF (2021) Effect of the matrix-edge-forest interior gradient on the phyllostomid bats assemblage in sub-Andean Forest fragments. Caldasia 43:274–285. https://doi.org/10.15446/caldasia.v43n2.85071

Palacio FX, Callaghan CT, Cardoso P, et al (2022) A protocol for reproducible functional diversity analyses. Ecography 2022:e06287. https://doi.org/10.1111/ecog.06287

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290. https://doi.org/10.1093/bioinformatics/btg412

Pasquini L, Fitzsimons J, Cowell S, Brandon K, Wescott G (2011) The establishment of large private nature reserves by conservation NGOs: key factors for successful implementation. Oryx 45:373–380. https://doi.org/10.1017/S0030605310000876

Pereira HM, Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology 87:1877–1885. https://doi.org/10.1890/0012-9658(2006)87[1877:MBDICL]2.0.CO;2

Piraquive-Bermúdez D, Behling H (2022) Holocene paleoecology in the Neotropical savannas of Northern South America (Llanos of the Orinoquia ecoregion, Colombia and Venezuela): what do we know and on what should we focus in the future? Front Ecol Evol 10:. https://doi.org/10.3389/fevo.2022.824873

R Development Core Team (2020) R: A language and environment for statistical computing.

Ramírez-Mejía AF, Urbina-Cardona JN, Sánchez F (2020) Functional diversity of phyllostomid bats in an urban–rural landscape: a scale-dependent analysis. Biotropica 52:1168–1182. https://doi.org/10.1111/btp.12816

Rex K, Michener R, Kunz TH, Voigt CC (2011) Vertical stratification of Neotropical leaf-nosed bats (Chiroptera: Phyllostomidae) revealed by stable carbon isotopes. J Trop Ecol 27:211–222. https://doi.org/10.1017/S0266467411000022

Rojas D, Warsi OM, Dávalos LM (2016) Bats (Chiroptera: Noctilionoidea) challenge a recent origin of extant Neotropical diversity. Syst Biol 65:432–448. https://doi.org/10.1093/sysbio/syw011

Romero-Ruiz M, Etter A, Sarmiento A, Tansey K (2010) Spatial and temporal variability of fires in relation to ecosystems, land tenure and rainfall in savannas of Northern South America. Glob Change Biol 16:2013–2023. https://doi.org/10.1111/j.1365-2486.2009.02081.x

Romero-Ruiz MH, Flantua SGA, Tansey K, Berrio JC (2012) Landscape transformations in savannas of Northern South America: land use/cover changes since 1987 in the Llanos Orientales of Colombia. Appl Geogr 32:766–776. https://doi.org/10.1016/j.apgeog.2011.08.010

Semper-Pascual A, Bischof R, Milleret C, et al (2022) Occupancy winners in tropical protected forests: a pantropical analysis. Proc R Soc B 289:20220457. https://doi.org/10.1098/rspb.2022.0457

Sikes RS (2016) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal 97:663–688. https://doi.org/10.1093/jmammal/gyw078

Straube FC, Bianconi GV (2002) Sobre a grandeza e a unidade utilizada para estimar esforço de captura com utilização de redes-de-neblina. Chirop Neotrop 8:150–152.

Suárez-Castro AF, Ramírez-Chaves HE, Noguera-Urbano EA, et al (2021) Vacíos de información espacial sobre la riqueza de mamíferos terrestres continentales de Colombia. Caldasia 43:247–260. https://doi.org/10.15446/caldasia.v43n2.85443

ter Braak CJF, Cormont A, Dray S (2012) Improved testing of species traits–environment relationships in the fourth-corner problem. Ecology 93:1525–1526. https://doi.org/10.1890/12-0126.1

ter Hofstede HM, Faure PA (2023) Predator–prey interactions between gleaning bats and katydids. Can J Zool 101:936–944. https://doi.org/10.1139/cjz-2023-0023

Velazco P, Lim BK (2014) A new species of broad-nosed bat *Platyrrhinus* Saussure, 1860 (Chiroptera: Phyllostomidae) from the Guianan Shield. Zootaxa 3796:175–193. https://doi.org/10.11646/zootaxa.3796.1.9.

Villalobos-Chaves D, Santana SE (2022) Craniodental traits predict feeding performance and dietary hardness in a community of Neotropical free-tailed bats (Chiroptera: Molossidae). Funct Ecol 36:1690–1699. https://doi.org/10.1111/1365-2435.14063

Voss RS, Fleck DW, Strauss RE, et al (2016) Roosting ecology of Amazonian bats: evidence for guild structure in hyperdiverse mammalian communities. Am Mus Novit 2016:1–43. https://doi.org/10.1206/3870.1

Weiss KCB, Ray CA (2019) Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. Ecography 42:2012–2020. https://doi.org/10.1111/ecog.04387

Williams BA, Watson JEM, Beyer HL, et al (2022) Global drivers of change across tropical savannah ecosystems and insights into their management and conservation. Biol Conserv 276:109786. https://doi.org/10.1016/j.biocon.2022.109786

Wordley CFR, Sankaran M, Mudappa D, Altringham JD (2017) Bats in the Ghats: agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. Biol Conserv 210:48–55. https://doi.org/10.1016/j.biocon.2017.03.026

Zou W, Liang H, Wu P, et al (2022) Correlated evolution of wing morphology and echolocation calls in bats. Front Ecol Evol 10:. https://doi.org/10.3389/fevo.2022.1031548