Multiple dimensions of phyllostomid bat biodiversity across ecosystems of the Orinoco Llanos

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Short title

Taxonomic, functional, and phylogenetic dimensions of bat biodiversity

Abstract

Understanding the impacts of habitat conversion on species assemblages across multiple biodiversity dimensions (taxonomic, functional, phylogenetic) and spatial scales is pivotal for implementing effective conservation strategies. Here, we surveyed phyllostomid bats using mist nets in riparian and unflooded forests, flooded savannahs, and conventional rice fields to investigate how changes in habitat quality affect multi-faceted diversity from two Colombian farming systems in the Orinoco Llanos: traditional farmlands with high-intensity agriculture (mainly rice production) and Civil Society Nature Reserves with greater ecosystem protection. We used a unified framework based on Hill numbers for quantifying bat taxonomic, functional, and phylogenetic diversity and modelled the relationship of these diversity facets with landscape variables (habitat cover and patch density) across three spatial scales (0.5, 1.5, 3 km) using Bayesian generalized linear mixed-effect models. Our results indicate that increasing human activity towards rice monocultures representative of traditional farmlands negatively affected all diversity facets. In contrast, forested habitats associated mainly with riparian forests within private reserves contained higher taxonomic, functional, and phylogenetic diversity than savannahs and rice fields. However, the differences between riparian forests and rice crops were significant only for phylogenetic diversity, indicating loss of evolutionary history after habitat conversion. At the landscape scale, forest cover was a significant predictor for functional (0.5 and 3-km scale) and phylogenetic diversity (0.5 km), and bats responded negatively at the 3-km scale to rice patch density from a functional diversity perspective. Increasing habitat quality through preserving forest cover and patches should minimize the harmful effects of habitat conversion on multidimensional bat biodiversity. Furthermore, the conservation of riparian forests and the creation of more wildlife-friendly farming, as practised in the reserves, should be prioritized to ensure high levels of bat taxonomic, functional, and phylogenetic diversity across Orinoco countryside landscapes.

Keywords: Chiroptera, Colombia, environmental filters, human land-use change, landscape composition and configuration, Llanos Orientales, multiple biodiversity dimensions, multiscale analysis

1. Introduction

Protecting biodiversity in complex and rapidly disappearing ecosystems is one of humanity's most critical environmental challenges (Martin, Maris and Simberloff, 2016). One of these challenges is habitat conversion, caused mainly by agriculture and livestock expansion, representing the primary cause of species loss and ecosystem services worldwide (Semenchuk et al., 2022; Buchadas et al., 2022). However, these trends have been particularly destructive in the tropics, with an increase of 50% in primary vegetation loss between 2016 and 2020 (Weisse and Goldman, 2021). In the same period, Colombia's rate of primary vegetation loss increased by ~118% – mostly in private areas (Weisse and Goldman, 2021). One of the most threatened, biodiverse, and poorly studied Colombian ecosystems is the Orinoco Savannah plains (Llanos) (Suárez-Castro et al., 2021; Williams et al., 2022). Unprecedented deforestation and degradation rates since the 1970s in the Llanos have resulted mainly in extensive areas of livestock production, croplands, urban settlements (Romero-Ruiz et al., 2012), and a few protected areas covering less than 15% of its original extent (Williams et al., 2022). These different human-modified habitats make the Llanos an excellent model system for understanding how land-use changes impact the structure of communities, ecosystem functioning, and services valued by humans.

The capacity of the natural habitats in countryside landscapes to provide resources for various organisms, deliver ecosystem services, and conserve species is associated with the level of human land-use intensity (Daily, 1997). This means some anthropized landscapes can retain considerable biodiversity and have an associated conservation value (Pereira and Daily, 2006). Future scenarios for biodiversity conservation will be determined by our capacity to understand species' responses in the rapidly expanding agriculture-livestock areas that increasingly dominate landscapes across the tropics (Pillay et al., 2022), and manage pristine and human-modified landscapes to preserve particular evolutionary histories and functionally unique species and their ecosystems (Brose and Hillebrand, 2016). Due to growing social demand for assessing the extent to which heterogeneous agricultural ecosystems can safeguard biodiversity in the Anthropocene, biogeographic and landscape ecological studies integrating multiple dimensions of diversity (species, functional traits, and evolutionary history) are a priority avenue for research, critical for informing land management and more adequately guiding changes in conservation policy (Smiley et al., 2020; Weeks et al., 2022; Willig et al., 2023).

Empirical evidence from a taxonomic diversity perspective has often been used to understand how human activity affects biodiversity-ecosystem-function relationships in the

Neotropics (Antonelli et al., 2018). Nevertheless, traditional species counts cannot appropriately assess the functional and evolutionary differences among taxa or assemblages since they consider species as independent entities of one another (Cadotte, Albert and Walker, 2013), and commonly fail to determine effective conservation units for mistaking species diversity for fixed evolutionary and niche differences (Isaac, Mallet and Mace, 2004; Zachos et al., 2013). For conservation and restoration purposes, a shift of focus from species counts to studies that embrace the interplay between the environment and multiple biodiversity dimensions is imperative (Flynn et al., 2009; Willig et al., 2023). From a conservation and diversity perspective, bats are an excellent group to study the impact of habitat conversion in the Neotropics because they exhibit a high richness/abundance of species, are sensitive to land-use changes (Meyer, Struebig and Willig, 2016), and fulfill diverse and valuable ecological functions such as pollination, seed dispersal, and control of arthropod and small vertebrate populations (Kunz et al., 2011).

Although the volume of research simultaneously assessing how multiple dimensions of Neotropical bat diversity are affected by human-modified landscapes has grown in the last decade (e.g., Cisneros, Fagan and Willig, 2015; Frank et al., 2017; Farneda et al., 2018; Pereira, Fonseca and Aguiar, 2018; Carrasco-Rueda and Loiselle, 2020; López-Baucells et al., 2022; Xavier et al., 2023), studies are nil for many tropical ecoregions. Furthermore, there is limited knowledge of how landscape composition and configuration may act as filters affecting multiple dimensions of bat diversity in countryside ecosystems (reviewed in Meyer et al., 2016). Landscape-scale studies have generally analysed bat richness, abundance, and community composition (e.g., Avila-Cabadilla et al., 2012; Arroyo-Rodríguez et al., 2016; Rocha et al., 2017), without a clear pattern emerging about how their varied results can be generalized across ecosystems, species, and spatial scales (Presley et al., 2019). Here, we assessed how Neotropical phyllostomid bats are affected by habitat disturbance in the Colombian Llanos from a taxonomic, functional, and phylogenetic diversity perspective. Additionally, taking a multi-scale approach, we assessed how compositional and configurational aspects of the landscape affect each diversity dimension. We predicted that:

(i) There are negative effects on bats concerning all three diversity facets as habitat complexity decreases towards rice monocultures and savannahs due to the decline in the availability of roosts and food (Carvalho et al., 2021), leading to biotic homogenization at the assemblage level.

(ii) Habitats characterized by assemblages comprised of species with closely related traits and lineages (i.e., greater functional and phylogenetic redundancy) may retain lower levels of functional and phylogenetic richness than taxonomic richness (Willig et al., 2023). Although taxonomic, functional, and phylogenetic diversity will all be negatively affected by habitat homogenization, the taxonomic diversity dimension will manifest a comparatively greater decline from riparian forests (the most preserved habitat) to rice crops (the most modified habitat), as several Neotropical bat species are functionally or phylogenetically redundant (Oliveira et al., 2016; Hurtado-Materon and Murillo-García, 2023).

(iii) For all three diversity facets, phyllostomid bats will exhibit positive relationships with forest cover and negative associations with rice cover. However, landscapes with small irregular patches have high patch density (Fahrig et al., 2011), and a high patch density is more representative of traditional farmlands in our study area. Consequently, we only predict negative effects of patch density on taxonomic, functional, and phylogenetic diversity in traditional farmland, but not in the more preserved landscapes, as in private reserves.

2. Material and methods

2.1 Study area and sampling design

Our study was centred in the macro-basin of the Colombian Orinoco, in the Civil Society Nature Reserves La Esperanza (5°42'N-71°14'W) and El Boral (5°19'N-71°47'W), and in the 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), Casanare state, Llanos ecoregion (Fig. 1). The Llanos cover ~17 Mha in Colombia, ~15% of the total area of the country (Borghetti et al., 2020). The study region is dominated primarily by flooded savannahs, riparian and unflooded forest patches, pasture-based livestock farming, urban areas, and agricultural systems composed mainly of rice (Romero-Ruiz et al., 2012; Sánchez-Cuervo et al., 2012). The climate in the region (tropical monsoon [Am], Köppen-Geiger classification) is characterized by a unimodal seasonality pattern: a dry season between December and March (monthly accumulated rainfall < 100 mm) and a wet season from April to November (150 to 600 mm), varying from a total of 1500 to 3000 mm year (IDEAM, 2015). Average annual temperatures vary from 27 to 30 °C during the dry season, and 23 to 26 °C during the wet season (Etter, 1997).

La Esperanza and El Boral (~137 m a.s.l.) are private reserves that protect part of a natural ecosystem and constitute a mix of flooded savannahs that still preserve native grasses with others used for cattle grazing, pastures planted with exotic grasses (Poaceae) for cattle production, and riparian forests that vary in size and experience seasonal inundation. Hato

California, Las Acacias, Sinaloa, and Finca Bella Vista (~164 m a.s.l.) are farmlands with the understory of unflooded and riparian forest partially removed and often used as a passageway for cattle. Naturally flooded savannahs were replaced entirely by monocultures, mainly conventional rice crops which were subjected to the use of synthetic pesticides and fertilizers between three and ten years ago when the paddies were established (mean of eight years prior to this study).

In all sampling sites, there is selective non-commercial logging of larger trees, and some exotic trees (e.g., *Mangifera* spp.) are present in riparian (La Esperanza) and unflooded forests (California). The canopy in riparian and unflooded forests is ca. 15 m tall, with occasional emergent trees reaching 20 m, and closed. Both habitats share forest pioneer species that produce fruits consumed by many frugivorous bat species, such as *Cecropia* spp., *Ficus* spp., and *Vismia* spp. The savannah has an open canopy composed mainly 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*).

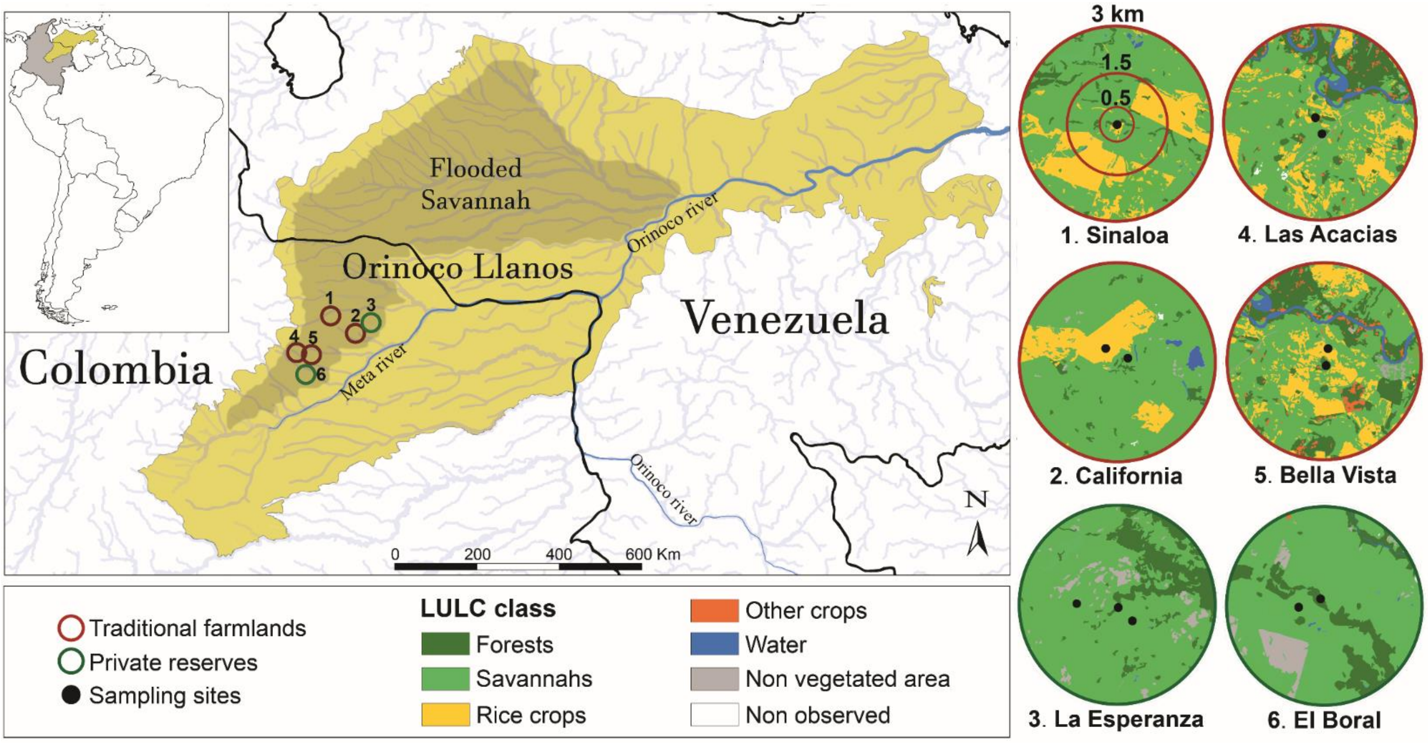

Fig. 1. Spatial distribution of the six Colombian landscapes in traditional farmlands and private reserves overlaid on a hydrographic mesh in the Orinoco Llanos ecoregion, Northern South America. The darkest area highlights the flooded (hyperseasonal) savannah. Each landscape is characterized by "Land Use Land Cover" (LULC) class and focal scales of 0.5, 1.5, and 3 km radii (as shown for Hato Sinaloa) centred on each mist net sampling site.

2.2 Bat sampling

Bats were sampled in four replicate surveys per habitat (one per season and rice production stage): riparian forests (three sampling units: La Esperanza, El Boral, and Sinaloa), unflooded forests (three: California, Las Acacias, and Finca Bella Vista), flooded savannahs (three: La Esperanza [two units] and El Boral), and conventional rice crops (three: California, Las Acacias, and Finca Bella Vista). Sampling sites in savannahs and rice crops were located between 150 and 400 m from the edge of riparian and unflooded forests. Bat sampling occurred during the four main stages of rice production: land preparation (transition dry-wet season), vegetative growth (wet), grain maturation (transition wet-dry), and post-harvest (dry).

Bat sampling was conducted in each habitat (riparian forests, unflooded forests, flooded savannahs, and rice crops) in all seasons: wet season in July-August 2022, transition wet-dry in November-December 2020, dry in January-February 2022, and transition dry-wet in March 2021. Bats were sampled using five ground-level mist nets (12 × 2.5 m, Ecotone, Poland, intercalating conventional and monofilament nets) deployed for a total of 23 to 26 nights per habitat/season (~ 8 nights per sampling unit). Bias in capture rates due to the bats' ability 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. Nets were deployed from dusk (~18:00 h) until 5 to 7 h after exposure (except during pouring rains) and revised at intervals of ~25 minutes. 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, savannahs = 26,901 m^2.h, conventional rice crops = 23,310 m^2.h, total = 97,479 m^2.h. Bats were individually marked with a unique numerical code using a tattoo in the right wing at the lower part of the plagiopatagium or with small and colored plastic rings on a plastic cable tie necklace (Sikes, 2016) and released at the capture site on the same night. These marking captures were 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 ANLA permit (resolution 0255/2014).

2.3 Species traits and phylogeny

We selected functional traits which are independent of the response variables and the particular landscape context, and are related to species responses to habitat conversion and their ability to provide ecosystem services: *body mass* (quantified with our capture data) is an important proxy for energy requirements, whereby larger Neotropical bats tend to be demographically more fragile due to smaller populations (Meyer et al., 2016), *wing morphology* (aspect ratio and relative wing loading calculated from our capture data) is a predictor of foraging behaviour and habitat use, affecting flight speed and maneuverability (Norberg and Rayner, 1987), *trophic level* (based on the literature) is a key trait associated with population dynamics since Neotropical bat species at the bottom of the food chain are less extinction-prone than those at higher trophic levels (Farneda et al., 2015), and *diet* (literature) is a more finely resolved categorization of dietary guilds describing the main food resources of each bat species (Cisneros et al., 2015). See Supplementary Material Table S1 for a more detailed explanation and Table S2 for individual values for each trait.

To quantify the phylogenetic diversity of phyllostomid bats we used the species-level phylogeny proposed by Rojas, Warsi and Dávalos (2016) as it avoids a known mislabelling error for *Phyllostomus discolor* present in other phylogenies (Dávalos et al., 2012). One of the 25 species (*Platyrrhinus angustirostris*) was not present in the phylogeny and was replaced by its closest congener (*P. incarum*) (Velazco and Lim, 2014). This supertree covered most of the species in the Llanos, and was pruned to obtain the local phylogeny (R package 'picante'; Kembel et al., 2010) and the respective pairwise phylogenetic distances using the 'cophenetic.phylo' function (R package 'ape'; Paradis, Claude and Strimmer, 2004). See Supplementary Material Fig. S1 for the pruned phylogenetic tree depicting relationships between bat species.

2.4 Landscape predictor variables

We included only aspects of landscape composition and configuration as predictor variables to equalize the representation of environmental characteristics between all four habitat types and avoid bias from over-representation of the local vegetation structure of riparian and unflooded forest habitats (Cushman, McGarigal and Neel, 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, savannahs, water, rice, and other crops in the landscape, with posterior verification in Google Earth Pro 7.3.4. We considered mature and secondary riparian and unflooded forests as "forest". This simplification reduces the probability of misclassification of the different habitats in our study area and is based on their influence on the distribution and abundance of Neotropical bats (e.g., Chambers et al., 2016; Falcão et al., 2021). Circular buffers with radii of 0.5, 1.5, and 3 km centred on each sampling site were used to calculate the landscape metrics *habitat cover* (composition) and *patch density* (configuration) of forests, savannahs, and rice crops. These metrics are frequently used in landscape-ecological studies of bats (Presley et al., 2019) and were calculated using the R package “landscapemetrics” (Hesselbarth et al., 2019). *Habitat cover* is represented by the total area in hectares (ha) of each habitat and *patch density* by the number of habitat patches per area (n/ha). Although it is acknowledged that collinearity effects between predictor variables do not necessarily constitute a problem in ecological studies (Morrissey and Ruxton, 2018), our metrics generally demonstrated low collinearity (Pearson correlation, $r < 0.50$ for all spatial scales, see Fig. S3). The exceptions ($r > 0.80$) were between rice cover and rice patch density (0.5 km scale), rice cover and savannah patch density (1.5 km scale), savannah cover and rice cover (0.5 and 1.5-km scale), savannah cover and savannah patch density (1.5 km scale), and savannah cover and rice patch density (3 km scale) (Fig. S3). While such landscape attributes can affect the distribution and abundance of tropical bats (Meyer et al., 2016), the focal scales encompass the home ranges of different-sized bat species (Jackson and Fahrig, 2015). Overlapping landscape buffers do not automatically violate statistical independence (Zuckerberg et al., 2020), but we chose to investigate these landscape metrics with radii no higher than 3 km to minimize spatial dependency between sites. See Table S3 in Supplementary Material for values and description of each landscape metric.

2.5 Data analysis

We excluded same-site recaptures and used only phyllostomid bat captures for statistical analysis since they are reliably sampled with mist nets (Kalko et al., 1996). This resulted in 25 species and 668 individuals for analysis (Table S4, see Table S5 for a complete list of species captured). Continuous traits (body mass, aspect ratio, and relative wing loading) and landscape variables were logarithmically transformed to normalized values, and traits were standardized to a mean of zero and a standard deviation of one to facilitate the comparison of their relative effects. Relative abundance based on the number of individuals of each species captured with mist nets was calculated based on the sampling effort ($m^2.h$) for each site, thus equalizing differences in capture effort between habitats. Analysis of relative abundance relies on the assumption of equal catchability of species, which is likely violated, owing to differences among bat species in traits and behaviours (Meyer et al., 2011). We consider potential implications for our results in the Discussion. Statistical analyses were performed in R software 4.0.2 (R Core Team, 2020).

We calculated the taxonomic, functional, and phylogenetic diversity for each habitat using Hill numbers (Hill, 1973), which have been widely applied to compare multiple diversity facets in a wide variety of taxa (Magurran, 2021). Hill numbers are effective ecological indicators that do not require assumptions about species extinctions to detect changes in the communities, and can be directly compared across multifaceted diversity metrics due to the standardization of measures expressed in common units by the q parameter (Chao, Chiu and Jost, 2014). Each diversity dimension was calculated using q values 0, 1, and 2 (‘hillR’ package; Li, 2018): $q = 0$, species abundance is ignored (species richness); as q approaches 1 (for simplicity hereafter referred to as "$q = 1$"), species are weighted by their abundance (Shannon diversity); at $q = 2$, greater weight is assigned to common than rare species (Simpson diversity or inverse Simpson concentration) (Chiu and Chao, 2014).

We analyzed all rice crop stages jointly because they did not differ significantly in species richness and abundance (Shapiro-Wilk test on residuals $P > 0.5$; Gaussian-GLM $P > 0.2$ for both response variables). We modelled diversity concerning habitat categories and landscape variables using Bayesian generalised linear mixed-effect models (GLMMs, ‘MCMCglmm’ package; Hadfield, 2010), which are valuable tools that allow the handling of data with various distributions (Bolker et al., 2009). We fitted one model for each q parameter (0, 1, and 2) of each biodiversity dimension (taxonomic, functional, and phylogenetic), with habitat type as fixed-effect and ‘sampling site’ incorporated as a random effect, totalling nine models. For the landscape analysis, we fitted one model per q parameter (0, 1, and 2) of each biodiversity facet (taxonomic, functional, and phylogenetic) for each spatial scale (0.5, 1.5, and 3 km radius), with “*habitat cover*” and “*patch density”* quantified for forests, savannahs, and rice crops as fixed-effect predictors and ‘sampling site’ incorporated as a random effect, totalling 27 models (nine for each scale). The models were fitted using a “weakly-informative” inverse-gamma prior (shape and scale = 0.001) with Gaussian distribution (iterations = 50000, burn-in period = 5000, thinning interval = 10). Results are reported as posterior means, 95% credible intervals, and p-values (pMCMC < 0.05). All model estimates achieved convergence as determined through trace plots and potential scale reduction factors (< 1.1, Gelman and Rubin, 1992).

3. Results

Riparian forests harboured the greatest taxonomic, functional, and phylogenetic diversity for all three levels of q (0, 1, 2), while all three diversity facets were lowest in savannahs and rice crops (Fig. 2). Species with more basal lineages associated with a diet composed of nectar and arthropods (e.g., *Glossophaga soricina*, *Lophostoma brasiliense, Micronycteris minuta*; Table S5) were lost in open habitats, such as rice fields. The rice crops harboured significantly lower phylogenetic diversity at all three levels of *q* (0, 1, 2) compared to riparian forests (Fig. 2). The Pearson correlation between net sampling effort and species richness was not significant (r = -0.59, *p* = 0.409) as the effort was roughly similar among habitats.

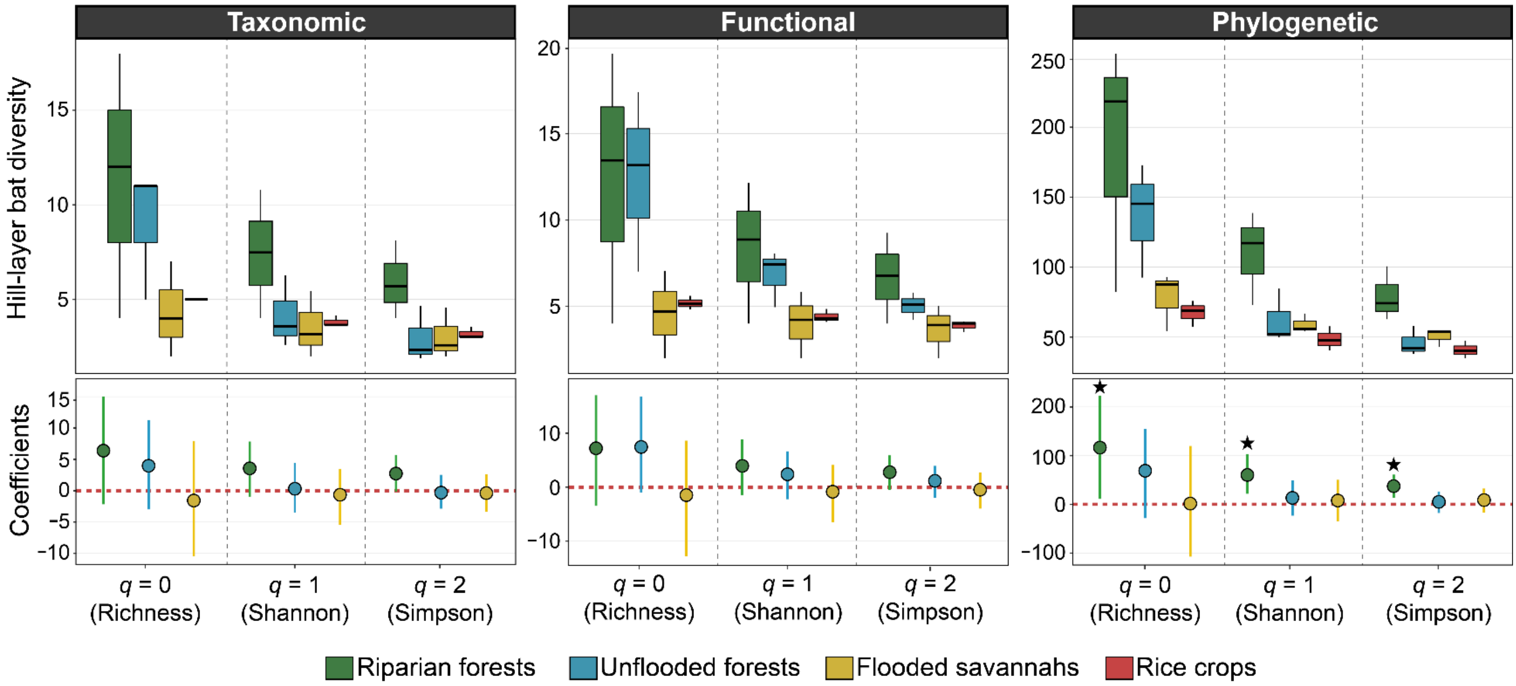

Fig. 2. Top: Comparison of taxonomic, functional, and phylogenetic bat diversity when only species richness is considered (*q* = 0), species are weighted by their abundance (*q* = 1), and greater weight is assigned to common than rare species (*q* = 2). The multiple biodiversity dimensions were quantified for phyllostomid bats sampled with mist nets in riparian forests, unflooded forests, flooded savannahs, and rice crops in the Colombian Llanos. Values represent medians (horizontal lines), lower and upper quartiles (colour bars) and maximum and minimum (vertical lines). Bottom: Predicted MCMCglmm differences between each habitat and rice crops (dashed red line), plotted with 95% credible interval and significance level (★pMCMC < 0.05). See Tables S6 and S7 in Supplementary Material for more detailed information on MCMCglmm model outputs.

The bat assemblage response to landscape-scale variables was significant at the 0.5 and 3-km scale and weaker at the intermediate scale of 1.5 km (Fig. 3). Forest cover was the most prominent predictor, which had a significant and positive relationship with functional (*q* = 1 and 2) and phylogenetic diversity (*q* = 1) at the 0.5 km scale, and with functional diversity (*q* = 1) at the 3 km scale. Functional diversity (*q* = 1) also responded significantly and negatively to rice patch density at the 3 km scale (Fig. 3). Savannah and rice cover, as well as savannah and forest patch density, did not show significant relationships with any of the three biodiversity dimensions (Fig. 3; Table S7). We did not find significant relationships with landscape variables for taxonomic diversity for any spatial scale, for functional diversity at the 1.5 km scale, and for phylogenetic diversity at the 1.5 and 3-km scale (Table S7).

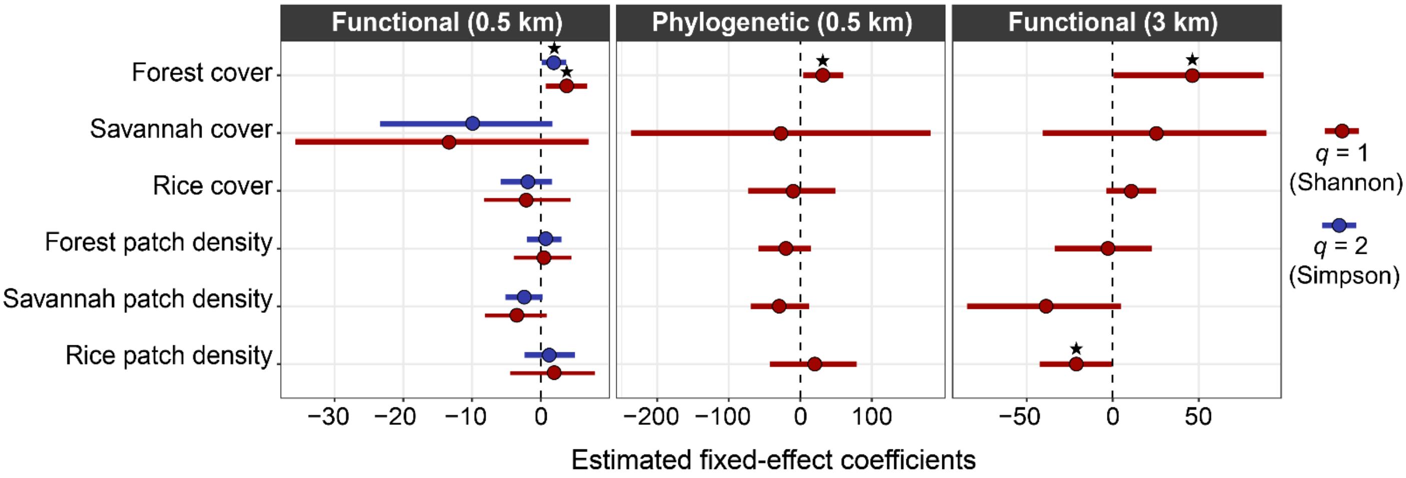

Fig. 3. Focal scales (0.5 and 3 km) with significant relationships (★*p*MCMC < 0.05) for functional and phylogenetic diversity (*q* = 1 when species are weighted by their abundance and *q* = 2 when greater weight is assigned to common than rare species) of phyllostomid bats and landscape predictor variables (habitat cover and patch density of forests, flooded savannahs, and rice crops) in the Orinoco Llanos, Colombia. Values represent posterior mean estimates ± 95% credible intervals. See Tables S6 and S7 in Supplementary Material for a complete list of results.

4. Discussion

Throughout the tropics, landscapes are typically constituted of a mosaic of different habitats modified by human activities that have led to the extinction of several species (Pereira and Daily, 2006; Buchadas et al., 2022). To assess responses to human-modified landscapes, most bat studies have focussed on a taxonomic diversity perspective (Meyer et al., 2016; Xavier et al. 2023). Here, we show how the cross-response congruence in taxonomic, functional, and phylogenetic diversity of phyllostomid bats to landscape configuration and composition associated with different human-disturbed habitats is the result of environmental sorting (Özkan, Svenning and Jeppesen, 2013): a process by which the number of species, ecological functions, and evolutionary history is higher in forested (riparian and unflooded forests) compared to non-forested habitats (savannahs and rice crops). Forested habitats contain a more complete set of species with functionally unique traits and particular evolutionary histories, thus leading to a positive effect in the taxonomic, functional, and phylogenetic community-level structure of bats in riparian and unflooded forests. Our results also indicated that forest cover is one of the most important landscape-scale predictors of bat functional and phylogenetic diversity. Furthermore, high-intensity agriculture acts as a strong environmental filter, shaping local bat assemblages in the Orinoco Llanos ecosystems (see Otálora-Ardila et al., 2024).

4.1 Influence of habitat type

In line with our first prediction, rice fields contained lower taxonomic, functional, and phylogenetic diversity of bats compared to forested habitats (riparian and unflooded forests), indicating loss of functionally and phylogenetically unique species (e.g., *Choeroniscus minor*, *Lampronycteris brachyotis*, *Trachops cirrhosus*), and likely resulting in negative impacts on evolutionary history and the provisioning of ecosystem services, such as pollination or arthropod suppression. However, contrary to our second prediction, the differences between riparian forests and rice crops were only significant for phylogenetic diversity (q = 0, 1, 2). This is an interesting result because although taxonomic and phylogenetic diversity might differentially respond to habitat conversion (Cisneros et al., 2015; Tucker et al., 2017; Willig et al., 2023), we observed that more basal evolutionary lineages (e.g., throughout the animalivorous bat clade) were missing in rice monocultures and retained only in more preserved ecosystems, such as riparian forests. The riparian forests acted as key reservoirs of bat diversity, but a higher taxonomic, functional, and phylogenetic diversity is likely only possible with the integral protection of native vegetation surrounding riparian habitats in the private reserves.

Neotropical bat studies elsewhere that employed Hill numbers also provided significant evidence of multi-faceted diversity loss from more to less complex ecosystems. For instance, while taxonomic and functional diversity (q = 1, 2) of phyllostomid bats decreased from primary forest to commercial *Acacia mangium* plantations (Carvalho et al., 2020) and taxonomic diversity (q = 1, 2) from primary montane cloud forest to pine-oak forest (Briones-Salas et al., 2019), taxonomic, functional, and phylogenetic diversity (q = 0, 1, 2) of aerial-hawking insectivorous bats decreased from continuous primary forest towards late-stage secondary forests with ~30 years of regeneration (López-Baucells et al., 2022). However, the opposite was observed by Morales-Martínez, López-Arévalo and Montenegro (2020) in Colombia, i.e., a decrease in taxonomic diversity of phyllostomid and aerial-hawking insectivorous bats (q = 2) in unflooded forests compared to casmophytic savannahs. In our study region, riparian and unflooded forests are highly complex and structurally similar habitats that possibly act together to provide connectivity, buffer the pervasive edge effects, and increase food availability (arthropods, fruits, nectar), expanding the foraging opportunities for generalist and specialist bat species (Kalcounis-Rueppell et al., 2013), and increasing multidimensional bat diversity. Riparian forest is particularly important for sustaining high landscape-scale diversity of phyllostomid bats due to the presence of water bodies, which offer vital resources. Higher complexity in vegetation structure representative of forested habitats associated with the presence of water bodies also were prerequisites for increased species richness and abundance of bats in a highly heterogeneous landscape in Colombia (Sánchez-Palomino, Pava and Cadena, 1996) and in the Brazilian Amazon (Martins et al., 2022).

4.2 Responses to landscape-scale predictors

In accordance with the results obtained for habitat type at the local scale, scale-sensitive associations with landscape metrics also manifested for bat functional and phylogenetic diversity rather than taxonomic diversity, driven by the loss of phylogenetically and functionally more distinct species. In line with our third prediction, forest cover was a significant predictor, showing positive associations at 0.5 km for functional (q = 1 and 2) and phylogenetic diversity (q = 1), and at 3 km for functional diversity (q = 1). Our results add to a growing body of evidence (e.g., Avila-Cabadilla et al., 2012; Arroyo-Rodríguez et al., 2016; Rocha et al., 2017; Farneda et al., 2022; Carvalho et al., 2023), indicating that forest cover embedded in a high-quality matrix is pivotal for mitigating some of the adverse effects of human land-use changes on Neotropical bat communities. Notably, optimal design recommendations for the conservation of forest-dwelling species in countryside ecosystems are associated with the protection of at least 40% of forest cover (Arroyo-Rodríguez et al., 2020).

Phyllostomid species also responded significantly and negatively to rice patch density at the 3 km scale from a functional diversity perspective (q = 1). An increase in patch density of forests, savannahs, and mainly rice is more representative of traditional farmlands in our study landscape, which might impose a greater barrier to the movement and foraging efficiency of some bat species. In this case, the bat assemblages in the Llanos may be structured according to the concept of area-restricted search (Dorfman, Hills and Scharf, 2022), concentrating the foraging activity in specific forested habitats that offer greater food abundance per unit effort, thereby reducing the use of rice patches for foraging. However, disturbance-tolerant bats, such as many frugivorous generalists (e.g., *Artibeus lituratus*, *A. planirostris*, *Carollia perspicillata*, *Uroderma bilobatum*), which are more adapted to open areas in the Llanos (Morales-Martínez et al., 2020), may benefit from a high patch density.

Our findings support Chambers et al. (2016), who postulate that patch density is important for predicting bat habitat selection across multiple spatial scales in tropical dry forests. Significant associations between bat diversity facets and landscape metrics were most prominent at the 0.5 km scale, followed by the 3 km scale, and were lacking at the 1.5 km scale. In the Llanos, landscape metrics quantified at the smallest scales (≤ 0.5 km) can be more representative of habitat composition and quality, as reflected in the significant effects on multiple bat diversity dimensions. On the other hand, larger scales (3 km) may better characterize landscape configuration, especially for rice paddies that occupy extensive areas. Although bat communities seem to respond at a small and large scale overall, species-specific analyses might show contrasting preferences in the home range of each species within an assemblage (Rodríguez-San Pedro et al., 2019; Martins et al., 2022). Furthermore, additional sampling effort is needed to determine whether the patterns described in the present study based on the La Niña influence (wetter periods) also occur during El Niño events and across the other ecosystems in the Orinoco Llanos, such as aeolian and highplain savannahs (see Romero-Ruiz et al., 2010).

Mist nets are the go-to method for sampling phyllostomid species, however catchability varies among species as they cover a wide range of traits, including foraging strategies (Meyer et al., 2011). Although this could have potentially biased our results, we assert that the effect of interspecific differences in catchability on taxonomic, functional, and phylogenetic diversity estimates is consistent across space and thus unlikely to significantly alter our conclusions. This is supported by the fact that the same suite of frugivorous generalist species was dominant across all habitats sampled (Fig. S4). Nevertheless, future ecological studies in the Orinoco Llanos, ideally with a larger sampling effort, should try to account for differences in species catchability, e.g. through capture-recapture models.

4.3 Conservation and management on private land

Human-induced habitat modification represents one of the primary causes of biodiversity loss worldwide (Semenchuk et al., 2022), and there is a general lack of private conservation areas for protecting biodiversity against increasing environmental disturbances in the Orinoco Llanos (Aldana and Mitchley, 2013). Our study shows that for phyllostomid bats the effects of habitat conversion manifest as similar responses across all three diversity dimensions, whereby riparian forests in Civil Society Nature Reserves harboured the greatest taxonomic, functional, and phylogenetic diversity. Bat assemblages in rice fields, in contrast, are impoverished from an evolutionary perspective. To maintain the pool of species, ecological functions, and evolutionary history within the riparian forests, our findings reinforce the irreplaceable value of surrounding native vegetation, such as flooded savannahs and unflooded forests. The long-term preservation of a savannah-forest mosaic landscape in the Orinoquia is of central importance for promoting natural corridors and stepping stones and supporting all dimensions of bat diversity.

The owners of private reserves have voluntarily carried out a central task of conserving natural resources commonly neglected by the Colombian and Venezuelan environmental governance (López and Arbeláez, 2016). Safeguarding the private reserves through payments for environmental services and implementing and encouraging more wildlife-friendly farming in the Colombian Orinoquia is of prime relevance if current governance is to fully realize its promise of environmental protection. Consequently, the results emerging from this potential engagement of private conservation policies (see López-Arévalo, Liévano-Latorre and Montenegro, 2021 and De Marco et al., 2023) will probably be accompanied by a significant improvement in the functional connectivity between forest and savannah patches. This may manifest in a multidimensional biodiversity increase in this ecoregion rarely safeguarded throughout protected areas (Williams et al., 2022), and with high biodiversity endangered mainly by the replacement of native vegetation by monocultures, illicit crops, and livestock (Romero-Ruiz et al., 2012). Our results support calls for promoting sustainable development in the Orinoco macro-basin to reduce trade-offs between food security and nature conservation, to improve the preservation of natural ecosystems outside protected and indigenous areas, and to stimulate scientific research to fill existing gaps in ecological knowledge. Therefore, we also recommended extending our line of research through ecological modelling to determine how scenarios of natural habitat conversion into monoculture systems, climate change, and fire management across the Orinoquia ecosystems affect bat communities.

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Authors’ contributions

AOA and FZF designed research; AOA and FZF performed the statistical analyses and FZF led the writing of the manuscript, supported mainly by AOA and CFJM; FZF and AOA collected data; AOA and FZF carried out the 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.

Supporting information

Additional supporting information may be found online in the Supporting Information section.

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