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Analysis of functional and phylogenetic diversity of bat communities: insights from resource use in the Pantanal and Cerrado

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Abstract

Background Assessing the structure of communities requires analysis of multiple dimensions of biological diversity. Such approaches provide a broader understanding of the ecological and historical factors involved in the formation and maintenance of communities. Metrics such as functional and phylogenetic diversity are crucial as they unveil how communities respond to environmental changes, providing a deeper understanding of their current state and resilience. This goes beyond species richness or community composition, enabling more profound insights into their present condition and resilience. Therefore, analysis in this sense allows accessing differences in the distribution of species, considering different landscape mosaics, and allowing strategic prioritization of conservation initiatives. In this sense, we investigated whether the composition of functional and phylogenetic groups of chiropteran species differs between the Pantanal and Cerrado biomes and various habitat types. We hypothesize that communities with greater conservation integrity are more diverse than communities that suffer anthropogenic influences.

Methods The surveyed communities include two areas in the Pantanal and two in the Cerrado, with one conservation unit and one that suffers anthropic influence, for each biome. We assessed the composition of bat assemblages by examining functional richness (FRic), functional uniformity (FEve), functional divergence (FDiv), and functional dispersion (FDis). Metrics that reflect phylogenetic richness and divergence were also used, such as phylogenetic diversity (PD), mean pairwise distance (MPD), and mean nearest taxon distance (MNTD).

Results and discussion Overall, conservation units sustain higher levels of functional and phylogenetic diversity compared to areas with anthropic influence. In the latter, species occupy fewer ecological niches, indicating that bats can persist in degraded environments, albeit the communities support only a portion of the functional groups.

Conclusion Our results showed, through analyses across multiple dimensions of functional and phylogenetic diversity, that bat populations are impacted by environmental degradation and fragmentation. Communities in more conserved areas exhibited higher functional and phylogenetic richness, indicating a greater number of occupied niches. These findings highlight the importance of exploring measures of biological diversity and their spatial scales to advance our understanding of biodiversity dynamics and optimize conservation planning for both species and communities.

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Keywords Anthropic influence, Bats, Conservation, Conservation unit, Diversity metrics

Background

Studies considering the relationships between landscape structure and patterns of habitat use by chiropterans remain limited and predominantly focus on the consequences of fragmentation [1–4]. Studies on landscape mosaic structure and evolutionary history have been developed to describe geographic gradients in species richness [5–7]. However, interest in phylogenetic and functional diversity has greatly increased in recent years, considering different taxonomic groups [6].

The multifaceted roles bats play in resource exploitation are better understood through understanding the structure and composition of their functional groups [8], incorporating various perspectives such as taxonomic, evolutionary, and ecological characteristics. Some classifications, derived from diverse methodologies [9–11], often categorize bats into groups such as aerial insectivores, trawling piscivore-insectivores, and gleaning carnivores, among others [11–13]. These foraging categories have contributed to a better understanding of the niches occupied by bats, thereby informing us about which species are more susceptible to deforestation [14]. Evaluating groups from a functional perspective has proven to be more effective than narrower assessments [15]. Chiropterans are excellent as a study group due to their wide range of dietary preferences, shelter uses, foraging behaviors, and ecological roles. They provide multiple ecosystem services including pollination, seed dispersal, and insect population control, and they are indicators of toxin accumulation [16, 17].

Metrics of functional and phylogenetic diversity provide valuable insights into community responses to environmental changes, offering a more comprehensive understanding of resilience and functional integrity than species richness or community composition alone [18, 19]. Assessing community phylogenetic diversity, especially by identifying regions rich in evolutionary history, deepens our understanding of structural constraints across different landscapes [20]. This framework suggests that areas with a higher number of phylogenetic branches tend to exhibit greater functional trait diversity, enhancing their potential for evolutionary adaptation to environmental changes [20, 21].

At the core of the concept of functional diversity is the role of functional traits, defined as the characteristics of organisms that influence both their fitness and the functioning of ecosystems [22–24]. The accuracy of functional diversity assessments largely depends on the selection of ecologically important traits [22–24]. In this context, functional diversity entails comparing trait differences among species and individuals to assess their effects on ecosystem function and their responses to environmental changes [23, 25]. Such analyses of functional diversity help quantify the elements of biodiversity that are essential for ecosystem operation [26].

The mammal fauna of the Pantanal region has been documented in several inventories [4, 27–33]. However, chiropteran diversity may be underestimated, especially due to differences in species composition between flooded and non-flooded areas. Some species are exclusively found in the floodplain, while the greatest richness of chiropterans is noted in the upland areas adjacent to it [33]. In the Cerrado, chiropteran surveys have identified between 11 and 25 species [34–42], which represent approximately 14% of Brazil's total chiropteran species [43]. This limited diversity is likely influenced by extensive deforestation, environmental degradation, habitat fragmentation, land use for agriculture, and livestock farming, which are the main factors influencing biological diversity in the Pantanal and Cerrado biomes [44–47].

Previous studies have demonstrated that communities in conserved areas exhibit greater heterogeneity in functional and phylogenetic groups compared to altered areas [48–51]. Research on the phylogenetic and functional relationships within bat communities remains scarce in these biomes. However, investigations into functional and phylogenetic diversity in the Cerrado have shown greater diversity than previously recorded [52]. Understanding the impacts of anthropogenic actions on species diversity and functional groups is crucial for developing effective landscape management guidelines, considering species persistence and resilience in these areas. In this study, we evaluated this hypothesis, in the context of the Pantanal and Cerrado regions.

Methods

Study area

In the Pantanal, western Brazil, the Reserva Particular do Patrimônio Natural (RPPN) Sesc Pantanal (SescPant) covering 108,000 hectares in Barão de Melgaço, Mato Grosso (16°41'S, 56°24'W), is characterized by a diverse mosaic of savannas and forest formations, including fields with murundus (rounded earthmounds covered by woody vegetation), shrubby areas, seasonally dry forests, and cambará forests (monospecific formation dominated by *Vochysia divergens*, Vochysiaceae). The cambará forest divides large open areas, characterizing a diversity of habitats within the conservation unit [53, 54]. In contrast, the Santa Lúcia Ranch (RanchPant), in the adjacent region (16°53'S, 55°54'W), left bank of the São Lourenço River, is more altered by human activity and cattle raising. The region comprises wet savanna with forest-islands (murundus), grasslands, and areas of sparse vegetation widely used as pasture. Denser forests along the rivers, interspersed with cambarazal forests and acurizais (forests of *Scheelea phalerata* palm), show a clear impact of livestock activity on the environmental heterogeneity [13] (Fig. 1).

In the Cerrado region, the Parque Sesc Serra Azul (SerAzul), Rosário Oeste, Mato Grosso (14º29'S, 55º44'W), is a conservation unit that spans approximately 5,000 hectares [55]. The region is a mix of dry and floodable pastures, with or without sparse trees, and various types of seasonal forests, including gallery forests and forests with babassu palms (*Orbignya phalerata*). Human influence in the surrounding areas, as in many other regions of the Cerrado, has resulted in a mosaic of agricultural exploitation interspersed with original vegetation [47, 56, 57]. On the other hand, the Serra da Mesa (SerMesa) region, encompassing the municipalities of Niquelândia, Colinas do Sul, Minaçu, and Uruaçu in Goiás (13°45' – 14°35'S and 47°50' – 49°15'W), includes a variety of landscapes ranging from open fields to dense, humid forests along watercourses. The area reflects the typical mesophytic habitats of the Cerrado core, with cerrado *sensu stricto* and cerradão (woodland savanna), contrasting with gallery forests that usually support a diversity of plant and animal species [56, 57] (Fig. 1).

The sampling periods lasted between 10 and 15 nights and were conducted using mist nets. The number of nets deployed per night ranged from 5 to 7, and each site was sampled for 1 to 3 days, with a sampling duration of six hours following sunset. The nets were checked every 15 to 30 min, depending on the number of animals captured. The nets were primarily set up in clearings or open corridors within forested areas, in locations with flowering or fruiting trees, and near rivers or bodies of water. All data presented in this study were obtained from previous sampling by the authors [4, 13, 55]. Sampling was conducted in four distinct areas over different periods. In the Pantanal region, data from RPPN Sesc Pantanal were collected between 1999 and 2008, covering all months of the year, while collections at Santa Lúcia Ranch took place in November and December 2014 and October 2015. In the Cerrado communities, sampling was conducted at Parque Sesc Serra Azul in August 2012, as well as in

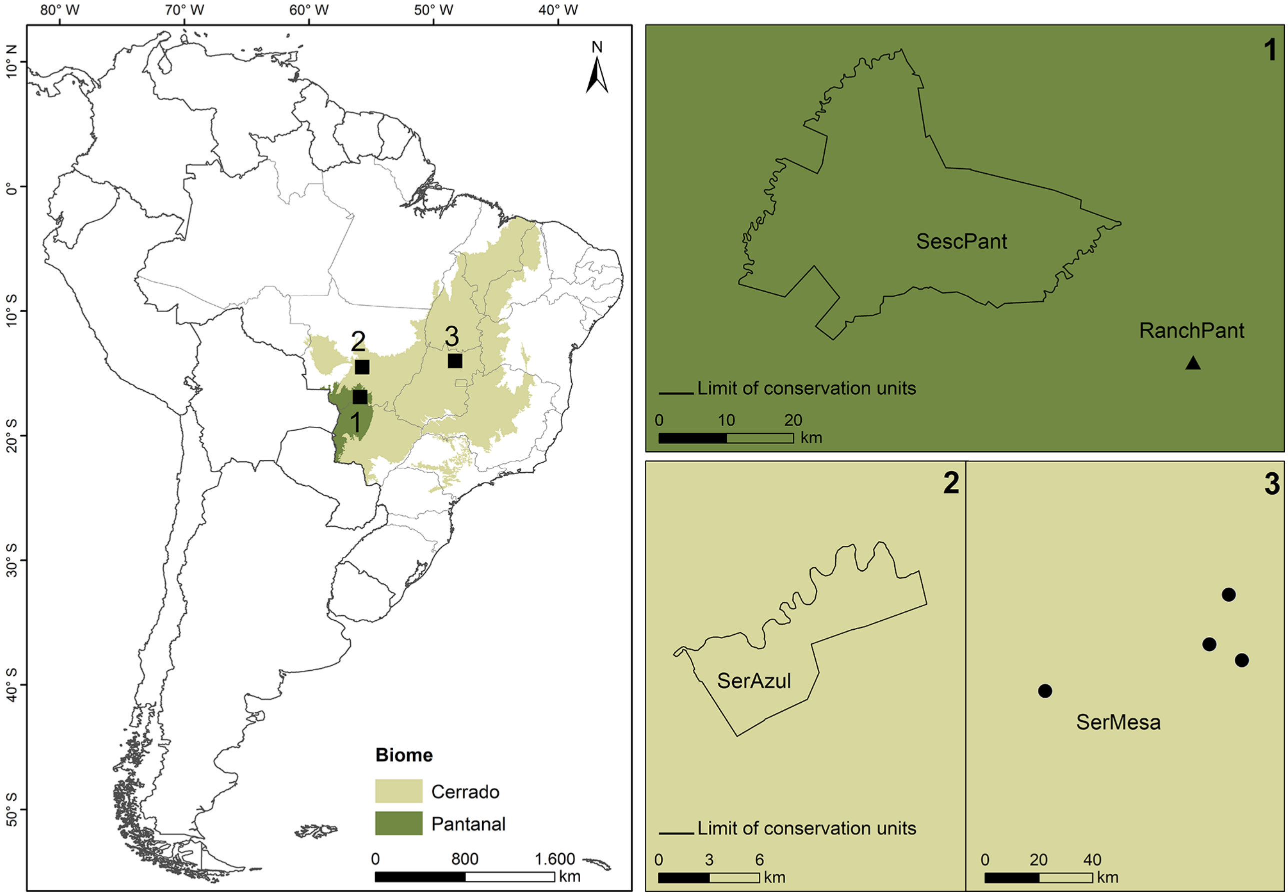

Fig. 1 The main map shows the neotropical region, highlighting the four sampled locations in Brazil. Smaller maps illustrate the communities in the Pantanal: (1) Sesc Pantanal (SescPant) and Santa Lúcia Ranch (RanchPant), Cerrado communities (2) Parque Sesc Serra Azul (SerAzul), and (3) Serra da Mesa (SerMesa). In 1 and 2 the polygons delimit the conservation units

March and August 2013. In the Serra da Mesa region, data were gathered in September, October, and December 1995, in addition to February and May 1996. To ensure comparability across communities and adjust for sampling effort variations, we standardized the data by normalizing each value relative to the total captures per community, using the 'decostand' function along with the 'total' method from the 'vegan' package [58].

Sample coverage

The sampling effectiveness was evaluated using Hill numbers, which are a measure of taxonomic species diversity within communities, based on the methodology detailed by Chao et al. [59]. Hill numbers (the effective number of species) are used to quantify species diversity by considering both species richness (the number of species) and their relative abundance. When $q=0$, the focus is solely on species richness, meaning the number of distinct species present is counted without regard to how abundant each species is. Using $q=0$ is particularly important in areas where the capture effort is unknown (one of the study areas), as the data are based on a substantial faunal survey effort that is not fully available. Although the data offers valuable information, it has limitations. However, it still allows for inferences about the communities and enables comparisons by equalizing sample sizes. The 'iNEXT' package [60] was utilized for this analysis, facilitating the computation and visualization of rarefaction and extrapolation sampling curves. This package also provided 95% confidence intervals and allowed us to estimate the asymptotic diversity values. This approach was particularly important given the different sampling efforts employed across the communities, ensuring that our diversity estimates accurately reflect the varying levels of sampling intensity.

Molecular data

The MEGA software [61] was used for aligning the sequences and manually editing alignments. Maximum likelihood gene tree estimations were carried out with IQ-TREE software [62], and the best-fit model was GTR + F + I + G4 chosen according to the BIC identified by ModelFinder [63] included in the IQ-TREE. Branch support was assessed using an approximate likelihood-ratio test based on the Shimodaira-Hasegawa-like procedure (SH-aLRT) [64] and nonparametric bootstrap frequencies. The tree was edited with FigTree software [65]. Overall, the bootstrap and SH-aLRT values were above 80, with only a few clades showing support values under this threshold.

A total of 70 sequences were used, 42 from the present study and 28 obtained from GenBank (Table S1). As an external group, sequences from GenBank of the bats *Rousettus aegyptiacus* (AB085740), *Rhinolophus ferrumequinum* (AB085731), and the Canidae *Cerdocyon thous* (KU253528), with 1,140 base pairs, were included. *Neoplatymops mattogrossensis* was removed from the phylogenetic diversity analysis due to a lack of samples for comparison. Details of the amplification conditions can be found in Table S2. The list of primers used in the amplification is available in Table S3. Additional information on the deoxyribonucleic acid (DNA) extraction and sequencing methods (cytochrome b gene) is described in detail in the study by de Oliveira et al. [66].

Phylogenetic diversity analyzes

Based on the phylogeny of the rooted maximum likelihood tree, we calculated: phylogenetic diversity (PD) [67], mean pairwise distance (MPD) [68], and mean nearest taxon distance (MNTD) [68].

The PD measure is the sum of the length of all branches in a phylogeny [68], and represents the sum of the evolutionary history in a sample; it is considered the first phylogenetic diversity metric. However, it does not consider species abundance within the sample; Faith's PD is expected to increase as the number of species in a sample rises.

The MPD measure quantifies the average pairwise phylogenetic distance between all species in an assemblage [22, 68]. MPD is a metric that weights the basal structure of the phylogeny (e.g., relationships between species from different families) [69]. The MNTD measure quantifies the pairwise phylogenetic distance between the closest relatives in an assemblage [22, 68]. It is a terminal metric that weights relationships at the ends of the phylogeny (e.g., species within the same genus) [69]. High values of MPD indicate that phylogenetically grouped. High values of MNTD suggest that closely related species do not co-occur in the community, that is, some species have branches much longer than average. On the other hand, low values suggest co-occurrence.

To eliminate metric redundancy, phylogenetic diversity was quantified using standardized effect size (SES) [22]. To calculate SES, species richness for each site was fixed, and species at the ends of the phylogeny were randomized 1000 times. A significant positive SES value indicates an over-dispersed phylogenetic structure, while significant negative values indicate phylogenetic clustering [69].

Phylogenetic signal

To assess whether functional traits present a phylogenetic signal, we used Blomberg's K and Significance Tests. These tests quantify the extent to which trait variation is explained by the structure of a given phylogenetic tree. To compare K values across different phylogenies and studies, standardization is required [22, 70]. This value is based on the expected value derived from the evolution of the trait under a Brownian motion model within the observed phylogenetic tree [70].

Characterization of food guild and foraging strategy as functional traits

To better understand bat assemblages, a species-level classification was employed based on diet and foraging behavior [71]. This classification system was based on the analysis of existing literature and included items such as seeds, fruits, nectar, invertebrates, vertebrates, fish, and blood. Each species was then categorized based on its predominant, secondary, and tertiary diets when applicable (Table S4). Some bat species may consume more than one type of resource, either regularly or occasionally, depending on the availability of the predominant resource. These variations may occur seasonally, as documented in various studies [72–74].

The foraging strategies have been characterized into five categories: aerial, gleaning, sedentary, nomadic, and trawling (Table S4). Aerial foragers capture prey while flying. Gleaning involves collecting food by picking it up from a solid surface, such as leaves, branches, or the ground. The trawling foraging strategy involves capturing prey on over water or, in some cases, in water. Nomadic foragers are associated with frugivores, and their populations move to different regions based on resource availability, suggesting more frequent shelter renewal. Sedentary foragers, also associated with a frugivorous diet, follow a regularly fixed route, typically when preference is linked to plants with continuous year-round production. The characterization of foraging strategies followed the propositions of Fenton [75], Soriano [76], Schnitzler and Kalko [12], Schnitzler et al. [11], and Denzinger and Schnitzler [77].

In addition, we performed Principal Coordinates Analysis (PCoA) using the 'ape' package to classify species into functional groups based on Bray-Curtis dissimilarities, utilizing the 'ecodist' package [78]. This analysis groups species based on their traits, thereby providing a better understanding of community composition and the dynamics of diversity.

Functional diversity analysis

Functional diversity was assessed using the widely known metric 'FD' [79]. It was calculated by generating a functional dendrogram from a matrix containing species and their associated functional traits, based on the total branch length. This approach yielded indices for functional richness (FRic), functional uniformity (FEve), functional divergence (FDiv), and functional dispersion (FDis) [22]. Additionally, mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) analyses were also performed for functional diversity [68].

Functional richness (FRic) quantifies the volume of niche space occupied by species based on their traits highlighting the range of ecological roles within a community [80, 81]. It is measure as the minimum convex polygon that encompasses all species and is particularly sensitive to species at the edges of the trait distribution [82]. Functional evenness (FEve) assesses how evenly species abundances are distributed across the occupied niche space, reflecting how efficiently a community uses available resources within its ecological limits [81].

Functional divergence (FDiv) and dispersion (FDis) measure niche differentiation and the average distance of species from the functional centroid, respectively, with high FDiv values indicating significant niche differentiation and high FDis values reflecting broader utilization of niche space edges [81].

Dietary traits were quantified by determining the proportion of various food types consumed by each species when they used multiple food sources. Foraging strategy traits were coded in binary terms. Quantitative traits, such as size and weight, were measured in millimeters and grams. Due to variability in measurement scales, standardization was necessary to mitigate scale effects, as stated in Pla et al. [83].

To ensure the accurate calculation of indices, all trait values were standardized to a range of zero to one using the 'decostand' function along with the 'range' method from the 'vegan' package [58]. This conversion ensured that the minimum value on the original scale becomes zero and the maximum value one, making all traits continuous [81, 83]. The 'FD' package was used to calculate functional diversity metrics using the 'dbFD' function for distance-based indices [84]. The 3D graphs were generated using the 'plotly' package [85]. All diversity analyses were conducted on the R platform [86].

Results

The collected samples varied considerably in size and composition, reflecting the ecological complexity of the analyzed environments. In the Pantanal, the SescPant site recorded 721 captures, including 40 species and 25 genera, while the RanchPant community had 659 captures, representing 29 species and 17 genera. In the Cerrado, the conservation area community SerAzul documented 562 captures with 39 species and 27 genera, and the SerMesa community recorded 490 captures, encompassing 33 species and 27 genera.

The rarefaction curves illustrate different levels of bat species richness among the four communities evaluated (Fig. 2). Within the Pantanal, the reserve community (SescPant) exhibits an extrapolation curve that has not reached an asymptote, indicating the potential for higher species richness than been recorded so far. In contrast, the curve for the ranch community (RanchPant), a more

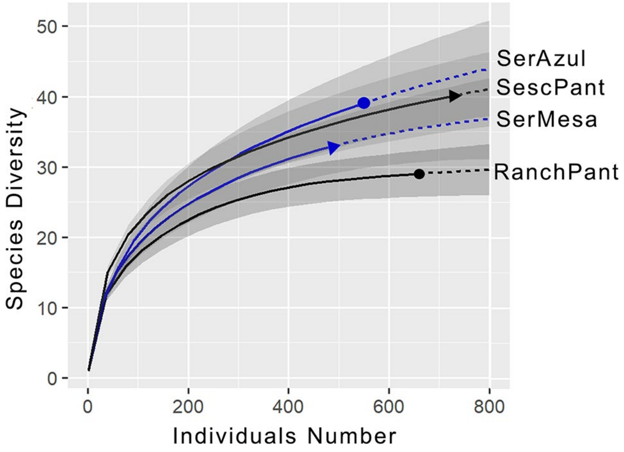

Fig. 2 Rarefaction curves, represented by solid lines for sample size and dotted lines for extrapolation, include 95% confidence intervals shown as shaded areas. These curves assess the number of individuals captured across various communities, which are categorized based on their conservation status: conserved areas (SescPant, SerAzul) and human-influenced areas (RanchPant, SerMesa). The communities are differentiated based on diversity, specifically q = 0 (species richness)

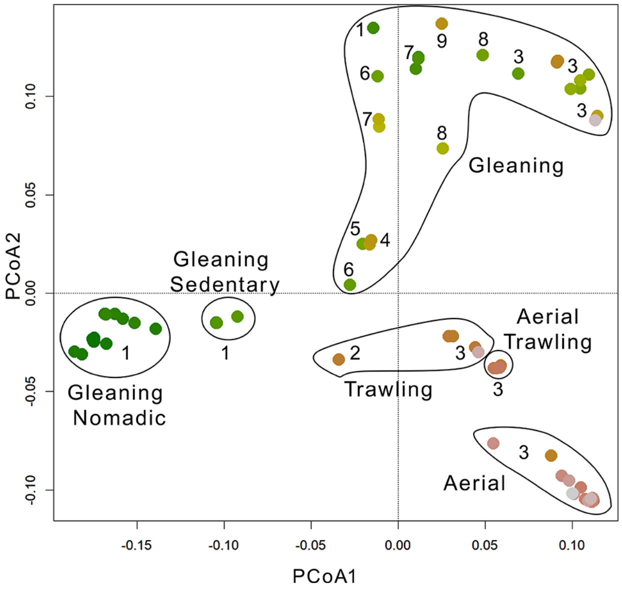

Fig. 3 Principal Coordinates Analysis (PCoA) was performed using Bray-Curtis dissimilarities to classify species into six groups representing foraging strategies: Gleaning (Nomadic and Sedentary), Trawling, and Aerial. Diets were categorized as (1) Frugivore, (2) Piscivore-Insectivore, (3) Insectivore, (4) Sanguivore, (5) Granivore, (6) Omnivore, (7) Nectarivore, (8) Carnivore-Insectivore, and (9) Frugivore-Insectivore

anthropogenically impacted area suggests lower species richness, with sampling approaching completion. Despite the proximity of the ranch and the reserve, which are separated by the banks of the São Lourenço River (with sampling points up to 20 km apart), the differences in bat communities between these areas are striking.

In the Cerrado region, the communities of Parque Sesc Serra Azul (SerAzul) and Serra da Mesa (SerMesa) show comparable species richness (Fig. 2), with both curves indicating that the species richness surpasses the sampled data. After rarefaction, there are no expressive differences in bat species richness across all studied communities in the Pantanal and Cerrado regions. However, within the Pantanal, the contrast between the conservation-oriented SescPant area and the livestock-driven RanchPant, is notably pronounced.

The effectiveness of the sampling effort was assessed by calculating the sample coverage at each community, which was particularly important as the sampling effort in some communities was smaller, requiring us to ensure equivalent effort per unit of area and time. In the Pantanal communities, sample coverage was 98% for SescPant and 99% for RanchPant. In the Cerrado communities, the sample coverage was 98.17% for SerMesa and 97.87% for SerAzul, indicating near-complete sampling for both communities.

In the Principal Coordinates Analysis (PCoA), a clustering pattern emerged based on species' foraging strategies. The foraging strategy delineated the groups, with some sharing similarities due to certain species consuming multiple types of food (Fig. 3).

The phylogenetic diversity (PD, Fig. 4a) observed in the SerAzul community is high, with positive sesPD values suggesting that this community has higher PD values than expected for its observed species richness. Conversely, negative sesPD values were observed for the other three communities (SescPant, RanchPant, SerMesa), indicating that their phylogenetic diversity is lower than expected given their species richness.

The MPD metric, which assesses the average phylogenetic distance among all individuals within a community (Fig. 4b), was high in the SescPant and SerAzul communities. This indicates the greatest phylogenetic distance among the species within these communities. Additionally, the positive sesMPD for SescPant suggests that this community has higher MPD values than expected (Table 1; Fig. 4b), showing exceptional phylogenetic diversity when contrasted with the others. The communities with the greatest average distance to the nearest taxon (MNTD) were the two from the Cerrado (SerMesa, SerAzul). However, the positive standardized effect size for MNTD (sesMNTD) in SerAzul indicates that this community has a higher phylogenetic diversity between species than observed (Table 1; Fig. 4c).

Mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) (Table 1) for phylogenetic diversity (Fig. 4) and functional diversity (Fig. 5) showed higher diversity in the conservation unit communities (SescPant, SerAzul). This finding is supported by the FRic values, which showed the highest functional richness in these communities (Fig. 6).

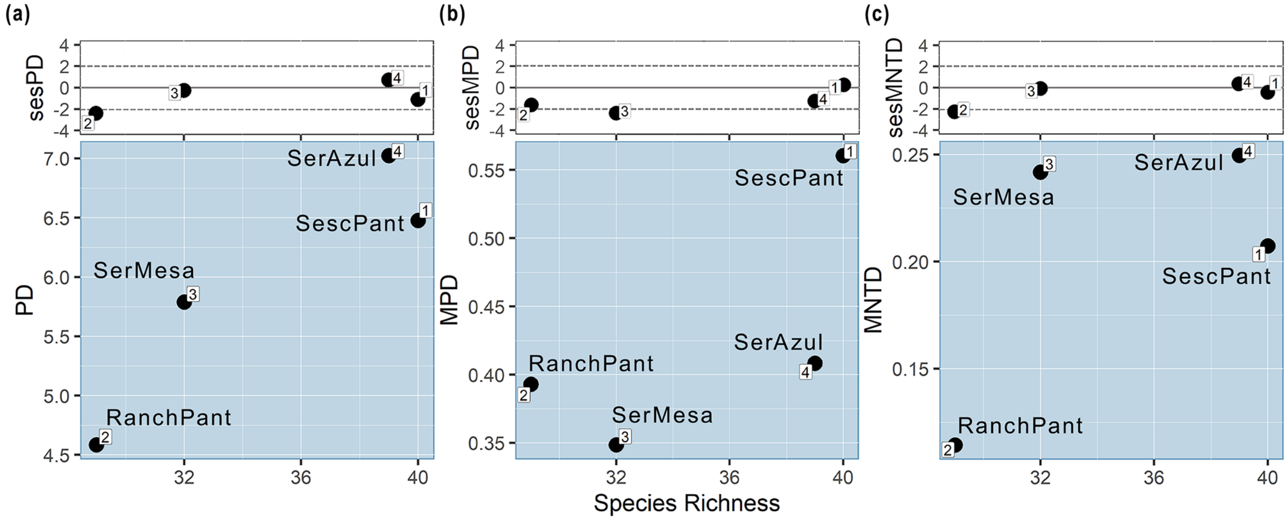

Fig. 4 Standardized effect size: (**a**) sesPD, (**b**) sesMPD, and (**c**) sesMNTD, along with 5% and 95% quantiles (dashed lines) of the simulated null communities of Faith's phylogenetic diversity (PD), mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) assessed for the communities sampled in Pantanal (SescPant, RanchPant) and Cerrado (SerMesa, SerAzul)

Table 1 Phylogenetic and functional diversity indices showing phylogenetic diversity (PD), mean pairwise distance (MPD), mean nearest taxon distance (MNTD) and standardized effect size (sesPD, sesMPD, sesMNTD), calculated for the Pantanal (SescPant, RanchPant) and Cerrado (SerMesa, SerAzul) communities. In bold are values statistically significant, with a p-value lower than 0.05

	SescPant	RanchPant	SerMesa	SerAzul
	Phylogenetic diversity			
PD	6.48	4.58	5.79	7.02
sesPD	-1.12	-2.40	-0.26	0.71
p	0.132	**0.010**	0.379	0.752
MPD	0.56	0.39	0.35	0.41
sesMPD	0.25	-1.62	-2.41	-1.26
p	0.612	**0.039**	**0.005**	0.102
MNTD	0.21	0.11	0.24	0.25
sesMNTD	-0.45	-2.27	-0.09	0.35
p	0.320	**0.003**	0.482	0.647
	Functional diversity			
MPD	1.54	1.26	1.29	1.32
sesMPD	1.59	-0.51	-0.57	0.13
p	0.950	0.278	0.258	0.516
MNTD	0.28	0.19	0.26	0.38
sesMNTD	0.65	-0.70	-0.06	1.34
p	0.758	0.242	0.567	0.899

Blomberg's K values were tested for all functional traits to evaluate the intensity of the phylogenetic signal of these characteristics in the phylogeny of these communities. The results suggest a phylogenetic signal with a high degree of variation for some phylogenetic traits, such as the insectivore, sanguivore, frugivore, and nectarivore diets, and the foraging strategies gleaning nomadic, gleaning, gleaning sedentary, aerial-trawling, aerial and trawling. Blomberg's K values show a non-significant or absent phylogenetic signal for the carnivore, piscivore-insectivore, and granivore diets, the same occurring for the forearm and weight traits (Table 2).

In terms of functional diversity, the high MPD (Fig. 5a) and low MNTD (Fig. 5b) values indicate that all communities exhibit substantial functional differentiation between species pairs, thereby indicating high functional diversity at the species level. However, conservation units exhibit even greater functional diversity compared to communities subjected to more anthropogenic influence.

In the Pantanal, the community experiencing the highest level of anthropogenic influence (RanchPant), exhibited the lowest functional and phylogenetic diversity. The low MPD and MNTD values, which were significant (p) in the context of phylogenetic diversity (Fig. 4), suggest that it is the most phylogenetically impoverished community. Moreover, the significant values of the standardized effect size suggest that the diversity measures may be overestimated, meaning that the phylogenetic diversity values reported by the metrics are higher than expected. Furthermore, the values of functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis, Table 3) were also low in this community, indicating few niche spaces occupied, many species closely related functionally, and low dispersal of functional traits.

Conversely, the conservation units' communities in both sampled biomes (SescPant, SerAzul) displayed the greatest richness (FRic), increased functional divergence (FDiv), and greatest functional dispersion (FDis, Fig. 6). These metrics indicate that a wide variety of niches are occupied and traits are broadly distributed within these communities (Table 3).

The community in the Cerrado with the most anthropogenic influence (SerMesa) had the lowest functional richness (FRic) and the second-lowest functional

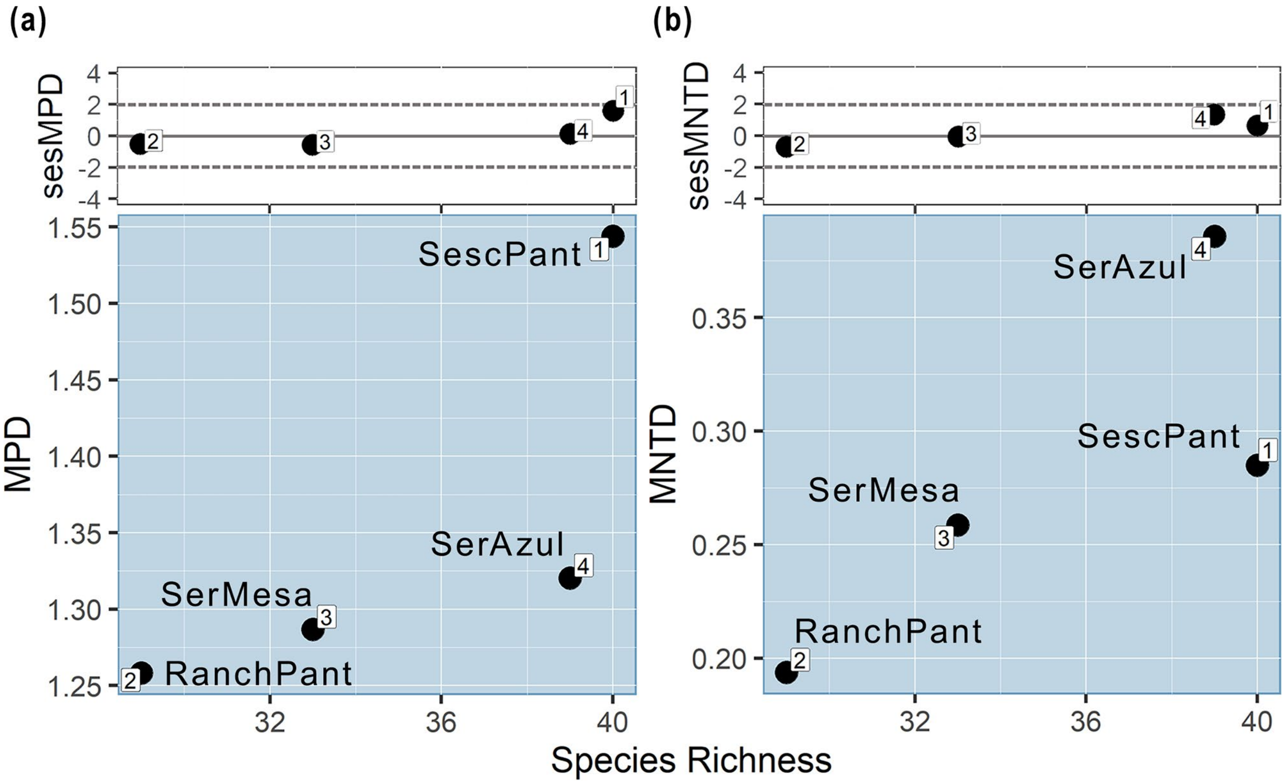

Fig. 5 Standardized effect size: (**a**) sesMPD, and (**b**) sesMNTD, along with 5% and 95% quantiles (dashed lines) of the simulated null communities of functional diversity (FD), mean pairwise distance (MPD), and mean nearest taxon distance (MNTD) assessed for the communities sampled in Pantanal (SescPant, RanchPant) and Cerrado (SerMesa, SerAzul)

dispersion (FDis, Fig. 6), indicating that few niches are occupied with restricted functional dispersion. However, this community showed the greatest functional uniformity (FEve) and elevated functional divergence (FDiv, Fig. 6), indicating that functional traits are evenly distributed across species, which fulfill a diverse array of ecological functions. These metrics, which represent MPD and MNTD, suggest that most species are closely related phylogenetically. However, phylogenetic divergence is greater among the basal taxa, while phylogenetic distances are smaller between the terminal taxa (Fig. 4b and c).

Discussion

We tested the hypothesis that conservation areas, which maintain habitat integrity in the Pantanal and Cerrado regions, support bat communities with greater functional and phylogenetic heterogeneity. Our findings validated this hypothesis, as we observed a positive association between habitat integrity and functional and phylogenetic diversity. This association was adjusted for species richness using a standardized effect size (SES). Previous studies have shown that vegetation homogeneity can act as an environmental filter, leading to the dominance of functional and phylogenetic clustering in bat communities [87–89]. In contrast, the heterogeneity of vegetation types found in more conserved areas increases phylogenetic diversity [89]. These results were consistent with our conclusions and support the importance of conservation efforts in maintaining habitat integrity and promoting biodiversity.

Land use for ranching, as exemplified by RanchPant in the Pantanal, has led to a marked decline in both functional and phylogenetic diversity within bat communities, as shown by the lower values of phylogenetic diversity indices (Table 1) and reduced functional richness (Table 3). This decline is indicative of a shrinking ecological niche space, which is particularly evident when compared to more conserved areas [6]. Previous studies have highlighted that biodiversity loss has been aggravated by substantial habitat reduction and fragmentation at the landscape level, one of the primary drivers of these observed patterns [87, 90, 91]. In RanchPant, anthropogenic influence has promoted conservative habitat filtering, favoring frugivorous species that are closely related phylogenetically and share similar functional traits, adapted to degradation and environmental fragmentation [6, 92]. This selection has resulted in bat communities that share advantageous traits for survival in degraded conditions, but with impoverished biological diversity compared to less anthropized areas [4, 28].

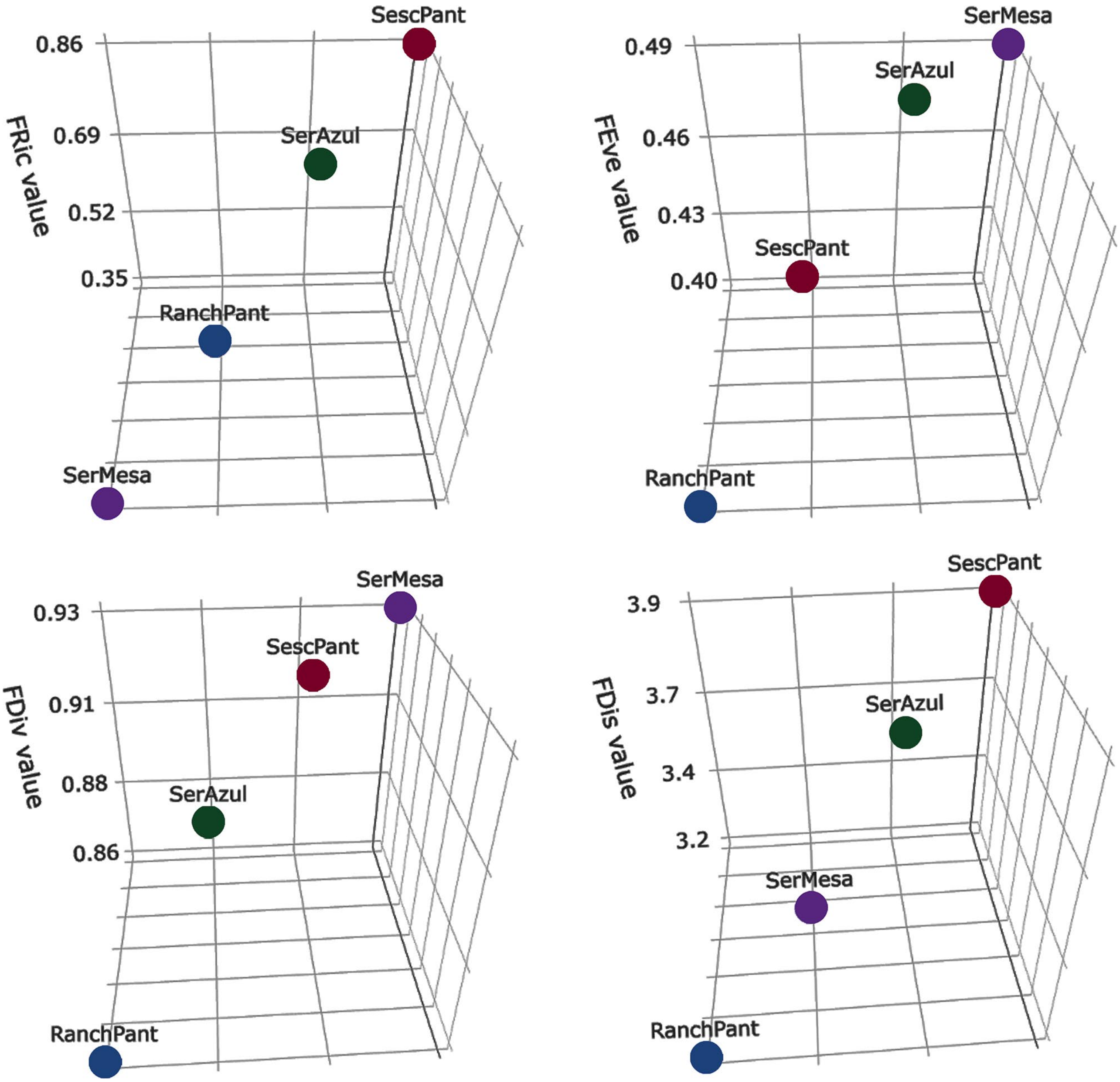

Fig. 6 Functional trait diversity plotted in a 3D graph, assessed for the sampled communities in the Pantanal (SescPant, RanchPant) and Cerrado (SerMesa, SerAzul). Spatial Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), and Functional Dispersion (FDis) were evaluated

Despite the pressures of habitat alteration, the present study reveals the prevalence of frugivores and nectarivores in all analyzed communities. This finding corroborates the results of previous studies, which indicate that in contexts of intensified land use, there is an expansion in the abundance of functional traits associated with plant-based diets [93]. This association suggests a potential adaptation of these animals specialized in fruits and nectar to environmental transformations induced by human activity, possibly facilitated by the availability of viable food resources, even in profoundly modified landscapes.

Bat species play crucial roles as seed dispersers and pollinators, especially in the Neotropical region, where many plant species rely on frugivores for dispersal services [94]. Additionally, bats contribute significantly to the pollination of numerous tropical crops, supporting a variety of economically and ecologically important plant species [95]. Therefore, conserved areas are crucial for maintaining the resilience of key species and functional groups that underpin the stability of these biomes. Meanwhile, even degraded areas continue to support constant regeneration, particularly in regions affected by livestock-induced fragmentation [96]. This underscores the

Table 2 Blomberg's K values tested for all functional traits. K represents the intensity of the phylogenetic signal for each functional trait in the phylogeny of the communities. Bold text indicates a significant statistical value with a p-value lower than 0.05

Functional traits	K	*p*
Insectivore	1.5208	**0.001**
Sanguivore	1.2349	**0.002**
Carnivore	0.3974	0.268
Piscivore-Insectivore	0.0590	0.891
Frugivore	3.5854	**0.001**
Nectarivore	0.8270	**0.001**
Granivore	0.4876	0.324
Gleaning nomadic	3.6773	**0.001**
Gleaning	2.0426	**0.001**
Gleaning sedentary	0.9893	**0.004**
Aerial-Trawling	4.0033	**0.001**
Aerial	2.6230	**0.001**
Trawling	2.2722	**0.001**
Forearm length	0.2571	0.072
Body mass	0.2376	0.260

Table 3 Values of the functional diversity metrics assessed include species functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). These metrics were evaluated for communities sampled in the Pantanal (SescPant, RanchPant) and Cerrado (SerMesa, SerAzul). The observed species richness (N) was recorded for each community

Community	*N*	FRic	FEve	FDiv	FDis
SescPant	40	0.8615268	0.4576685	0.9249708	3.864872
RanchPant	29	0.5243205	0.4031926	0.8607402	3.230387
SerMesa	33	0.3456373	0.4910184	0.9311993	3.398253
SerAzul	39	0.7412666	0.4901894	0.9039586	3.665258

importance of bats in both protected and anthropized areas in supporting essential ecological functions.

Phylogenetic signal analyses indicate limited variation in the evolution of traits such as forearm length, body mass, and diet (carnivore, granivore and piscivore-insectivore), with a low phylogenetic signal observed when testing the value of K. This suggests that only a small portion of the variation in these functional traits can generally be attributed to adaptive selection occurring after the divergence of a common ancestor [97]. The bat superfamily Noctilionoidea exhibits a remarkable ecological breadth, with divergent echolocation, specialized flight strategies linked to insectivory, and parallel evolution of diverse plant-based diets, such as nectar, pollen, and fruits, evolving from the ancestral insectivorous condition [98]. Frugivorous, nectarivorous, and insectivorous conditions appear to evolve before carnivorous and hematophagous ones in bat phylogeny. The insectivorous condition within the order is considered the oldest, with all other guilds evolving from this initial condition [98]. However, the lack of data on closely related community traits may reduce the ability to detect a phylogenetic signal for functional traits, especially those that have evolved recently [99].

Conclusions

Our study focuses on the biodiversity of bat communities in the Pantanal and Cerrado regions and how it is affected by local-scale land use. We found that degraded areas have lower functional and phylogenetic diversity, which is consistent with previous studies confirming the sensitivity of bats to local-scale deforestation [51, 87, 100, 101]. However, there is still a lack of research on the mechanisms behind these changes and the impact of habitat complexity and disturbance on bat diversity.

Therefore, our results emphasize the importance of integrating both functional and phylogenetic dimensions into conservation strategies to ensure the preservation of species, their evolutionary histories, and the functional roles they play, which are essential for sustaining ecosystem functions and services. They also reinforce that the effects of different forms of landscape use should not only be viewed from the perspective of species arrangements (losses or gains) but also under the traits of their components, with potential implications for the functionality of ecological systems, particularly through the recognized contributions of bats in regeneration processes. Within each bat community in the Pantanal and Cerrado, functional and phylogenetic diversity is shaped by environmental filtering and limiting similarity pressures. In protected areas, environmental filtering supports greater functional and phylogenetic diversity, while in anthropized areas, limiting similarity pressures and the effects of degradation tend to reduce this diversity.

In summary, our research uncovered strong spatial patterns in the functional diversity of bat communities across two biomes, when contrasting community structures in more intact and anthropized areas. This suggests that anthropogenic pressures not only reduce species richness but also homogenize the functional attributes of communities, potentially compromising ecosystem resilience and functionality. Such insights are critical for developing and implementing conservation programs aimed at preserving biodiversity.

Abbreviations

FRic	Functional richness
FEve	Functional uniformity
FDiv	Functional divergence
FDis	Functional dispersion
PD	Phylogenetic diversity
MPD	Mean pairwise distance
MNTD	Mean nearest taxon distance
SES	Standardized effect size
sesPD	Standardized effect size phylogenetic diversity
sesMPD	Standardized effect size mean pairwise distance
sesMNTD	Standardized effect size mean nearest taxon distance

PCoA	Principal Coordinates Analysis
DNA	Deoxyribonucleic acid
SescPant	Sesc Pantanal
RanchPant	Santa Lúcia Ranch
SerAzul	Parque Sesc Serra Azul
SerMesa	Serra da Mesa
RPPN	Reserva Particular do Patrimônio Natural

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40693-025-00137-z.

Supplementary Material 1: Table S1. List of specimens used in phylogenetic diversity analyses, with taxon, GenBank accession number or voucher number, and font. *Due to the lack of data on *Promops nasutus* in the present study, a congener, *Promops centralis*, was utilized. Table S2. Standardized PCR amplification cycles for the cytochrome b gene of the analyzed chiropteran genera. Some genera had two standardized cycles. Table S3. Primer list employed in the amplification (A) and sequencing (S) steps of the cytochrome b gene. Table S4. Compilation of functional traits for the sampled bats. Mean forearm length (mm) and body mass (g) were calculated based only on adult individuals of species with more than ten captures* in the present study. For species with few individuals, data from the literature were sourced from Velazco et al. (2010), Moratelli et al. (2013), Reis et al. (2017), and Velazco and Patterson (2019). A species-level classification based on diet and foraging behavior was employed based on Findley (1993), Fenton (1999), Soriano (2000), Schnitzler and Kalko (2001), and Schnitzler et al. (2003).

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Author contributions

Conceptualization (MBO, LFBO, CRB); data curation and analysis (MBO); funding acquisition (LFBO, CRB); investigation (MBO, LFBO, CRB); writing (MBO) – original draft; writing – review and editing (MBO, LFBO, CRB).

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All data generated or analyzed during this study are included in this published article.

Declarations

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Competing interests

The authors declare that they have no competing interests.

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