



# Habitat Heterogeneity and Geographic Location as Major Drivers of Cerrado Small Mammal Diversity Across Multiple Spatial Scales

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The Cerrado biome is one of the global hotspots of biodiversity, and non-volant small mammals represent a significant portion of Cerrado species richness (45%) and endemism (86%). Nevertheless, we still lack a comprehensive picture of small mammal diversity patterns and drivers throughout the Cerrado. Here we surveyed small mammals across 45 sites to address species richness, abundance, and composition patterns and their drivers within and across sites, habitats, and localities at the world's most diverse tropical savanna. As hypothesized, we found: (1) rich assemblages (12–21 species) characterized by few abundant and several intermediate-level and rare species; dominated by oryzomyine and akodontine cricetid rodents, and thylamyine and marmosine within marsupials, each tribe showing distinct habitat requirements; (2) strong habitat selectivity, with assemblages composed of forest dwellers, savanna specialists, and grassland inhabitants; and (3) similar species richness ( $\alpha$ -diversity) but high species turnover ( $\beta$ -diversity) across sites, habitats, and localities, suggesting that horizontal stratification (within localities) and geographic location (across the Cerrado) are key drivers of small mammal diversity in tropical savannas. Thus, habitat heterogeneity and geographic location can be inferred as the main factors shaping species richness, abundance, and composition across the analyzed multiple spatial scales. Moreover, we found that geographical distance as well as the distance to neighbor biomes better explained species turnover, indicating landscape history and phylogenetic constraints as the major determinants of Cerrado small mammal diversity, as also evidenced for plants and other animal groups. These data highlight the need to preserve the mosaic of habitats across the different regions of the biome to conserve most of the Cerrado biodiversity.

**Keywords:** abundance, composition, habitat selectivity, inventory, marsupials, rodents, species richness

## INTRODUCTION

Understanding how species richness, composition, and endemism vary across space is a long-standing, central question in ecology and biogeography (Rosenzweig, 1995; Webb et al., 2002; Lomolino et al., 2006), which can also support setting priorities for biodiversity conservation (Wiens and Graham, 2005; McKnight et al., 2007; Jetz and Fine, 2012). In particular, knowledge on large-scale variations in species richness ( $\alpha$ -diversity, the number of species in a given site), and species turnover ( $\beta$ -diversity, changes in species composition across sites), helps creating a comprehensive picture of diversity patterns and their drivers—critical to the understanding of the biogeographic history and diversification of biomes and/or species groups (Melo et al., 2009; Maestri and Patterson, 2016), as well as to pinpoint regions with high diversity and distinct composition for conservation (Socolar et al., 2016; Gianuca et al., 2017; Franoso et al., 2020).

Species richness in tropical savannas is influenced by a variety of factors, including natural fires, herbivore density, precipitation levels, and soil fertility—which ultimately determine habitat heterogeneity among open and forest habitats within these biomes (e.g., Solbrig et al., 1996; Radford et al., 2014; Pringle et al., 2016; Andersen, 2020)—as key drivers. Efforts to understand species turnover and changes in community composition across savannas have shown the importance of both environmental factors, such as bioclimatic gradients (e.g., Bond et al., 2001; Rugemalila et al., 2016; Morales-Martinez et al., 2018), and evolutionary constraints, such as niche conservatism, as drivers of  $\beta$ -diversity (e.g., Campos et al., 2011; Schmidt et al., 2017; Schoeman and Monadjem, 2018).

Tropical savannas are characterized by a highly seasonal climate and a mosaic of grasslands, savannas, woodlands, and forests (Cole, 1986; Solbrig et al., 1996). They represent unique ecosystems, harboring high numbers of endemic plants and animals (Pennington et al., 2018) that have evolved and adapted to their particular environmental conditions (Scholes and Archer, 1997; Mishra and Young, 2020). Although these open biomes represent a large portion of the world's area and biodiversity (Furley, 2006; Dinerstein et al., 2017), savannas have been neglected in scientific research in comparison to tropical forests (Werneck, 2011). These rich and distinctive ecosystems have also been undervalued in terms of conservation (Colli et al., 2020; Dudley et al., 2020). They are currently threatened by human development, representing a great part of the world's agricultural and livestock area (Suttie et al., 2005; Ryan et al., 2016), besides facing high rates of native vegetation loss (Van der Walt et al., 2015; Alencar et al., 2020).

The Cerrado, the largest and most diverse of South American savannas (Cole, 1986; McNaughton et al., 1993), is characterized by high species richness and endemism (Ribeiro et al., 2007; Silva et al., 2007; Nogueira et al., 2011; Carmignotto et al., 2012; Valdujo et al., 2012). Yet, only 8.3% of Cerrado native remnants are legally protected (Franoso et al., 2015), thus setting the Brazilian savannas as one of the 36 global hotspots for biodiversity conservation (Myers et al., 2000; Myers, 2003). Cerrado richness is known to vary according to the number and

type of habitats in the landscape, reinforcing the importance of habitat heterogeneity, as in savannas worldwide (e.g., Colli et al., 2002; Batalha and Martins, 2007; Camargo et al., 2018). The Cerrado is also characterized by high  $\beta$ -diversity, with compositional changes strongly influenced by the distance to neighboring biomes, environmental conditions (climate and topography), and evolutionary constraints (e.g., Ratter et al., 1996, 2003; Silva, 1996; Brown and Gifford, 2002; Silva and Bates, 2002; Nogueira et al., 2011; Valdujo et al., 2013).

Despite an increase in the number of studies in the last decades, there are still large gaps in our knowledge of Cerrado landscapes and biota (Colli et al., 2020). For Cerrado small mammals, the composite nature of their assemblages, characterized by open vegetation and forest specialists, has long been highlighted (e.g., Alho et al., 1986; Bonvicino et al., 1996; Santos-Filho et al., 2012), as well as the role of gallery forests (GFs) in increasing community diversity due to their higher vertical complexity, allowing access to different forest strata and resources for scansorial and arboreal species (e.g., Redford and Fonseca, 1986; Johnson et al., 1999; Hannibal and Cáceres, 2010). While for lizards the open formations of the Cerrado have shown to be richer than forests (Colli et al., 2002; Nogueira et al., 2009), for birds and mammals, studies advocate the opposite (Silva and Bates, 2002; Camargo et al., 2018). Indeed, the relative contribution of horizontal (number of habitats) and vertical (habitat complexity) stratification for species richness and composition within and across sites and localities has not yet been properly accessed for small mammals. As known to researchers for quite some time, field research in large biomes such as the Cerrado is not geographically balanced, being largely concentrated around the core area of the biome, near Brasília, the capital of Brazil, where main university campi are located (see also Mendona et al., 2018). Research has also been in large part limited to single localities and/or habitat types, focusing on local-scale questions (e.g., Ribeiro and Marinho-Filho, 2005; Bezerra et al., 2009; Godoi et al., 2010), or varying in sampling design and effort, which compromise the strength of comparative analyses across the Cerrado (Marinho-Filho et al., 1994; Vieira and Palma, 2005; Ribeiro et al., 2020).

We conducted a field study to address these shortcomings by covering a much broader geographical extent compared to previous studies in the Cerrado biome, to assess small mammal diversity within and across distinct spatial scales. Our dataset comprises a standardized sampling effort across 45 sites and 7 localities encompassing distinct habitats and portions of the Cerrado, including its core area as well as areas nearby all adjacent biomes. We aim to verify the importance of habitat complexity and heterogeneity, large-scale environmental variables, and phylogenetic constraints, on small mammal richness, abundance, and composition within and across sites, habitats, and localities. We hypothesize that richness will vary across habitats, with forests being richer than savannas, and grasslands presenting the lowest number of species, according to the vertical complexity hypothesis (e.g., Camargo et al., 2018). We also anticipate a high species turnover across habitats, with assemblages dominated by both forest dwellers and open formation specialists, as previously found based on high habitat selectivity and distributional data

of small mammals (e.g., Carmignotto et al., 2012; Ribeiro et al., 2020). As such, richness at localities should be strongly influenced by habitat heterogeneity (McCleery et al., 2018; Loggins et al., 2019). Across localities, we expect assemblage turnover to be influenced by the distance to neighbor biomes, large-scale environmental variables, and phylogenetic constraints, as previously shown for anurans (Valdujo et al., 2012, 2013), lizards (Nogueira et al., 2009, 2011), and plants (Françoso et al., 2016, 2020). Consequently, total richness in the Cerrado should have a greater contribution from species turnover across habitats and localities than from average species richness within sites. Finally, we hypothesize that different clades, represented by lineages descended from open habitat or forest dwellers' ancestors, will present different habitat requirements, as found for lizards and birds at the Cerrado (Silva, 1995, 1997; Nogueira et al., 2009).

## MATERIALS AND METHODS

### Study Area

The Cerrado, the largest Neotropical savanna, covers an area of about 2 million km<sup>2</sup> at the center of South America (Oliveira and Marquis, 2002; Veblen et al., 2007), being limited by other dry and/or highly seasonal vegetation formations such as the Caatinga and Chaco (Prado and Gibbs, 1993). The Cerrado is also delimited by the two major South America's rainforests: the Amazonian to the north, and the Atlantic Forest in its southern and eastern limits (Ab'Saber, 1977; Hueck and Seibert, 1981; **Figure 1**). The Cerrado is characterized by a defined seasonal climate, with a wet (October to April) and a dry (May to September) season, with the former concentrating around 80–90% of annual rainfall (Coutinho, 2006). Annual precipitation varies from 1,200 to 2,300 mm, with mean annual temperature ~22°C (Nimer, 1989; Alvares et al., 2013; **Figure 1**). Major drainages cut the Cerrado across the central Brazilian plateau, where altitudes around 1,000–1,300 m dominate, descending to adjacent valleys and depressions (Parada and Andrade, 1977). The ancient plateaus, now covered by Cenozoic sediments, gave rise to sandy soil and lato soil, which are poor in nutrients and rich in minerals (Furley and Ratter, 1988).

As a biome, the Cerrado presents the development of several facies as a result of the interaction between climate, soil types, and drainage (Furley, 1999; Oliveira-Filho and Ratter, 2002). These facies represent distinct habitats that were considered in the sampling design of the study as follows: “campo úmido” (CU)—flooded grasslands; “campo limpo” (CL)—a grass-dominated habitat; “campo sujo” (CS)—open grasslands with some trees and shrubs; “campo cerrado” (CC)—shrubby vegetation with a higher density of trees and the intervening ground covered by grasses; “cerrado *sensu stricto*” (CE)—woodlands with an open canopy and some grass covering the ground; “cerrado rupestre” (RC)—woodlands at rocky landscapes; “carrasco” (CAR)—woodlands with denser understories at transitional areas with Caatinga; “cerradão” (CD)—dense woodlands with a closed canopy; GF—forest formations along watercourses; seasonal forests (SF)—forest formations usually located at hillsides; and wet gallery forests (WGF)—open-canopy forests composed of

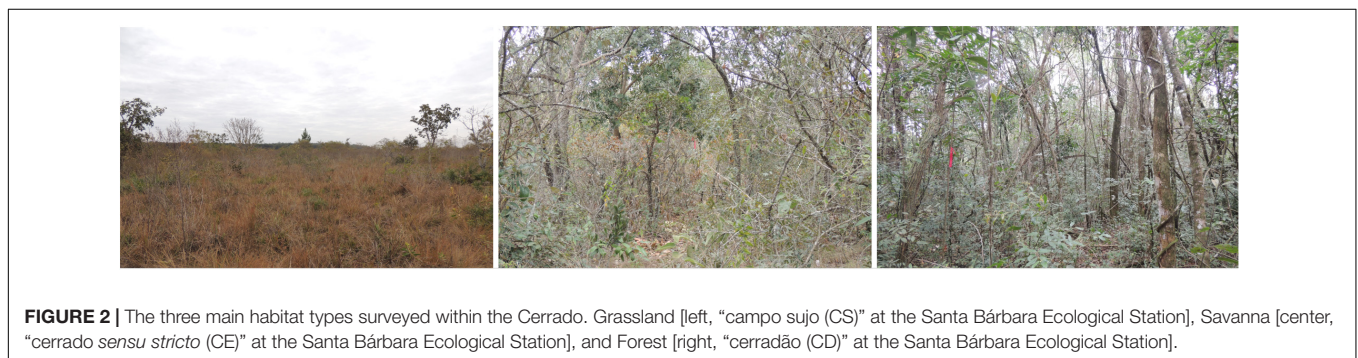
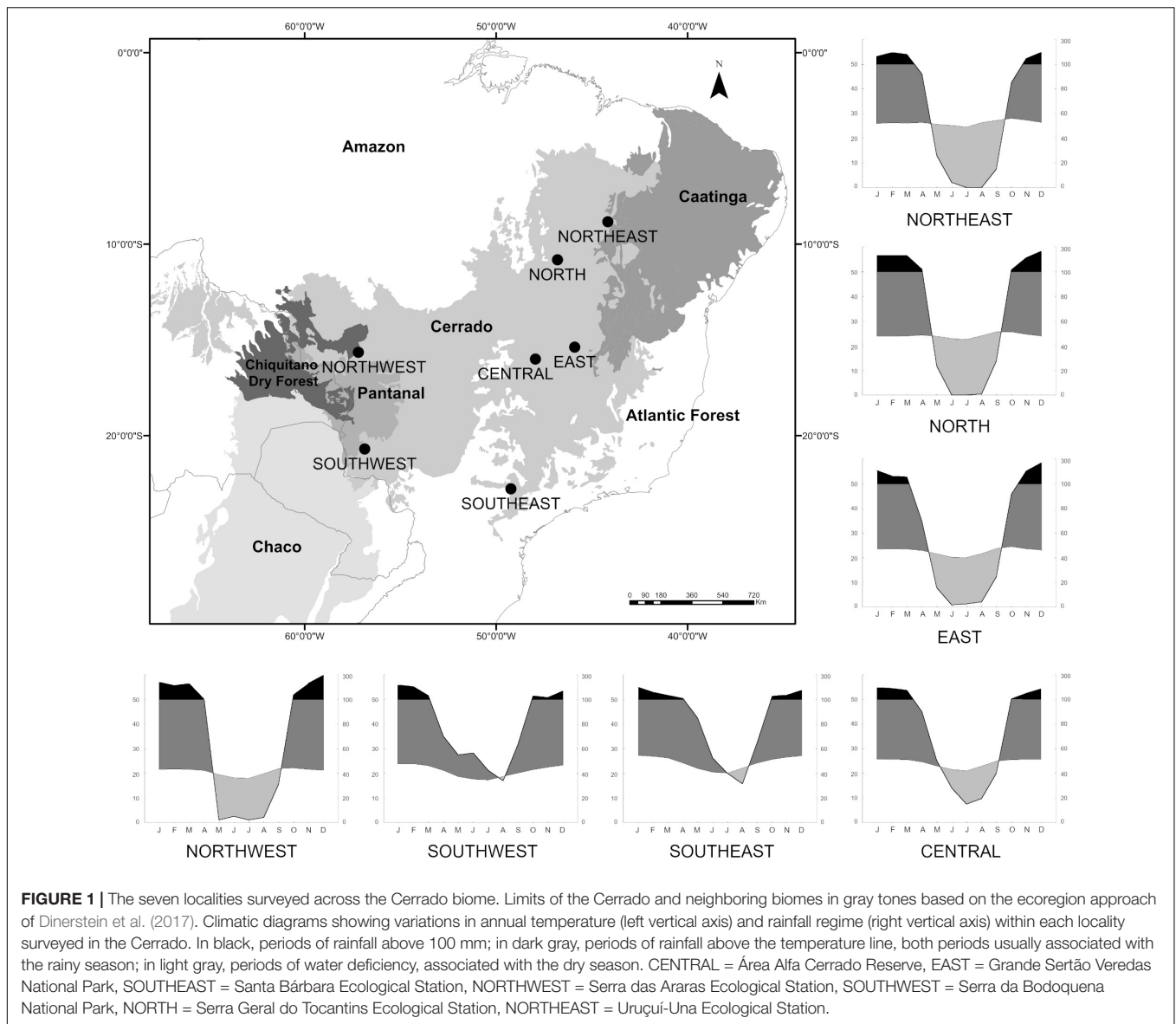
palms and trees in a water-saturated soil (Ribeiro and Walter, 1998; **Figure 2**). These habitats were also classified into the three major habitat types present in the Cerrado: grasslands—comprising the different grassland facies (CU, CL, CS, and CC); savannas—representing the woodlands (CE, RC, and CAR); and forests—all surveyed forest formations (CD, GF, SF, and WGF; **Supplementary Table 1**).

### Standardized Sampling Design

Small non-volant mammals were surveyed across seven distinct protected areas chosen across the entire range of the Cerrado and at different distances to the adjacent open or forest biomes, as follows: (1) Uruçuí-Una Ecological Station (a locality situated at northeastern Cerrado, hereafter NORTHEAST) in February/March 2000; (2) Grande Sertão Veredas National Park (a locality situated at eastern Cerrado, hereafter EAST) in October 2001; (3) Área Alfa Cerrado Reserve (a locality situated at central Cerrado, hereafter CENTRAL) in January/February 2002; (4) Serra da Bodoquena National Park (a locality situated at southwestern Cerrado, hereafter SOUTHWEST) in April 2002; (5) Serra das Araras Ecological Station (a locality situated at northwestern Cerrado, hereafter NORTHWEST) in October 2002; (6) Santa Bárbara Ecological Station (a locality situated at southeastern Cerrado, hereafter SOUTHEAST) in January/February 2003; and (7) Serra Geral do Tocantins Ecological Station (a locality situated at northern Cerrado, hereafter NORTH) in March/April 2003 (**Figure 1**). All localities were sampled for 10 consecutive days of capture during the rainy season (October to April), with ~2,000 pitfall trap (PT) nights and ~2,000 live trap (LT) nights per locality (except NORTHEAST, surveyed for 19 days, with ~3,500 PT nights and ~3,500 LT nights) (**Supplementary Table 1**). At each locality, sampling sites comprising both PTs and LTs were set at the different habitats representing the vegetation mosaic typical of the Cerrado (**Figure 2**), at least 1 km apart. All sampling sites in a given locality were distributed around a 20-km radius from a central point (usually the reserve lodge). The number of sampling sites varied from 5 to 7 per locality, according to the number of habitats available (from 4 to 7), including at least one sampling site in each major habitat type: grassland, savanna, and forest per locality (except for NORTHEAST and SOUTHWEST localities where grassland patches were not available) (**Figure 3** and **Supplementary Table 1**).

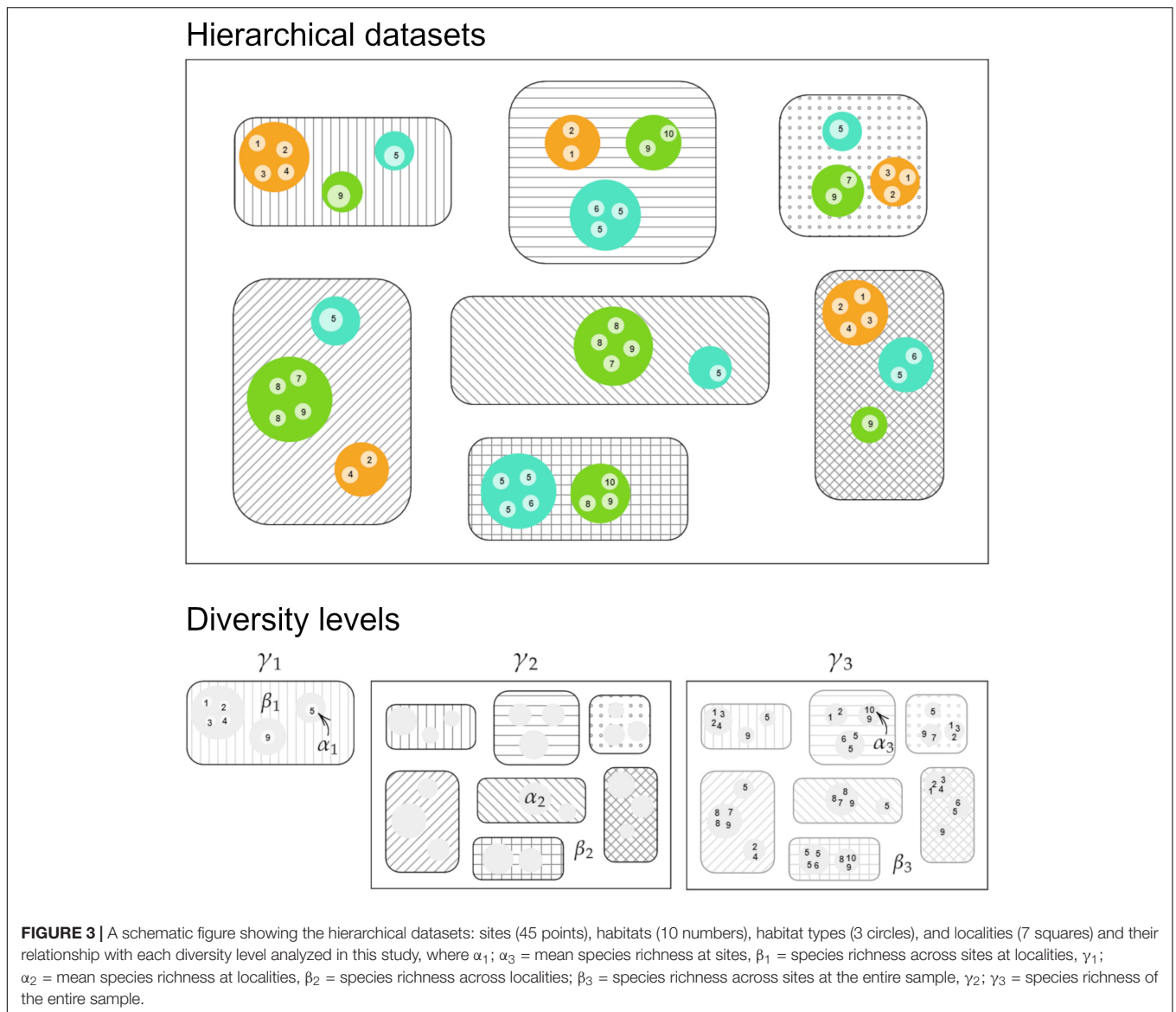
### Data Collection and Sampling Effort

Each sampling site was comprised of two transects: 40 PTs and 30–40 LTs (except at humid and rocky habitats generally surveyed only by LTs—**Supplementary Table 1**), spaced ~15 m from each other. LTs were set at the ground to ~1.5 m high, in line, with Sherman (7.5 cm × 8.5 cm × 23.0 cm; H.B. Sherman Traps, Tallahassee, FL, United States) and mesh-wire LTs (19.5 cm × 20.0 cm × 32.0 cm) interspersed (20–27 Sherman and 10–13 mesh-wire traps) and spaced 15 m from each other, comprising transects 450–600 m long, and a capture effort of ~350 trap nights (**Supplementary Table 1**). LTs were baited with a mixture of peanut butter, sardine, and ground maize, adding a slice of manioc in the mesh wire traps. PTs were set in a “Y”



configuration, with four 35-L buckets buried in the ground and connected with 50 cm high × 5 m long plastic drift fences at each capture station, with 10 stations spaced 15 m from each other, comprising a transect around 250 m long, and a capture effort of

~400 trap nights (see also Nogueira et al., 2009; **Supplementary Table 1**). PT and LT transects were checked daily. Capture effort was estimated by multiplying the total number of traps with the number of nights they remained open in the field for each



trap transect, site, habitat, and locality (**Supplementary Table 1**). A total of 45 sampling sites representing the mosaic of habitats of the Cerrado, which were classified as grasslands (15 sites), savannas (13 sites), and forests (17 sites) across the 7 localities, were surveyed, summing 15,963 PT nights and 16,121 LT nights (**Supplementary Table 1**).

Voucher specimens were deposited at the mammal collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. When capture numbers exceeded 20, individuals were temporarily marked (with non-toxic colored enamel) and released at the capture site, to identify recaptures. Additionally, tissue samples were obtained for all vouchers and preserved in the above-mentioned collection, and chromosome preparations were made in the field for most collected specimens. The capture and collection of small mammals were approved by the IBAMA (permits no. 172/99; 065/2001; 353/2001; 355/2001; 150/2002; and 002/2003), and they followed the ASM

guidelines for the use of wild mammals in research (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists, 2016). Taxonomic identifications were based on morphological, karyological, and/or molecular data. Nomenclature and classification follow Voss and Jansa (2009) for the marsupials and Patton et al. (2015) for the rodents, and also follow recently published arrangements and species descriptions (Nascimento et al., 2013; Bonvicino et al., 2014a; Hurtado and Pacheco, 2017; Weksler et al., 2017; Suárez-Villota et al., 2018; Silva et al., 2019; Brandão et al., 2021; Fegies et al., 2021).

## Data Analyses

### Taxonomic $\alpha$ -Diversity Across Scales

To evaluate sampling effort and to estimate and compare species richness across sites, habitats, and localities, we used abundance data to calculate the coverage estimator and to generate sample

size-based rarefaction and extrapolation sampling curves (Chao and Jost, 2012; Colwell et al., 2012). The coverage estimator represents the proportion of the total number of individuals in an assemblage belonging to a species represented in the sample, estimated in percentage, as a measure of completeness. We used the online iNEXT platform (Hsieh et al., 2016) with 1,000 bootstraps, considering as an endpoint setting for extrapolation curves, the double reference sample size (Chao et al., 2014), and treating the reference sample as the mean sample size for localities, as 50 individuals for sites, and as the small sample size for habitat types, to obtain extrapolated data for all samples. CIs of 95% were used as threshold in comparisons (Chao and Chiu, 2016).

iNEXT platform also estimates diversity measures based on the parameter “ $q$ ” of the Hill numbers (Hill, 1973; Jost, 2006), which takes into account species richness and relative abundance data, with increasing sensitivity for dominant species (Chiu and Chao, 2014), and are recommended for biologically interpretable comparisons among samples (Moreno et al., 2018). Thus, besides species richness ( $q = 0$ —abundance data not considered), we also estimated the Shannon–Wiener diversity index ( $q = 1$ ; the exponential of Shannon entropy—same weight for all species abundance data) and the Simpson diversity index ( $q = 2$ ; the inverse of Simpson concentration—common species more important). Species richness was compared across habitats and habitat types (grasslands, savannas, and forests) to verify the contributions of habitat diversity and complexity in assemblage’s diversity.

Species were classified by abundance data, based on Whittaker plots, as rare (summing up to 10% of total abundance), abundant (summing up to 50%), and intermediate level, and also by family, subfamily and tribe as follows: marsupials from Didelphidae family were classified into Caluromyinae and Didelphinae subfamilies, and this latter into Didelphini, Marmosini, and Thylamyini tribes; rodents from Cricetidae family into Akodontini, Oryzomyini, Phyllotini, Thomasomyini, and Wiedomyini tribes; and rodents from Echimyidae family into Eumysopinae subfamily, and Caviidae family into Caviinae subfamily.

### Taxonomic $\beta$ -Diversity Across Scales

Our dataset is hierarchical and encompasses sites ( $n = 45$ ), localities ( $n = 7$ ), habitats ( $n = 10$ : CU, CL, CS, CC, CE, RC/CAR, CD, GF, SE, and WGF), and habitat types ( $n = 3$ : grasslands, savannas, and forests; **Figure 3** and **Supplementary Table 1**). As such, we applied the additive partitioning concept of diversity:  $\gamma$ -diversity =  $\alpha$ -diversity +  $\beta$ -diversity (Loreau and Hector, 2001; Veech et al., 2002; Chao et al., 2012) to investigate the contribution of species richness ( $\alpha$ -diversity) and species turnover ( $\beta$ -diversity) across scales, i.e., within and across sites, habitats, and localities.  $\alpha$ -diversity ( $\alpha_1$ ) was treated as the mean observed and extrapolated number of species recorded in each site,  $\beta$ -diversity ( $\beta_1$ ) as the species richness found across sites (or habitats), and  $\gamma$ -diversity ( $\gamma_1$ ) as the mean number of species in a given locality.  $\alpha$ -diversity ( $\alpha_2$ ) was treated as the mean observed and extrapolated number of species recorded in each locality ( $\alpha_2 = \gamma_1$ ),  $\beta$ -diversity ( $\beta_2$ ) as the species richness

found across localities, with  $\gamma$ -diversity ( $\gamma_2$ ) as the observed and estimated number of species found in the entire sample.  $\alpha$ -diversity ( $\alpha_3$ ) was also treated as the mean observed and extrapolated number of species recorded in each site ( $\alpha_3 = \alpha_1$ ),  $\beta$ -diversity ( $\beta_3$ ) as the number of species recorded across all sites (or habitats) encompassing all localities, with  $\gamma$ -diversity ( $\gamma_3$ ) as the observed and estimated number of species found in the entire sample ( $\gamma_3 = \gamma_2$ ) (see **Figure 3**). Sample-based rarefaction and extrapolation curves for sites (or habitats) and localities were used to estimate species richness ( $q = 0$ ) across scales. Additionally, to evaluate  $\beta$ -diversity for the three main habitat types: grasslands, savannas, and forests, we also generated the curves based on species richness ( $q = 0$ ), the Shannon–Wiener ( $q = 1$ ), and Simpson ( $q = 2$ ) diversity indices considering all sites grouped by habitat type (**Figure 3**).

### Community Structure

We used non-metric multidimensional scaling (NMDS) ordination based on the Bray–Curtis similarity index (Clarke, 1993; Moreno et al., 2018) to graphically illustrate differences in community structure across sites, habitats, and localities; a Shepard plot was performed to verify the goodness of fit of the data in the NMDS analysis. The capture success for each species per site was computed as the total number of individuals divided by the capture effort and used in this analysis. Only species with at least five captures considering all sites were included, to prevent biasing the results due to a small sample size (see Linzey and Kesner, 1997; Carvalho et al., 2020). NMDS ordination was performed with the “vegan” R package (Oksanen et al., 2020), function *metaMDS*; and the Shepard plot (or stress plot) using the *stressplot* R function.

The Jaccard similarity index based on the presence/absence of data between pairwise localities was used to investigate spatial autocorrelation due to its robustness, where rare and abundant species are similarly weighted, being sensitive to species turnover in rare species and less biased regarding the presence of a few dominant species in assemblages (Moreno et al., 2018). The pairwise matrix of dissimilarity ( $1 - \text{Jaccard index}$ ) was correlated with the pairwise matrix of geographic distances (Ludwig and Reynolds, 1988; Nekola and White, 1999) *via* the Mantel test (Manly, 1994).

Previous studies have shown the influence of the biota of neighboring biomes in the formation of the species pool of the Cerrado (Valdujo et al., 2012, 2013; Françoso et al., 2016, 2020). Species currently occurring in the Cerrado, which have originated from ancestors that occupied adjacent biomes, would—through niche conservatism—be restricted to areas in the Cerrado with similar environmental conditions to those required by their ancestors, that is, similar to those found in the neighboring biomes. Environmental variables are also known to influence species turnover in animal groups in the Cerrado (Brown and Gifford, 2002 for butterflies; Nogueira et al., 2009 for lizards; and Valdujo et al., 2013 for anurans). Based on these findings, we performed Mantel tests to investigate the relationship between species composition and: (1) geographic distance to neighboring Cerrado biomes: Atlantic Forest, Amazonian Forest, Caatinga, Chaco, and Pantanal. Geographic distances, in kilometer, were

calculated in ArcMap 10.1 (Environmental Systems Research Institute [ESRI] Inc, 2012) based on the Dinerstein et al. (2017) ecoregion-based approach map for the biome limits; (2) large-scale environmental variables categorized, as follows, to homogenize the different types of variables for comparisons (McCune and Allen, 1985; Urban, 2000): (1) the length of dry season (1/2 months = 1; 3/4 months = 2; and 5 months = 3), (2) rainfall deficit (1 = 0–50 mm; 2 = 50–100 mm; 3 = 100–150 mm; 4 = 150–200 mm; and 5 = 200–250 mm), (3) annual mean temperature (1 = 20–22°C; 2 = 22–24°C; 3 = 24–26°C; and 4 = 26–28°C), (4) temperature variation between means of the hottest and coldest months (1 = 2–4°C; 2 = 4–6°C; and 3 = 6–8°C), (5) dominant habitat (1 = grasslands; 2 = savannas; and 3 = forests), (6) dominant soil type (1 = sand; 2 = lato soil; 3 = rendzine soil; and 4 = lito soil), and (7) relief (1 = smooth, 2 = mixed; and 3 = steep), and (8) altitude (1 = 0–500 m; 2 = 500–1,000 m; and 3 = >1,000 m). The chosen environmental variables were those revealed as the most significant in previous studies. Climatic data were extracted from Leemans and Cramer (1991) and were also used as the basis for the Walter's climatic diagrams (Figure 1). Geomorphological data were based on RADAMBRASIL (1982a,b,c). The environmental variable matrix was based on Euclidian relative distances (Ludwig and Reynolds, 1988; Urban, 2000). The Mantel tests were performed in PAST software (Hammer et al., 2008).

## RESULTS

We captured 792 individuals of 58 small mammals across sites, habitats, and localities in the Cerrado. PTs captured 299 individuals (38%) of 38 species (66%), while LTs captured 499 individuals (62%) of 47 species (81%) (Supplementary Table 2), highlighting the importance of using both traps in small mammal surveys: 11 species (19%) were recorded exclusively by PTs and 20 species by LTs (34%). Capture success also varied among taxonomic groups (i.e., marsupials from the Order Didelphimorphia, Family Didelphidae, and rodents from the Order Rodentia, Families Cricetidae, Caviidae, and Echimyidae). Cricetid rodents were the dominant group, with 500 (63%) individuals and 30 (52%) species, followed by didelphids, with 175 (22%) individuals and 17 (30%) species, echimyids with 113 (14%) individuals and 9 (15%) species, and cavies with 4 (1%) individuals and 2 (3%) species (Supplementary Table 2). Didelphids and cavies were mostly captured by PTs while LTs captured most cricetids and echimyids. Body size played an important role in differential capture rates, with LTs capturing, in general, larger species, such as echimyids, which were almost exclusively captured by this trap (Supplementary Table 2).

### Species Richness and Diversity Across Scales

Analyzing the 45 sampling sites, species richness varied from 2 to 11 species (mean  $\pm$  SD = 5.44  $\pm$  2.56, Table 1), with the estimated richness ranging from 2.00 to 15.71 (mean  $\pm$  SD = 7.28  $\pm$  4.02). The sample-based rarefaction and extrapolation curves showed inflection points between 20 and 40 individuals, and a high

overlap in species richness ( $q = 0$ ) were observed across sites at the seven localities (Supplementary Figure 1). There was also a great variation in the number of individuals captured per site, ranging from 2 to 65 (mean  $\pm$  SD = 17.60  $\pm$  12.81), with sampling coverage varying accordingly, from 0.00 to 1.00 (mean  $\pm$  SD = 0.82  $\pm$  0.19, Table 1). However, most sites ( $n = 38$ ; 84%) presented high levels of sampling coverage, above 0.75, evidencing that sites were properly surveyed (mean effort = 355 PT nights and 358 LT nights, Supplementary Table 1). Sites also showed a high overlap in species diversity considering both the Shannon–Wiener ( $q = 1$ ) and the Simpson diversity ( $q = 2$ ) indices (not shown), with most species represented by a few individuals—less than 10—across sites.

Grouping the 45 sites by habitat, we also observed a high overlap in the observed species richness ( $q = 0$ ), which did not increase from grasslands to forests (Figure 4A). The mean observed richness varied from 3.00  $\pm$  1.00 (in the areas of “CC”) to 6.67  $\pm$  4.51 (in the areas of “CD,” Table 1). Analyzing the sites by the three major habitat types (grasslands, savannas, and forests), they also presented similar mean observed richness (mean  $\pm$  SD = 4.53  $\pm$  2.07 for grasslands; mean  $\pm$  SD = 5.69  $\pm$  3.01, for savannas; and mean  $\pm$  SD = 6.06  $\pm$  2.51, for forests; Figure 4B). This is consistent with the results from rarefaction and extrapolation curves that show overlapping across habitats and higher mean species richness values associated with distinct habitats across localities (Supplementary Figure 1). The number of individuals was found to be higher in sites representing different habitats, such as “CL,” “CS,” “CE,” “CD,” GF, and SF, with no relationship to specific habitats (Table 1).

Sample-based rarefaction and extrapolation curves showed high richness ( $q = 0$ ) and also an overlap across habitat types, especially between grasslands (mean  $\pm$  SD = 27.73  $\pm$  6.31) and savannas (mean  $\pm$  SD = 30.48  $\pm$  5.79), with forests showing a somewhat higher richness (mean  $\pm$  SD = 39.69  $\pm$  5.74) (Supplementary Figure 2A). The results for the Shannon diversity ( $q = 1$ ), however, point savannas and forests as more diverse than grasslands, and savannas as the most diverse habitat type considering the Simpson index (Supplementary Figures 2B,C). This is consistent with the fact that grasslands were hyper dominated by one species (*Necomys lasiurus*), whereas savannas have shown the most even distribution across species (Supplementary Table 3).

While small mammal diversity greatly overlapped across sites, habitats, and habitat types, taxonomic representativeness was strongly related to habitat. Forests were dominated by oryzomyines, with echimyids and marmosines also comprising an important component of these denser habitats, while thylamyines were more associated with savannas, as well as phyllotines and wiedomyines, with akodontines predominating in grasslands (Figure 5 and Supplementary Table 3).

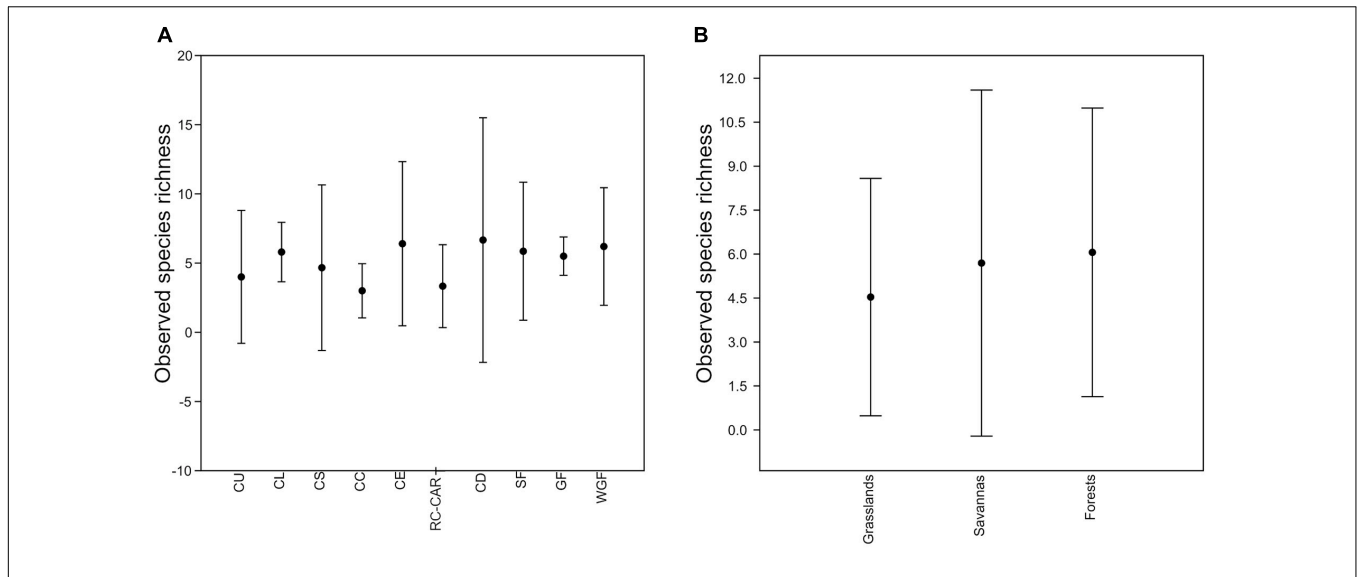
The observed species richness ( $q = 0$ ) varied from 12 to 21 species per locality (mean  $\pm$  SD = 16.00  $\pm$  3.56), with the estimated richness ranging from 13.50 to 23.92 species (mean  $\pm$  SD = 18.19  $\pm$  3.78, Table 1). The sample-based rarefaction and extrapolation curves showed inflection points between 100 and 150 individuals (Figure 6A),

**TABLE 1** | Sampling coverage (SC), sample size ( $n$ , number of individuals), and the observed species richness (SR,  $q = 0$ ), at each site, habitat, habitat type, and locality; and extrapolated SR ( $q = 0$ ), the observed Shannon index ( $q = 1$ ), and Simpson index ( $q = 2$ ) for each locality, and mean and SD for all sampled localities.

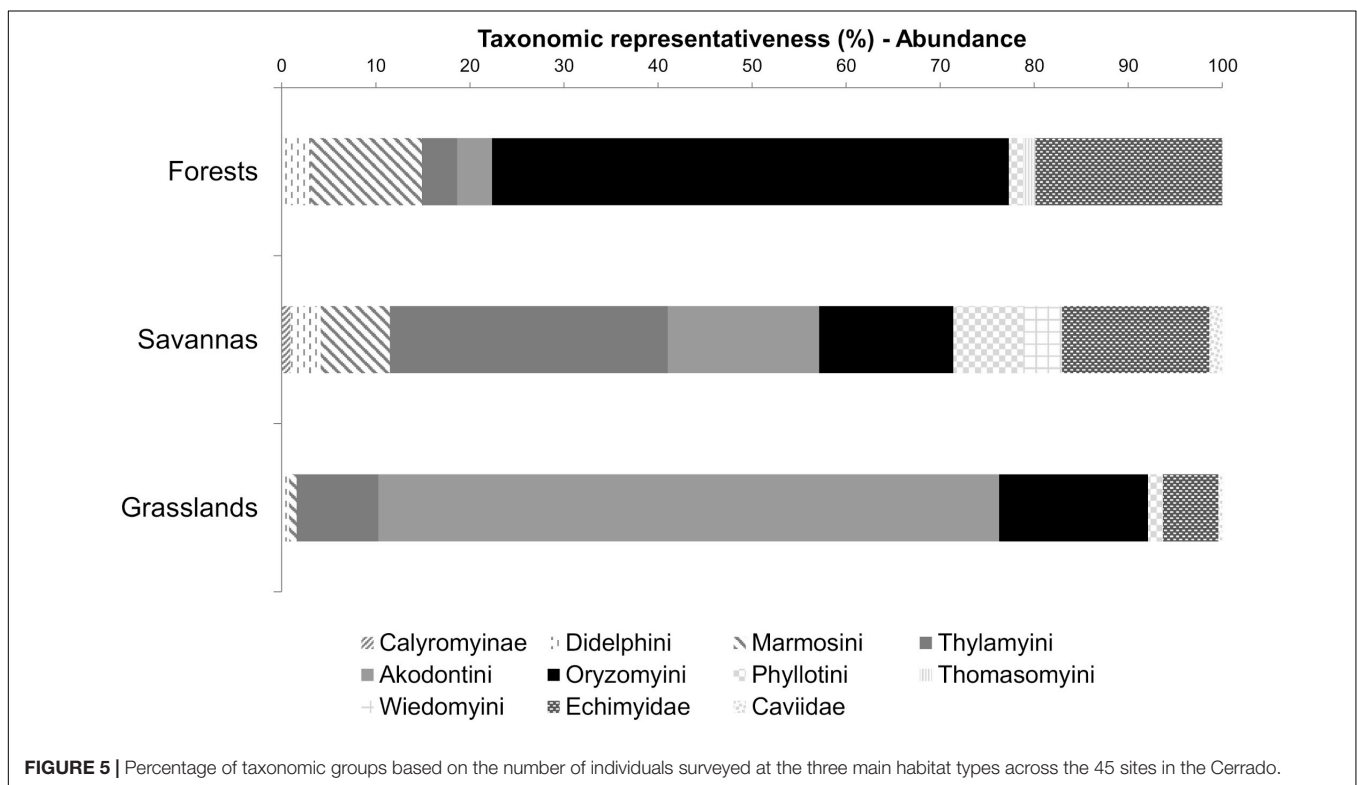
| Site       | Locality                          |               |               |               |               |                |               | Habitat        | Habitat type    | Total           |                 |
|------------|-----------------------------------|---------------|---------------|---------------|---------------|----------------|---------------|----------------|-----------------|-----------------|-----------------|
|            | CENTRAL                           | EAST          | SOUTHEAST     | NORTHWEST     | SOUTHWEST     | NORTH          | NORTHEAST     |                |                 |                 |                 |
|            | SC - N - SR                       | SC - N - SR   | SC - N - SR   | SC - N - SR   | SC - N - SR   | SC - N - SR    | SC - N - SR   |                |                 |                 |                 |
| Grasslands | Campo Úmido (CU)                  | 0.91 - 20 - 7 | 0.80 - 5 - 2  | 0.82 - 9 - 5  |               |                | 0.75 - 4 - 2  |                | 0.92 - 38 - 9   | 0.97 - 253 - 24 | 0.99 - 792 - 58 |
|            | Campo Limpo (CL)                  | 0.84 - 10 - 6 | 0.50 - 10 - 6 | 0.92 - 47 - 7 | 0.76 - 7 - 4  |                |               | 0.82 - 17 - 6  |                 | 0.88 - 91 - 19  |                 |
|            | Campo Sujo (CS)                   | 1.00 - 10 - 2 |               | 0.97 - 65 - 8 |               |                |               | 0.94 - 12 - 4  |                 | 0.99 - 87 - 10  |                 |
|            | Campo Cerrado (CC)                | 1.00 - 17 - 3 |               |               | 0.49 - 5 - 4  |                |               | 1.00 - 15 - 2  |                 | 0.92 - 37 - 8   |                 |
| Savannas   | Cerrado <i>sensu stricto</i> (CE) | 1.00 - 17 - 3 | 0.43 - 7 - 5  | 0.56 - 9 - 5  | 0.67 - 11 - 7 | 0.87 - 22 - 8  | 0.60 - 5 - 3  | 0.95 - 36 - 9  | 0.97 - 185 - 27 | 0.98 - 217 - 28 |                 |
|            | Cerrado <i>sensu stricto</i> (CE) |               | 1.00 - 14 - 3 |               |               |                |               | 0.93 - 24 - 10 |                 |                 |                 |
|            | Cerrado <i>sensu stricto</i> (CE) |               |               |               |               |                |               | 0.95 - 40 - 11 |                 |                 |                 |
|            | Rocky Cerrado (RC)                |               |               |               |               |                | 0.91 - 11 - 2 |                | 0.88 - 32 - 10  |                 |                 |
| Forests    | Carrasco (CAR)                    |               | 0.80 - 15 - 5 |               |               |                |               | 1.00 - 6 - 3   |                 |                 |                 |
|            | Cerradão (CD)                     |               |               | 0.83 - 3 - 2  | 0.95 - 38 - 7 | 0.88 - 31 - 11 |               |                | 0.93 - 72 - 17  | 0.97 - 322 - 37 |                 |
|            | Seasonal forest (SF)              |               |               |               | 1.00 - 13 - 3 | 0.91 - 33 - 9  |               | 0.76 - 11 - 6  | 0.93 - 109 - 22 |                 |                 |
|            | Seasonal forest (SF)              |               |               |               |               | 0.96 - 22 - 6  |               |                |                 |                 |                 |
|            | Babaçu forest (BF)                |               |               |               | 0.90 - 30 - 7 |                |               |                |                 |                 |                 |
|            | Gallery forest (GF)               | 0.86 - 20 - 8 | 0.87 - 14 - 5 | 0.00 - 2 - 2  | 0.91 - 9 - 4  | 0.79 - 24 - 8  | 0.79 - 14 - 5 | 0.82 - 22 - 9  | 0.88 - 105 - 27 |                 |                 |
|            | Wet Gallery forest (WGF)          |               | 0.88 - 15 - 6 |               |               |                |               | 1.00 - 21 - 5  | 0.98 - 36 - 10  |                 |                 |
| Total      | Sample coverage (SC)              | 0.98          | 0.94          | 0.99          | 0.97          | 0.97           | 0.94          | 0.99           | 0.97 - 0.02     |                 |                 |
|            | Sample size - individuals (N)     | 94            | 80            | 135           | 113           | 132            | 78            | 160            | 113.14 - 30.90  |                 |                 |
|            | Obs. Species richness ( $q = 0$ ) | 12            | 21            | 13            | 16            | 17             | 13            | 20             | 16.00 - 3.56    |                 |                 |
|            | Ext. Species richness ( $q = 0$ ) | 13.50         | 23.92         | 13.57         | 17.04         | 19.26          | 19.61         | 20.47          | 18.19 - 3.78    |                 |                 |
|            | Obs. Shannon Wiener ( $q = 1$ )   | 8.16          | 16.74         | 4.14          | 7.89          | 10.33          | 7.56          | 15.45          | 10.04 - 4.53    |                 |                 |
|            | Obs. Simpson ( $q = 2$ )          | 6.41          | 14.41         | 2.23          | 4.76          | 7.68           | 5.65          | 13.46          | 7.80 - 4.52     |                 |                 |

CENTRAL = Área Alfa Cerrado Reserve; EAST = Grande Sertão Veredas National Park; SOUTHEAST = Santa Bárbara Ecological Station; NORTHWEST = Serra das Araras Ecological Station; SOUTHWEST = Serra da Bodoquena National Park; NORTH = Serra Geral do Tocantins Ecological Station; NORTHEAST = Uruçuí-Una Ecological Station.





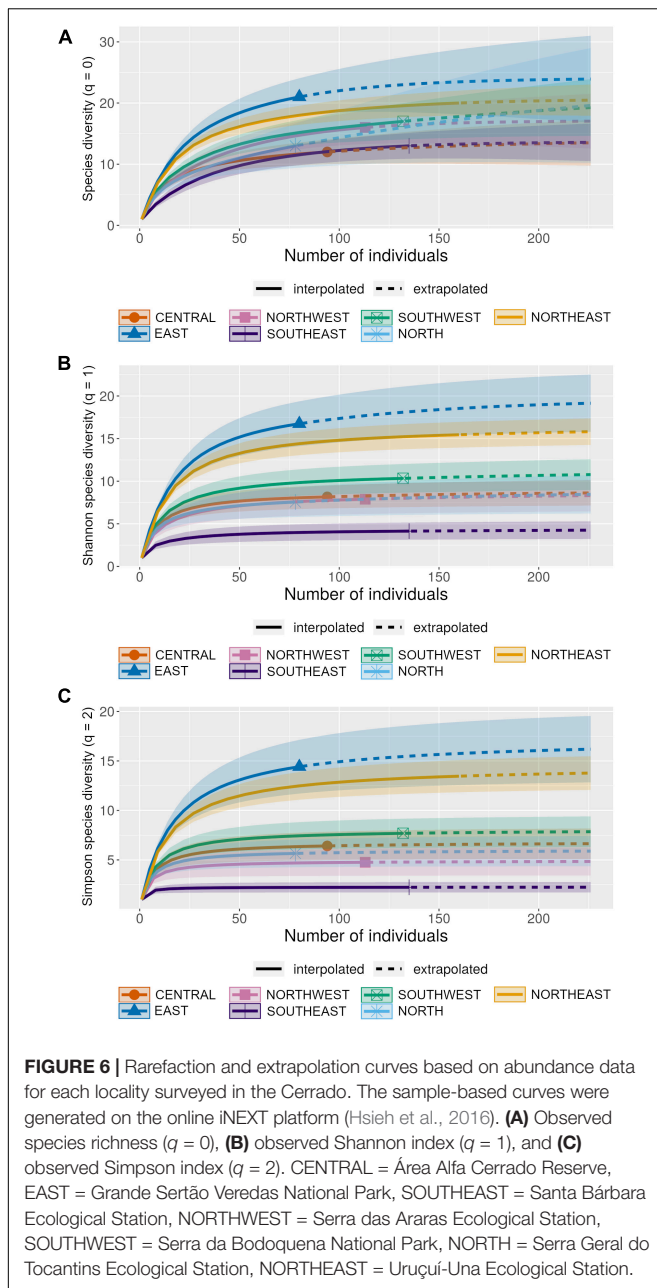
**FIGURE 4 |** Mean observed species richness across the different habitats (A) and the three main habitat types (B) based on the 45 sites surveyed within the Cerrado. Point = mean, lines = SD, CU = “campo úmido,” CL = “campo limpo,” CS = “campo sujo,” CC = “campo cerrado,” CE = “cerrado *sensu stricto*,” RC = “cerrado rupestre,” CAR = “carrasco,” CD = “cerradão,” GF = gallery forest, SF = seasonal forest, WGF = wet gallery forest.



**FIGURE 5 |** Percentage of taxonomic groups based on the number of individuals surveyed at the three main habitat types across the 45 sites in the Cerrado.

and, despite a varying number of individuals per locality (78–160, mean ± SD = 113.14 ± 30.90), all localities presented high values of sampling coverage, from 0.94 to 0.99 (mean ± SD = 0.97 ± 0.02, **Table 1**), evidencing the robustness of sampling effort (mean = 2,280 PT-nights and 2,303 LT-nights, **Supplementary Table 1**). Species richness

rarefaction and extrapolation curves showed a great overlap, varying from 10 to 31 species, and not differing significantly across localities (**Figure 6A**). However, the results from both the Shannon–Wiener ( $q = 1$ ) and the Simpson diversity ( $q = 2$ ) indices, which consider species abundance, differed across localities, being possible to identify three distinct levels of



diversity: the lowest values were found at SOUTHEAST, with four localities (NORTHWEST, NORTH, CENTRAL, and SOUTHWEST) showing intermediate diversity levels, and NORTHEAST and EAST representing the most species-rich localities (Figures 6B,C).

Relative abundance varied greatly across species, with assemblages encompassing few abundant ones (from 1 to 6 species)—summing up from 8 to 29% of individuals per locality, and several species being either in the intermediate level (from 5 to 9 species)—comprising 38 to 46% of individuals, or rare (from 4 to 7 species)—representing between 29 and 46% of individuals (Supplementary Figure 3). Indeed, only 5 species (9% of all species) were frequently captured, with more than 20 individuals

in a given locality, and most species not reached 10 individuals per locality (Supplementary Table 2). SOUTHEAST locality, the less diverse in relation to the Shannon–Wiener and Simpson indices (Figures 6B,C), also showed lower species richness and lower evenness in abundance distribution across species.

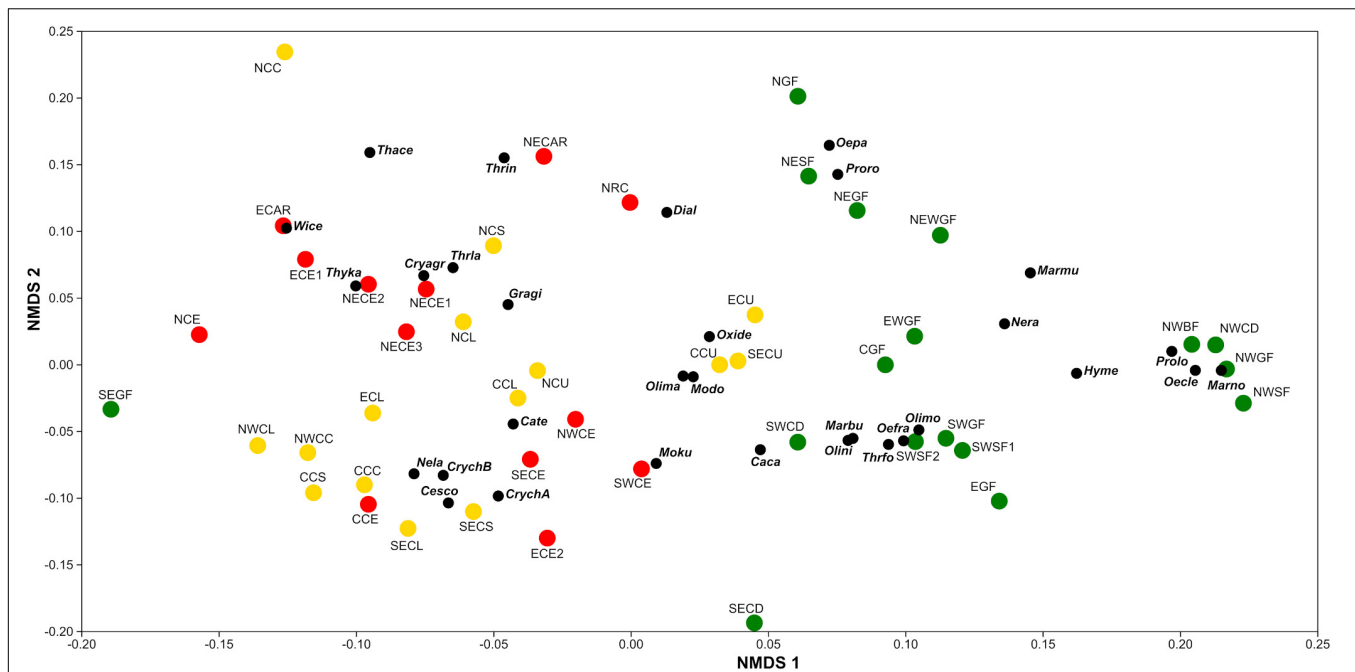
Taxonomic representativeness pointed didelphids (tribes Marmosini and Thylamyini), cricetids (tribes Akodontini, Oryzomyini, and Phyllotini), and echimyids (subfamily Eumysopinae) as the most representative groups. However, the importance of each group varied across localities (Supplementary Figure 4). While oryzomyines dominated in the number of species and individuals in most localities, akodontines were the major group in abundance in SOUTHEAST and NORTH. Echimyids, usually representing around 5–20% of species richness and abundance, summed 33% of NORTH individuals. Among didelphids, thylamyines were the most important group, but marmosines also contributed in NORTHWEST and SOUTHWEST. At NORTHEAST, for instance, didelphids represented 50% of all individuals. The two richest localities, EAST and NORTHEAST (Figures 6A–C), were also the ones with the highest taxonomic diversity, represented by 8 and 10 distinct taxonomic groups, respectively (Supplementary Figure 4).

## Contributions of $\alpha$ - and $\beta$ -Diversity Across Scales

Observed and estimated mean  $\alpha_1$ -diversity (at sites; varying from 2 to 11 species) represented a small portion (34–40%) of  $\gamma_1$ -diversity (at localities; varying from 12 to 21 species), with  $\beta_1$ -diversity (the species turnover across sites or habitats) mostly contributing (66–60%) (Supplementary Figure 5). Considering the entire sample for the Cerrado ( $\gamma_{2,3}$ -diversity; 58 species), the importance of  $\beta_2$ -diversity (72.4–70.9%—species turnover across localities) and  $\beta_3$ -diversity (90.6–88.4%—species turnover across habitats and localities, all sites) was even greater compared to  $\alpha_2$ -diversity (27.6–29.1%—species richness per locality) and  $\alpha_3$ -diversity (9.4–11.6%—species richness per site; Supplementary Figure 5).

## Community Structure

The NMDS analysis (stress = 0.15; see also the Shepard plot in Supplementary Figure 6) based on the Bray–Curtis similarity index shows distinct small mammal assemblages across sites, habitats, and localities. Considering only species with at least five captures during this study ( $n = 31$ ; 53%), we found two major clusters, with all forests (except SOUTHEAST GF) segregated from grasslands and savannas (Figure 7). This community structure—of forest vs. open habitat—was observed across all seven localities. Community structure also differed within major habitat types, with the areas of “CU” clustering together irrespective of the locality, and the areas of dry grasslands being more similar to each other than with the areas of savannas, whereas savannas presented distinct community structures—two distinct clusters—evidencing a marked regionalization across savannas (Figure 7). This is consistent with a strong species turnover across localities ( $\beta_2$ ; Supplementary Figure 5), which



**FIGURE 7 |** A non-metric multidimensional scaling (NMDS) ordination plot based on a Bray–Curtis similarity matrix, considering the capture success of species with at least five captures across the 45 sites surveyed in the Cerrado. Sites in color, with forests represented by green circles, savannas by red circles, and grasslands by yellow circles. Black circles represent the species. Site acronyms are the junctions of localities and habitats, as follows: CENTRAL (C) = Área Alfa Cerrado Reserve, EAST (E) = Grande Sertão Veredas National Park, SOUTHEAST (SE) = Santa Bárbara Ecological Station, NORTHWEST (NW) = Serra das Araras Ecological Station, SOUTHWEST (SW) = Serra da Bodoquena National Park, NORTH (N) = Serra Geral do Tocantins Ecological Station, NORTHEAST (NE) = Uruçuí-Una Ecological Station, CU = “campo úmido,” CL = “campo limpo,” CS = “campo sujo,” CC = “campo cerrado,” CE = “cerrado *sensu stricto*,” RC = “cerrado rupestre,” CAR = “carrasco,” CD = “cerradão,” GF = gallery forest, SF = seasonal forest, WGF = wet gallery forest, Species acronyms: Caca = *Calomys callosus*, Cate = *Calomys tener*, Cesco = *Cerradomys scotti*, Cryagr = *Cryptonanus agricolai* A, CrychA = *Cryptonanus chacoensis* A, CrychB = *Cryptonanus chacoensis* B, Dial = *Didelphis albiventris*, Gragi = *Gracilinanus agilis*, Hyme = *Hylaeamys megacephalus*, Marbu = *Marmosa budini*, Marmo = *Marmosops noctivagus*, Modo = *Monodelphis domestica*, Moku = *Monodelphis kunsii*, Nela = *Necomys lasiurus*, Nera = *Necomys rattus*, Oecle = *Oecomys cleberi*, Oefra = *Oecomys franciscorum*, Oepa = *Oecomys paricola*, Olima = *Oligoryzomys mottogrossae*, Olimo = *Oligoryzomys moojeni*, Olini = *Oligoryzomys nigripes*, Oxide = *Oxymycterus delator*, Prolo = *Proechimys longicaudatus*, Proro = *Proechimys roberti*, Thace = *Thalpomys cerradensis*, Thrla = *Thrichomys cf. laurentius*, Thrfo = *Thrichomys fosteri*, Thrin = *Thrichomys inermis*, Thyka = *Thylamys karimii*, Wice = *Wiedomys cerradensis*.

is also pointed by the rarefaction and extrapolation curves of the three major habitat types (Supplementary Figure 2).

Assemblages were characterized by high habitat selectivity, with 14 species associated to forests, and 17 species mostly occurring on grasslands and savannas. Among the first group, there are species clearly associated with different portions of the Cerrado, with species from NORTHWEST clustering together and apart from others (e.g., *Marmosops noctivagus*, *Oecomys cleberi*, and *Proechimys longicaudatus*), in the same manner as those from SOUTHWEST (e.g., *Marmosa budini*, *Oecomys franciscorum*, and *Thrichomys fosteri*), and those from NORTHEAST and EAST (e.g., *Oecomys paricola* and *Proechimys roberti*), demonstrating high regionalization also across forests. *Oxymycterus delator* and *Oligoryzomys mottogrossae* showed a strong relationship with “CU” while others were more associated to dry grasslands (e.g., *Cryptonanus chacoensis* B, *N. lasiurus*, and *Cerradomys scotti*), and to savannas (e.g., *Cryptonanus agricolai* A, *Thylamys karimii*, and *Thrichomys cf. laurentius*). Distinct species composition was also found across localities, with NORTH, NORTHEAST, and EAST (e.g., *Thalpomys cerradensis*, *Wiedomys cerradensis*, and *Thrichomys inermis*)

segregating from NORTHWEST, SOUTHWEST, and CENTRAL (e.g., *C. chacoensis* A, *Monodelphis kunsii*, and *Calomys tener*; Figure 7), reinforcing the species turnover pattern found in open habitats as well.

All taxonomic groups (didelphids, cricetids, and echimyids) showed similar patterns of habitat selectivity, with species segregation between forest and open habitats (Figure 7). Yet, thylamyines among didelphids, and wiedomyines and akodontines among rodents, were mostly associated with savannas and grasslands, respectively, as was also pointed by taxonomic representativeness in the three major habitat types (Figure 5).

The Jaccard similarity index based on the presence/absence of species between localities showed low values in most pairwise comparisons (Supplementary Table 4). These results point to distinct assemblages across the Cerrado, characterized by several exclusive species in a given locality (Supplementary Table 2). Despite a significant spatial correlation (Mantel test,  $r = 0.467$ ,  $t = 1.988$ ,  $p = 0.047$ ), geographic distance between localities explained a small portion of the variation in species composition ( $R^2 = 0.218$ ; Supplementary Figure 7). The correlation between

composition similarity and the distance to adjacent biomes was also significant (Mantel test,  $r = 0.557$ ,  $t = 2.350$ ,  $p = 0.019$ ), pointing the importance of geographic location and the influence of neighbor biomes for Cerrado small mammal composition ( $R^2 = 0.314$ ). Large-scale environmental variables, however, showed no correlation with the composition similarity (Mantel test,  $r = 0.365$ ,  $t = 1.852$ ,  $p = 0.064$ ). Although environmentally similar localities, such as NORTHWEST and NORTH, were more similar regarding species composition, CENTRAL and SOUTHEAST represent very distinct environments but presented quite similar faunas (Figure 1 and Supplementary Tables 4, 5).

## DISCUSSION

### Species Richness and Diversity Across Scales

Species richness in the 45 sites (2–11, mean = 5.44) was very similar to the results reported by Vieira and Palma (2005; 2–10, mode = 5) in a study compiling 82 sites (the capture effort of at least 500 LT nights and 10 individuals) and by Mendonça et al. (2018; 1–26 species, mean = 5.82) in a literature review encompassing 446 sites. Although highly variable,  $\alpha$ -diversity at sites ( $\alpha_1$ ) has been properly assessed in most studies (e.g., Cáceres et al., 2010, 2011a; Bonvicino et al., 2012; Carmignotto et al., 2014; Gomes et al., 2015), contributing to the species richness found across habitats and localities at the Cerrado, as discussed below.

In relation to the habitat mosaic, however, we found unexpected results: similar species richness across habitats. According to the vertical complexity hypothesis, richness would vary across habitats, with forests being richer than savannas, and grasslands presenting the lowest number of species (e.g., Redford and Fonseca, 1986; Johnson et al., 1999; Hannibal and Cáceres, 2010). Although some authors have found similar species richness across habitats in a given locality (Bonvicino et al., 2005; Bezerra et al., 2009; Carmignotto and Aires, 2011), a positive relationship between habitat complexity and richness was mostly observed, with higher values associated to forests (Marinho-Filho et al., 1994; Vieira and Palma, 2005; Godoi et al., 2010; Santos-Filho et al., 2012; Gomes et al., 2015). Because savannas and forests are the best sampled habitats across the Cerrado (Mendonça et al., 2018), one explanation could be related to a sampling bias toward more forest habitat types, with grasslands being neglected in most studies and potentially influencing previous results. In fact, we obtained high richness for both forest and open habitats across sites and localities, indicating that horizontal heterogeneity is as important as vertical stratification for small mammal assemblages, as emphasized for other tropical savannas at both local and landscape scales (Price et al., 2010; Nyirenda et al., 2020).

At localities, sampling methodology and taxonomic resolution might explain the higher richness associated to forests found in previous studies. The survey of a significant portion of species by PTs here, including several open-habitat specialists (e.g., *Cryptonanus* spp., *M. kunsi*, and *Microakodontomys transitorius*), may explain the lower richness found in grasslands and savannas

in studies not using this methodology. Also, some open-habitat taxa have been recently reviewed, evidencing sympatric species at the Cerrado (e.g., *Cerradomys*; Percequillo et al., 2008; Bonvicino et al., 2014a), as well as sympatric and morphologically cryptic species, identified by karyotype and/or molecular data (e.g., *Cryptonanus* and *Oligoryzomys*; Weksler et al., 2017; Fegies et al., 2021), revealing a hidden diversity for these groups, and increasing species richness at open habitats.

Moreover, the sampling methodology currently used was designed to capture terrestrial and scansorial species. Thus, similar to the relevance of using intense sampling effort and complementary trap types to effectively characterize the number of species in the Cerrado habitat mosaic (up to 7–11 species per site; Ribeiro and Marinho-Filho, 2005; Bezerra et al., 2009; Carmignotto et al., 2014), sampling the canopy should also increase species richness in forests (Camargo et al., 2018). In fact, arboreal marsupials (e.g., *Caluromys lanatus* and *C. philander*) and rodents (e.g., *Phyllomys centralis*) were not or rarely captured in our study, suggesting that these species are exclusively or mostly captured using traps set in the canopy (Hannibal and Cáceres, 2010; Machado et al., 2018).

Although less studied, fine-scale habitat variables (e.g., grass cover, canopy cover, number of termite mounds, and soil type) might also be related with Cerrado small mammal richness and abundance patterns at local scale (Vieira et al., 2005; Rocha C. R. et al., 2011; Furtado et al., 2021). Vegetation structure was shown to influence savanna vertebrate diversity, especially by altering the availability of food resources, refuge sites, presence of competitors, and/or predators, as well as their dispersal capacity (Kutt and Woinarski, 2007; Price et al., 2010; Sirami and Monadjem, 2012; Ribeiro et al., 2019). Such microhabitat selectivity, not measured in this study, may also contribute to the understanding of the great variation in abundance observed here across sites (2–65 individuals).

Species richness, in a similar manner as found across sites and habitats, overlapped across localities. This is the first study to analyze this variable in a standardized way, evidencing rich small mammal assemblages throughout the Cerrado, reinforcing the high richness previously found in independent surveys at different portions of the biome (12–24 species; e.g., Bonvicino et al., 2005, 2012, 2014b; Cáceres et al., 2007, 2011a; Bezerra et al., 2009; Pereira and Geise, 2009; Carmignotto and Aires, 2011; Rocha R. G. et al., 2011, 2014; Santos-Filho et al., 2012; Carmignotto et al., 2014; Gomes et al., 2015; Carmignotto, 2019; Ribeiro et al., 2020). Long-term inventories comprising the wet and dry seasons typical of the Cerrado may also yield a higher number of individuals and species, especially considering naturally rare species (e.g., 1–4 individuals across localities), and those that present a great variation in abundance between seasons (Bonvicino et al., 2014b; Gomes et al., 2015; Rocha et al., 2017; Ribeiro et al., 2019). In fact, higher sampling effort in the NORTH raised the previous species richness to 23 (Carmignotto and Aires, 2011), and the same was found for NORTHWEST (21 species; Santos-Filho et al., 2012); SOUTHEAST (18 species; Furtado et al., 2021), and CENTRAL (16 species; Carmignotto, 2005). These studies extrapolated the expected richness for these localities, and suggest that richer assemblages, around

18–24 species—as estimated here—are the rule for Cerrado. Similar results were obtained in standardized surveys for other terrestrial vertebrates, such as squamates and anurans (Nogueira et al., 2009; Valdujo et al., 2013), evidencing the high richness across this Neotropical savanna, and highlighting that the Cerrado is still a poorly sampled biome, with a few localities properly surveyed.

As hypothesized, richness at localities was strongly influenced by habitat heterogeneity, as advanced for other tropical savannas (McCleery et al., 2018; Loggins et al., 2019). The high number of habitats here surveyed (5–7) including at least one major habitat type (grasslands, savannas, and forests) represented well both the horizontal and vertical stratification at landscapes, and therefore, assemblages' species richness. These results point to the importance not only of sampling methodology and capture effort, but also of sampling coverage, where the survey of multiple and distinct habitats plays a major role in species richness completeness (e.g., Nogueira et al., 2009; Price et al., 2010).

The Shannon and Simpson indices, on the other hand, showed that species richness together with evenness varied, with five of the seven localities presenting lower diversity indices, associated with lower species richness and a high number of individuals of few species (e.g., SOUTHEAST characterized by hyper dominance of one species, *N. lasiurus*). These results are in accordance with the abundance pattern of Cerrado assemblages, composed of a few abundant and several intermediate and rare species (Marinho-Filho et al., 1994; Mares and Ernest, 1995; Carmignotto et al., 2014). In fact, most species were represented by a few individuals, with only *N. lasiurus*—the most common species recorded in the Cerrado (Mendonça et al., 2018)—and *Hylaeamys megalcephalus*, surpassing 35 individuals across localities. Although local abundance is related to distributional range (Vieira and Palma, 2005; Mendonça et al., 2018), and several locally abundant species in our study are widely distributed in the Cerrado (e.g., *Oligoryzomys nigripes*, *C. scotti*, and *T. cerradensis*), some species with restricted ranges (e.g., *T. fosteri*, *P. roberti*, and *T. inermis*) were also locally common.

Taxonomic representativeness varied across localities, but in general, cricetids dominated, followed by didelphids and echimyid rodents (Vieira and Palma, 2005; Carmignotto et al., 2012; Mendonça et al., 2018). In our study, however, didelphids were an important component of most assemblages both in terms of species richness (19–35%) and abundance (15–48%), suggesting that differences in sampling methodology, especially the use of PTs, uncovered more robust diversity patterns for this group and, consequently, for assemblages. In fact, PTs provided a higher number of individuals and species not only for didelphids but also for some small cricetids (e.g., *Microakodontomys*, *Oligoryzomys*, and *Calomys*) in comparison with LTs, including species exclusively recorded using this method (*M. kunsii*, three *Cryptonanus* species, *Pseudoryzomys simplex*, and *Cavia aperea*; see also Cáceres et al., 2011b; Ribeiro-Júnior et al., 2011). These results evidence that sampling methodology can also compromise the diversity patterns uncovered for small mammals as a substantial portion of individuals, and species, are exclusively caught by either live or PTs (e.g., Umetsu et al., 2006; Ardente et al., 2017; Bovendorp et al., 2017).

At the tribal level, we observed a strong relationship between landscape context—represented by the most common habitats in each locality—and taxonomic representativeness (see habitat selectivity mentioned below), attesting distinct habitat requirements by small mammal lineages, as hypothesized here and previously documented for birds (Silva, 1995, 1997) and lizards (Nogueira et al., 2009). Such groups represent distantly related lineages (distinct orders, in the case of marsupials and rodents; distinct families in the case of cricetids and echimyids; and even the tribes within each subfamily are not sister lineages) with very distinct biogeographical histories (e.g., Jansa et al., 2014; Steppan and Schenk, 2017; Courcelle et al., 2019; Percequillo et al., 2021), evidencing the importance of phylogenetic constraints shaping Cerrado small mammal current diversity (Carmignotto et al., 2012).

## Contributions of $\alpha$ - and $\beta$ -Diversity Across Scales

Because this is the first study on small mammals to apply standardized sampling across sites, habitats, and localities throughout the Cerrado, one important contribution concerns the critical relevance of species turnover—across scales—in shaping small mammal diversity in this biome. Although Cerrado harbors high  $\alpha$ -diversity at sites ( $\alpha_1 = 40\%$ ;  $\alpha_3 = 10\%$ ) and at localities ( $\alpha_2 = 30\%$ ),  $\beta$ -diversity across habitats ( $\beta_1 = 60\%$ ), and particularly across localities ( $\beta_2 = 70\%$ ), and across both habitats and localities ( $\beta_3 = 90\%$ ) represent most part of the diversity through all analyzed scales. Hence, as anticipated, total richness in the Cerrado has a greater contribution from species turnover across habitats and localities than from average species richness within sites.

Ribeiro et al. (2020), partitioning the two components of  $\beta$ -diversity, found that species replacement is much more important than nestedness, reinforcing species turnover and not the net gain or loss of species as a major driver of Cerrado small mammal diversity. A few small mammal studies assessing  $\beta$ -diversity have suggested savannas and forests as the habitats concentrating a higher variation across sites (Marinho-Filho et al., 1994; Vieira and Palma, 2005; Ribeiro et al., 2020). Despite not statistically different, we have also found mean higher richness for forests, evidencing a high species turnover within this habitat type across the Cerrado, mainly represented by restricted-range shared species with the neighboring forest biomes, as observed for plants and other vertebrates (e.g., Silva, 1997; Valdujo et al., 2012; Françoiso et al., 2016). However, we also found high and similar richness for grasslands and savannas, stressing the importance of species turnover across these open habitats as well, mostly represented by restricted-range endemic species and species shared with adjacent open biomes (e.g., Nogueira et al., 2011; Valdujo et al., 2013), emphasizing the importance of all three major Cerrado habitat types for small mammals regional species pool.

High species richness obtained by summing the 45 sites in our study (representing  $\sim 11\%$  of the total effort reported for the Cerrado by Mendonça et al., 2018) represents 51% of the total richness obtained by these authors for GF, 47% for typical savanna ("CE"), and 36% for wet grasslands ("CU"), evidencing the

spatially concentrated nature of Cerrado inventories performed so far, which did not properly access the high  $\beta$ -diversity, which is proving to be typical of the biome (Nogueira et al., 2011; Valdujo et al., 2013; Franoso et al., 2020; Ribeiro et al., 2020). In fact, 113 native small mammals were recorded along the 446 sites in the review of Mendona et al. (2018), and 58 species were recorded in our study, reinforcing the distinctiveness among species composition we found across localities. Indeed, biogeographic regions based on differential plant and invertebrate and vertebrate community composition were previously proposed (Silva, 1995; Ratter et al., 1996, 2003; Brown and Gifford, 2002; Azevedo et al., 2016; Franoso et al., 2016, 2020; Amaral et al., 2017), stressing the importance of  $\beta$ -diversity in structuring plant and animal assemblages across the Cerrado.

## Community Structure

As expected, a high species turnover across habitats can be associated with the strong habitat selectivity, with most species segregating between forest and open habitats (e.g., Bonvicino et al., 1996, 2005; Lacher and Alho, 2001; Santos-Filho et al., 2012; Ribeiro et al., 2020). Although didelphids have been often associated to forests (Vieira and Palma, 2005; Santos-Filho et al., 2012; Mendona et al., 2018), we observed genera among marmosines (*Monodelphis*) and thylamyines (*Cryptonanus* and *Thylamys*) strongly associated with savannas and grasslands. This habitat dichotomy was also evident among oryzomyines, with *Hylaeamys*, *Oecomys*, *Nectomys*, and some *Oligoryzomys* species preferring forests while *C. scotti* and *O. mattogrossae* selected open habitats; among phyllotines, with *Calomys callosus* more frequently captured at forests and savannas, and *C. tener* at grasslands and savannas; and among echimyids, with *Proechimys* associated with forests and *Thrichomys* with open habitats. Akodontines and wiedomyines, on the other hand, preferred open formations. A strong historical component is the most likely explanation to this pattern as habitat preferences are related to the evolutionary history of lineages (Silva, 1997; Azevedo et al., 2016; Fenker et al., 2020). Carmignotto et al. (2012) have already advanced the composite nature of Cerrado endemic mammals, with lineages dispersed and diversified into the Cerrado descending from neighboring forest biomes (Amazonian or Atlantic Forests), where they occupy forests (e.g., niche conservatism, the colonization of similar habitats) or open habitats (e.g., ecological opportunity, the colonization of distinct habitats; see Lv et al., 2016), and those descended from adjacent open biomes (Caatinga, Chaco, or Seasonally Dry Forests) maintaining their specialized open-habitat preferences (e.g., niche conservatism). New data on systematics and biogeography of these lineages demonstrate the complex evolutionary history of Cerrado small mammals, presenting a remarkable heterogeneous diversification across landscapes and time periods, with ancient lineages associated with both forest and open formation ancestors, as well as recent diversification events occurring throughout the open and forest Cerrado habitats (Giarla and Jansa, 2014; Pavan et al., 2016; Courcelle et al., 2019; Fegies et al., 2021; Percequillo et al., 2021; Prado et al., 2021; Saldanha and Rossi, 2021).

Our study revealed that the distance between localities explained, in part, the dissimilarity in composition found across localities (see also Marinho-Filho et al., 1994; Vieira and Palma, 2005; Nogueira et al., 2009; Coelho et al., 2018), while the distance to adjacent biomes better contributed, as hypothesized. The influence of the distance to neighboring biomes in shaping regional species pools was shown to be mostly based on evolutionary constraints as several taxa colonized the Cerrado in areas similar to or nearby their ancestors' range (e.g., niche conservatism; see Wiens and Graham, 2005), evidencing the importance of the historical component for anurans (Valdujo et al., 2012, 2013), squamates (Nogueira et al., 2009, 2011), birds (Silva, 1996, 1997; Silva and Bates, 2002) and now, small mammal assemblage composition. Although environmental correlates, mainly represented by rainfall gradient and topography, also constitute important determinants for species richness and turnover across savannas (Owen, 2013; Radford et al., 2014; Rugemalila et al., 2016), large-scale environmental variables tested here were not significantly related with composition dissimilarity. This result, contrary to our expectations, was also found by other authors working with Cerrado small mammals, leading them to consider local-scale processes, such as habitat selectivity and limited dispersal, as more important factors for species sorting in the Cerrado (e.g., Ribeiro et al., 2020). Our standardized surveys, however, have shown similar species richness patterns across sites, habitats, and localities, with a greater contribution given by species turnover across habitats, but especially across localities, evidencing the importance of large-scale evolutionary processes on local species composition (see Wiens and Graham, 2005). Given the fact that several organisms with very distinct ecological requirements (e.g., plants, anurans, squamates, and birds) present similar patterns across the Cerrado, we may agree with the authors who suggest the influence of large-scale historical, biogeographical processes, as the main drivers of Cerrado diversity (e.g., Nogueira et al., 2009; Fenker et al., 2020).

## CONCLUSION

Based on standardized surveys, we evidenced that habitat heterogeneity is a major determinant of small mammal species richness at multiple spatial scales here analyzed, pointing to a general pattern across tropical savannas. We also found high  $\beta$ -diversity across habitats and localities, emphasizing a greater contribution of species turnover in structuring small mammal communities across the biome. The replacement of open-area specialists as well as forest dwellers across localities throughout the Cerrado highlights the importance of evolutionary constraints shaping small mammal communities, revealing the complex and distinct history of this Neotropical savanna. Summing to similar results found for other animals and plants at the Cerrado, our study contributes to the understanding of the biogeographic history of the biome, evidencing the need to preserve the habitat mosaic typical of the Cerrado landscapes, as well as different portions of the biome to properly preserve the

diversity of small mammals at this Neotropical savanna. Taken the fact that almost 50% of the biome has been lost or converted into agriculture and pasture in the last decades, the continuing rate of landscape change, and a few conservation units across the biome (Beuchle et al., 2015; Françoso et al., 2015; Strassburg et al., 2017; Alencar et al., 2020), it is urgent to implement new conservation units at different portions of the Cerrado.

Inventories based on standardized sampling design and high capture effort, with the use of complementary sampling methodologies in poorly surveyed areas, are highly recommended [e.g., central and eastern Mato Grosso (Brandão et al., 2019); southeastern and western Goiás (Hannibal et al., 2021); central Minas Gerais and eastern Mato Grosso do Sul (Mendonça et al., 2018)], as shown here, to provide robust datasets and increased knowledge on species diversity and distribution in the biome. The collection of vouchers and tissue samples, as well as karyotype data from the surveyed small mammals, is the basis for the description of new taxa (e.g., Bonvicino et al., 2014a; Brandão et al., 2021). Indeed, improvements on the systematics of several genera have contributed with the high richness found in open habitats, as well the high  $\beta$ -diversity found across localities, as previously widely distributed taxa are currently represented by distinct restricted-range species [e.g., former concepts of *Oligoryzomys fornesi* (Wekslers and Bonvicino, 2005, 2015); *Oryzomys subflavus* (Percequillo et al., 2008); *Thrichomys apereoides* (Nascimento et al., 2013); and *Micoureus demerarae* (Silva et al., 2019)]. This diversity will also continue to increase based on recent findings of cryptic lineages in didelphid and cricetid genera (e.g., Suárez-Villota et al., 2018; Fegies et al., 2021; Prado et al., 2021), reinforcing the existence of yet higher taxonomic richness than have been recorded so far in the Cerrado.

## DATA AVAILABILITY STATEMENT

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

## ETHICS STATEMENT

Ethical review and approval were not required for this animal study because during the time the research was conducted, in the years of 2000–2003, the animal ethics committees were being implemented at the universities, and the current laws regulating this type of research, with wild animals, followed by the committees (CEUAs – Federal law 11.794/2008 and State law 11.977/2009), are not yet in effect.

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## AUTHOR CONTRIBUTIONS

AC collected and analyzed the data and wrote the initial draft of the manuscript. All authors helped to design the study, made a critical contribution to the data analysis and manuscript writing and review, and gave final approval for submission.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.739919/full#supplementary-material>

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