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Drivers of small-mammal community structure in tropical savannas

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Drivers of small-mammal community structure in tropical savannas

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Editorial: Drivers of small-mammal community structure in tropical savannas

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Editorial on the Research Topic
Drivers of small-mammal community structure in tropical savannas

Background

Tropical and subtropical savanna ecosystems (TSE; Figure 1) contribute ∼30% of terrestrial primary productivity globally (Grace et al., 2006), while covering 20% of the land area of the Neotropics, sub-Saharan Africa, southern Asia, and northern Australia (Bond, 2016). The tremendous productivity of intact TSE is consumed by—among others—a diverse mammalian fauna of small herbivores and omnivores and both native and domestic large herbivores. Much of it, though, is pre-emptively consumed by fire. Large fires are conspicuously concentrated in regions of TSE, particularly sub-Saharan Africa, the Cerrado of Brazil, and northern Australia (Giglio et al., 2021). Herbivores help shape fire regimes, and fire regimes in turn shape herbivory (Young et al., 2022). We opened this Research Topic because, relative to their counterparts in tropical forests and temperate grasslands, the ecological roles of smaller mammals (small rodents, marsupials, shrews, etc.) in TSE are poorly understood (Schieltz and Rubenstein, 2016). Our particular focus was what habitat-related factors drive species composition, abundance, diversity, and trophic and non-trophic relationships. We invited participation of small-mammal ecological researchers with field experience on all four continents hosting TSE.

We were particularly interested in studies of the effects on small-mammal community structure of three major endogenous disturbances with which TSEs have evolved: fire, large-mammalian herbivory (LMH), and drought (Buisson et al., 2019). Only in African and parts of southern Asian TSE are native large herbivores still an important component of the trophic system, but domestic livestock herbivory is an important force shaping landscapes and biota in nearly all areas of intact TSE. Shrub encroachment is another driver of small-mammal community changes; this phenomenon may be an indirect effect of long-term changes to the other three disturbance regimes, or it may result from introduction of invasive exotic shrubs. Anthropogenic habitat destruction, alteration, and fragmentation, directly and indirectly through climate change make it even more urgent that we understand how habitat factors influence abundance and diversity of TSE small mammals. Murid rodents, a speciose family occurring in all areas of TSE, are especially important because of their diverse roles as dispersers and predators of savanna trees and shrubs (e.g., Maclean et al., 2011; Schoepf and Pillay, 2023) and as reservoirs of zoonotic disease arising in the tropics (Lecompte et al., 2006; Limongi et al., 2016).

What we know includes, for example, that heavy grazing by both native and domestic LMH in African TSE suppresses abundance and diversity (taxonomic and functional) of small mammals (Bergstrom et al., 2018; McCleery et al., 2018), that the same effect is caused by cattle in Australia (Radford et al., 2015), and that wildfires in the Brazilian Cerrado can cause a temporary shift in dominance from a diurnal species to a more insectivorous, nocturnal one (Vieira and Briani, 2013). In all three regions, data show that some small-mammal species are "increasers" in response to loss of cover, even when most others respond negatively to loss of cover due to fire, grazing, or drought, at least over the short term (McDonald et al., 2016; Loggins et al., 2019). Mostly from Australian TSE studies, we know that loss of cover exposes many small mammals to increased predation, especially by feral cats (Leahy et al., 2015); this, and lack of evidence for post-disturbance food limitation (Radford, 2012) argues that the responses of "decreasers" reflect top-down control. "Increaser" species may use non-vegetative cover (rock crevices, burrows), be more nocturnal, and/or may prefer early successional food resources (McDonald et al., 2016; Bergstrom et al., 2018). Whether this holds true for southern Asian species is currently unknown (Bergstrom et al.).

Summaries of articles in the Research Topic

While fire is a variable in the background of any study of TSE habitats of small mammals, three studies in this Research Topic explicitly examined the effects of fire on small-mammal communities: occurrence of fire in gallery forests within the Brazilian Cerrado increased the density of understory plants and herbaceous cover, decreased small-mammal species richness and abundance, and reduced seed removal rates by small rodents (Cazetta and Vieira); in northern Australian TSE, small-mammal abundance and diversity were enhanced at local scales by rock

FIGURE 1
Views of tropical savanna habitats from three of the continents indicative of where small-mammal studies in this Research Topic were conducted: **(A)** open savanna on red sandy loam soils of the Laikipia Plateau, central Kenya, overstory dominated by *Senegalia mellifera, S. brevispica* and *Vachellia etbaica*, with a discontinuous understory layer dominated by the grasses *Digitaria milanjiana, Cynodon dactylon, Pennisetum mezianum*, and *P. stramineum* (photo by Bradley J. Bergstrom); **(B)** overall view of a typical savanna landscape (known as cerrado *sensu stricto*) associated with sandy soils of the Cerrado biome (photo by André F. Mendonça, taken at Jatobá Farm, Jaborandi municipality, state of Bahia, northeastern Brazil); **(C)** typical *Eucalyptus miniata* dominated open savanna forest characteristic of tropical, high-rainfall savannas (>1000 mm) in the Top End of the Northern Territory and parts of the Kimberley region, Western Australia (photo by Ian Radford, taken on the Mitchell Plateau, north Kimberley); **(D)** typical southern African savanna dominated by acacia trees, with *Dichrostachys cinerea* in the shrub layer, and a dense tall grass layer; southern Kruger National Park, South Africa (photo by Ara Monadjem; note termite mound, a conspicuous landscape feature of TSE in Africa, South America, and Australia).

and shrub cover, by reduced late-dry-season burning, and by maximization of long-unburned and ungrazed habitat patches–presumably as predator refuges–but not by a mosaic of burned patches (Radford et al.). In a long-term compilation of studies of the rodent *Necromys lasiurus* in the patchy Alter do Chão savannas of the Amazon region, neither fire at a regional scale nor climate change was found to influence the species' population dynamics as much as food availability (da Rosa et al.). A fourth study looked at the effects of loss of tree cavities (hollows)—driven largely by fires, but also by LMH and tropical cyclones—on three threatened, regionally endemic, semi-arboreal savanna small mammals on northern Australia's Melville Island and found that their abundance was associated with availability of shrubby habitat patches rather than tree hollows, with the former providing refuges from feral cat predation (Penton et al.).

No study in the Research Topic focused primarily on LMH as a predictor of small-mammal community structure, although LMH was one of the indirect influences on habitat variability in the study by Penton et al. and 18 previously published studies on LMH effects on TSE small mammals were reviewed by Bergstrom et al.

Three studies in the Research Topic examined small-mammal communities in areas undergoing woody shrub encroachment: in native dry grasslands of western India, some rodents responded negatively to the invasion of the exotic *Prosopis* and the concomitant loss of grassy cover, whereas others responded positively to heavy encroachment (Misher et al.); murid rodents of southern African savannas depredated seeds of the invading shrub *Dichrostachys* a third more than those of the native canopy tree *Senegalia* (Teman et al.), suggesting they might control this invasion; and in the Brazilian Cerrado, woody encroachment driven by active fire suppression had species-specific consequences for small mammals, with some open-grassland specialists being negatively affected including two Cerrado endemic and regionally vulnerable murid species (Furtado et al.).

Two papers examined effects of loss of habitat amount and quality and of patch size due to fragmentation on the small-mammal community: habitat generalists were less affected by variation in these three attributes than habitat specialists in the Brazilian Cerrado, and species composition was better explained by habitat features at the local scale, whereas species richness was better explained by landscape-scale metrics (Melo et al.). Studying 36 forest patches within a Cerrado savanna matrix, smaller patches had higher small-mammal abundance, richness of generalist species increased with amount of habitat in the landscape, and richness of specialists increased with increasing quality of the habitat (Mattos et al.).

Two other papers examined cross-habitat comparisons of small-mammal richness and abundance in TSE: in a large-scale study across half of the Cerrado biome that has not been lost to agricultural conversion, heterogeneity of habitats (grassland, typical savanna, and forest formations) at all spatial scales examined was a good predictor of species richness and abundance and occurrence of narrowly distributed species (Carmignotto et al.). The miombo of Tanzania is unusual within the African savanna biome in that the unpalatability of grasses leads to absence of LMH and their predators. This camera-trap study had a detection threshold for body sizes larger than the focal mammals of other studies in this Research Topic (including several small carnivores), but for 19 species of meso-mammals detected, site utilization was greater in gallery forest than in woodland, and for several of these species—including a large murid—detections were significantly associated with termite mounds (D'Ammando et al.).

A global review of mostly experimental field studies of the effects of habitat-altering disturbances on TSE small-mammal community structure found 63 studies, of which 33 studied effects of fire, 18 of LMH, and eight of shrub encroachment. Most conclusive studies found that either loss of cover, or a combination of cover loss and alteration of food resources, explained small-mammal responses, which were mostly negative to loss of cover (Bergstrom et al.). Research gaps include any studies of LMH (cattle grazing) from South America, and any studies at all from southern Asia (but see Misher et al.).

We hope the new studies published in this Research Topic will advance our understanding of habitat-driven effects on TSE small-mammal communities and of certain species of interest due to their endangerment, their provision of ecosystem services, or their potential as zoonotic disease reservoirs. We further hope this set of studies will encourage small-mammal ecologists to fill research gaps by conducting experimental studies in all TSE areas, particularly south Asia, and LMH studies in the Neotropics.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Conflict of interest

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

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BRIEF RESEARCH REPORT
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Savanna Rodents' Selective Removal of an Encroaching Plant's Seeds Increased With Grass Biomass

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In savannas across the planet, encroaching woody plants are altering ecosystem functions and reshaping communities. Seed predation by rodents may serve to slow the encroachment of woody plants in grasslands and savannas. Our goals for this study were to determine if rodents in an African savanna selectively removed seeds of an encroaching plant and if foraging activity was influenced by the local vegetation structure or by the landscape context. From trials with two species of seeds (encroacher = *Dichrostachys cinerea*, non-encroaching overstory tree = *Senegalia nigrescens*) at 64 seed stations, we recorded 1,065 foraging events by seven species of granivorous rodents. We found a strong positive relationship between rodent activity and the number of seeds removed during trials. Foraging events were dominated by rodent seed predators, with <10.6% of events involving a rodent with the potential for secondary dispersal. Rodents selectively removed the seeds of the encroaching species, removing 32.6% more *D. cinerea* seeds compared to *S. nigrescens*. Additionally, rodent activity and the number of seeds removed increased at sites with more grass biomass. Our results suggest a potential mechanistic role for rodents in mitigating the spread of woody plants in grass dominated savannas.

Keywords: ecosystem service, Eswatini, foraging, *Dichrostachys cinerea*, *Senegalia nigrescens*

INTRODUCTION

Globally, savannas are experiencing an increase in woody vegetation, known as woody encroachment (Stevens et al., 2016a,b). Savannas are characterized by a coexistence of trees and grasses, with woody vegetation historically limited by rainfall, fire, herbivory, and competition with grasses (Bond, 2008; Lehmann et al., 2014; Staver and Bond, 2014). However, in the last century, tropical savannas in Africa, South America, and Australia (Stevens et al., 2016b) have seen an increased in abundance of woody plants due to poorly understood and interacting factors, such as atmospheric carbon dioxide, fire regimes, and overgrazing (Sala and Maestre, 2014; Archer et al., 2017). Encroachment, often dominated by a few native plant species, can alter vegetation structure to shade out vegetation in the grassy layer (Scholes, 2003; Charles-Dominique et al., 2018).

This structural and compositional change can alter the ecosystem functions and services that savannas provide, such as altering carbon storage, decreasing water availability, reducing biological diversity, and disrupting socioeconomic conditions through reduced grazing (Huxman et al., 2005; Soto-Shoender et al., 2018). To maintain savannas and their beneficial services, it is important to understand factors that can limit the establishment of woody encroachers, particularly at the seed germination and establishment stage.

One under-studied process that can limit woody plants during the seed germination and establishment stage is post-dispersal seed predation (Ostfeld et al., 1997; Vaz Ferreira et al., 2010). Post-dispersal seed predation can influence the colonization, distribution, and composition of plant communities (Hulme, 1997; Lindquist and Carroll, 2004; Zamora and Matías, 2014). Compositional changes can occur when predators selectively consume seeds of certain species over others (Meiners and Stiles, 1997; Orrock et al., 2006). One group of effective seed predators that can reshape the structure of vegetation are granivorous rodents (Davidson et al., 1984; Brown and Heske, 1990; Hulme, 1993). Rodents can mitigate populations of invasive and exotic plants by predating their seeds (Parker et al., 2006; Pearson et al., 2012) and may have the potential to slow woody encroachment in savannas (Busch et al., 2011; Stanton et al., 2018). However, there is minimal information on how rodents could limit the establishment and spread of encroaching woody plants (Busch et al., 2011; Bergstrom, 2013; Gordon et al., 2016).

Seed consumption by some rodents, other mammals, birds, and insects, can increase the viability of seeds and disperse them to new areas (Schupp, 1993; Miller, 1994b; Crawley, 2000). However, many non-caching granivorous rodents are effective seed predators that destroy the seed upon consumption (Ostfeld et al., 1997; Honek et al., 2009). The extent of rodents' predation and dispersal of seeds is likely a function of environmental conditions. At a local scale, rodents' movements are shaped by vegetation structure, such as grass biomass and shrub cover, which provide cover from predators (Hulme, 1993; Monadjem, 1999a; Loggins et al., 2019b). While less pronounced, rodent activity may also be influenced by different types and configurations of surrounding landscapes (Nupp and Swihart, 2000; Orrock and Damschen, 2005; Ness and Morin, 2008).

Our goals for this study were to determine if rodents in an African savanna selectively removed different woody seeds and varied their activity with changes in local vegetation structure or landscape context. Working in a shrub encroached savanna embedded within a complex landscape matrix, we predicted rodents would selectively remove seeds of a woody encroacher (*Dichrostachys cinerea*). We predicted that the nutritious *D. cinerea* herbivore-dispersed seeds would also be highly palatable for rodents (Irie and Tsuyuzaki, 2011; Xiao and Zhang, 2016) and selected (i.e., removed at a higher rate) over a non-herbivore dispersed tree species (*Senegalia nigrescens*). Additionally, we predicted that fine-scale habitat conditions would have a greater influence on seed removal than the surrounding landscape because of rodents' strong behavioral responses to local vegetation structure (Lima and Dill, 1990; Loggins et al., 2019a).

MATERIALS AND METHODS

Study Area

We conducted our study in the subtropical savannas of northeastern Eswatini. This region falls within the Maputaland-Pondoland-Albany biodiversity hotspot, recognized for its high endemism and biodiversity (Smith et al., 2008). A variety of land uses in the region creates a mosaic landscape of irrigated commercial monocultures and rain-fed subsistence agriculture, grazing lands, and protected areas (Bailey et al., 2016; Reynolds et al., 2018).

The native savanna vegetation in this area is characterized by a continuous grass layer dominated by *Themeda triandra* and *Panicum maximum* and interspersed with woody trees and shrubs. The dominant canopy tree is *S. nigrescens* and the shrub layer is dominated by *D. cinerea.* The woody shrub cover in the region has increased steadily over the last 70 years, from 2% to currently >40% (Roques et al., 2001; Sirami and Monadjem, 2011; McCleery et al., 2018; Stanton et al., 2020). The region has mild, dry winters and hot, wet summers. We conducted our study during the winter, June–July 2018, when average temperatures range from 8 to 26°C and the region receives approximately 0–50 mm of its average 600 mm of annual rainfall (Goudie and Price-Williams, 1983).

We conducted our experiments within the Mbuluzi Game Reserve, Mlawula Nature Reserve, Hlane Royal National Park, and the Inyoni Yami Swaziland Irrigation Scheme (IYSIS) cattle ranch. These savannas were embedded within a land-use matrix consisting of protected natural areas, cattle ranches, subsistence agriculture, and intensive sugarcane plantations (Monadjem and Garcelon, 2005; LaScaleia et al., 2018). Our study sites host a variety of rodents with different feeding and habitat preferences. The most common species at our sites (*Mastomys natalensis, Lemniscomys rosalia, Aethomys ineptus,* and *Micaelamys namaquensis*) have variable diets that include seeds (Field, 1975; Kerley and Erasmus, 1991;Monadjem, 1997a, 1998; Chimimba and Linzey, 2008; Hagenah et al., 2009; Mulungu et al., 2011). We have found no evidence suggesting these widespread and well-studied rodents contribute to secondary seed dispersal (Miller, 1994a; Skinner and Chimimba, 2005; Scholtz, 2008; Happold, 2013; White and Midgley, 2021). However, three less common granivorous species (*Saccostomus campestris*, *Steatomys pratensis,* and *Mus minutoides*) on our sites are known to eat seeds and cache food in their burrows or nests (Hanney, 1965; Ellison, 1993; Hoole et al., 2017) and may facilitate seed dispersal. However, caching by *M. minutoides* has only recently been demonstrated in a laboratory setting and *S. campestris* and *S. pratensis* often reduce their activity during the austral winter (Kern, 1981; Korn, 1987; Monadjem, 1999b), which is when we conducted this study because seeds from the dominant woody plants are most abundant (Donaldson, 1993; Hoffman, 2006).

Site Selection and Landscape Metrics

To understand the influence of the surrounding landscape on the interaction between rodents and seed predation, we created

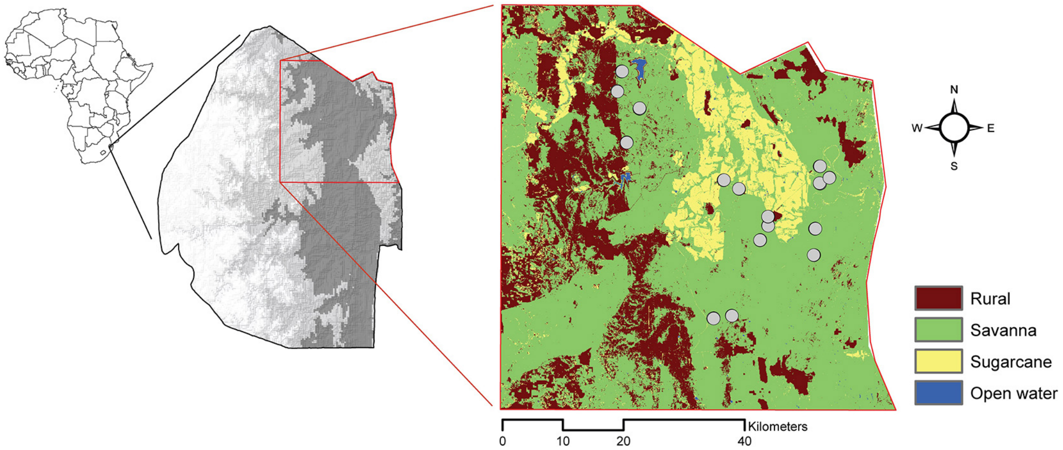

FIGURE 1 | Map detailing the country of Eswatini (gray scale depicts elevation; darker gray is lower elevation) and our study area. Our study area is delineated in red, and our sampling sites (gray circles) are overlayed on our classification of land-cover types.

a land-cover map from Google Earth Engine which included savanna, agriculture, homestead, and open water (Reynolds et al., 2018; **Figure 1**). We derived a value for each site for compositional (the type and diversity of land cover) and configurational (the shape and arrangement of land cover) landscape heterogeneity (Gustafson, 1998). To derive these measures, we used the *raster* and *SDMTools* packages in R statistical software V 3.5.0 to implement a moving-window analysis and identify gradients in landscape composition and configuration based on variations in land cover (Zhang et al., 2013; Tolessa et al., 2016, R Core Team, 2018). To capture areas of savanna with a variety of surrounding landscapes, we set a window with a 2 km radius and centered sampling landscapes around cells surrounded by at least a 500 × 500 m buffer. Within the 2 km buffer, we calculated two measures of compositional heterogeneity (Shannon diversity index of land cover types and land cover richness) and three measures of configuration heterogeneity (total length of edge between land cover classes, total number of patches, and patch cohesion and landscape division) (Fahrig et al., 2011; **Supplementary Table 1**).

We used principal components analysis (PCA) from the *psych* package to create two orthogonal components of landscape heterogeneity, representing compositional, and configurational heterogeneity (Revelle, 2014). We ranked cells based on their PCA value for compositional and configurational heterogeneity. Using stratified sampling, we then selected 16 sampling landscapes across gradients of compositional and configurational heterogeneity.

We scored sites as low (<33%), medium (34–66%), or high (>67%) compositional and configurational heterogeneity. We stratified the 16 sites based on the following classifications: high compositional and high configurational heterogeneity (n = 3), high compositional and medium configurational heterogeneity (n = 2), high compositional and low configurational heterogeneity (n = 2), medium compositional and medium configurational heterogeneity (n = 1), medium compositional and low configurational heterogeneity (n = 2), low compositional and high configurational heterogeneity (n = 2), low compositional and medium configurational heterogeneity (n = 2), and low compositional and low configurational heterogeneity (n = 2).

Vegetation Structure

Our sampling sites were located within relatively open savanna habitats (woody cover 25–40%). To quantify the vegetation structure of the local environment (0.25-ha), we sampled three 50 m transects at each site. We ran two parallel transects at 10 m distance from the center of the site, and a third perpendicular transect through the center point. We measured grass biomass with a disc pasture meter (DPM) every 5 m on each transect (Bransby and Tainton, 1977). We averaged the measures and used a previously calibrated estimate to generate an estimate of biomass in kg/ha (Zambatis et al., 2006). We measured the average canopy cover at each site by taking spherical densiometer readings at every 5 m along each of the three transects and we estimated shrub cover (woody cover <5 m) using the line intercept method on each transect (Canfield, 1941).

Foraging Trials

We conducted foraging trials with seeds from the two dominant woody species in our study area, *S. nigrescens* and *D. cinerea* (family Fabaceae). They are both widespread in southern African savannas (Palgrave and Palgrave, 2015). *D. cinerea* is a common woody encroacher that relies on ingestion by non-rodent herbivores (e.g., ungulates) for both dispersal and dormancy-breaking (Van Staden et al., 1994; Miller, 1995; Dudley, 1999; Tjelele et al., 2012, 2015). The seeds of *D. cinerea* are round and ≈ 4 mm × 5 mm (**Supplementary Figure 1**). The pods are nutritious and are eaten by large herbivores. *S. nigrescens* is a canopy tree with disc-shaped seeds that form in a pod and are dispersed through ballistic dispersal. The seeds of *S. nigrescens* are ≈ 10 mm × 10 mm and flat (**Supplementary Figure 1**). These larger seeds do not require herbivore-assisted dispersal to break dormancy and are damaged if consumed (Miller, 1994b, 1995).

At each sampling site (50 × 50 m plot, 0.25 ha) we established four seed stations around the center of the site. We placed the seed stations (30 cm diameter tray) halfway under shrubs to increase foraging rates (Loggins et al., 2019b). Prior to trials, we pre-baited trays for 24 h with oats and peanut butter. Then we randomly assigned two seed stations to receive *S. nigrescens* seeds (*n* = 40) and two to receive *D. cinerea* seeds (*n* = 60). We obtained our seeds from Silverhill Seeds and Books[1]. We used 50% more *D. cinerea* seeds than *S. nigrescens* seeds to account for the former's smaller mass and volume. We ran each trial for 24 h and then collected and recorded the number of intact seeds remaining. We classified seeds as remaining seeds if they were scarred or damaged but had an intact cotyledon that could potentially germinate (Bell and van Staden, 1993). The small and hard seeds used in this study often shatter with damage to the cotyledon; thus, to be conservative we considered seeds with >25% damage to the cotyledon as removed (Barnes, 2001). For the next 24-h period, we switched seed species at each station and ran the trial again. Finding no evidence that the common seed predators (*M. natalensis, L. rosalia, A. ineptus,* and *M. namaquensis*) contribute to secondary seed dispersal (Miller, 1994a; Skinner and Chimimba, 2005; Scholtz, 2008; Happold, 2013; White and Midgley, 2021), we assumed the seeds removed by these species were predated. Alternatively, we acknowledged that foraging by the less common *M. minutoides*, *S. campestris*, and *S. pratensis* may have led to secondary dispersal.

Rodent Activity

To link seed predation to rodent activity, we monitored each seed station with a short-focused camera [Spartan, model SR1-IR(S100), Norcross, GA, United States]. We placed the camera 55 cm above each seed station facing downwards (**Supplementary Figure 2**). Seed trays were marked with a scale bar to aid in identification of rodents using tail and body length (McCleery et al., 2014). We set the motion-sensitive camera to photo, three bursts, with a 5 s trigger interval. To calculate the length of foraging bout we measured the duration of time each individual rodent first and last appeared on camera, with new bouts starting after 20 min of non-detection (Loggins et al., 2019b). When multiple individuals of the same species appeared on camera simultaneously, we noted a foraging bout for the maximum number of individuals seen in the frame. We grouped the ecologically similar *A. ineptus* and *M. namaquensis* as a single species due to the difficulty of distinguishing them on camera; however, the latter species is rarely captured away from rocky outcrops in Eswatini (Monadjem, 1997b) and was therefore not likely to be encountered in this study. All methods were approved by the University of Florida's Institutional Animal Care and Use Committee (#201509045).

Statistical Analyses

Seed Selection

To determine if rodents selected one seed species over the other, we modeled the proportion of seeds removed during each trial as a function of the species of seed. We used proportions to account for the different number of seeds used for each species. We used a mixed effects model with each seed station as a random effect and fitted to a binomial distribution using the *lme4* package for R (Bates et al., 2015). We considered the proportion of seeds removed to be significantly different if the 95% confidence intervals (CI) of β estimate for seed species did not include zero.

Variation in Seed Removal

To explain variation in seed removal for each species separately, we used the raw count of the number of seeds remaining at each tray. For each species, we considered variation as a function of factors at two different scales, the local scale (vegetation structure at the 0.25 ha scale) and the landscape scale (land use composition and configuration at the 2 km scale). We developed seven *a priori* models to explain differences in the number *D. cinerea* and *S. nigrescens* seeds remaining. We included models with only one fixed variable (canopy cover, shrub cover, grass biomass, compositional heterogeneity, and configurational heterogeneity), as well as global and null models (**Table 1**). We fitted generalized linear mixed models using a generalized Poisson distribution and site as a random effect using the *glmmTMB* package in R (Brooks et al., 2017). We evaluated model fit using Akaike's information

TABLE 1 | Degrees of freedom (DF), Akaike's information criterion corrected for small sample size (AICc), difference in AIC scores (ΔAICc), and AICc weight (AICcwt) of models to explain differences in the numbers of *Dichrostachys cinerea* seeds remaining at seed trays (a), the number of *Senegalia nigrescens* seeds remaining at seed trays (b) and the total time (i.e., number of minutes) rodents foraged at each seed station (c).

Model	DF	AICc	ΔAICc	AICcwt
(a) Number of *D. cinerea* seeds remaining				
Grass biomass	4	386.2	0	0.868
Compositional heterogeneity	4	392.4	6.20	0.039
Null	3	392.8	6.57	0.032
Canopy cover	4	394.1	7.85	0.017
Global	8	394.2	7.97	0.016
Configurational heterogeneity	4	394.2	7.98	0.016
Shrub cover	4	395.0	8.74	0.011
(b) Number of *S. nigrescens* seeds remaining				
Grass biomass	4	435.6	0	0.274
Null	3	435.8	0.20	0.248
Shrub cover	4	436.7	1.10	0.158
Configurational heterogeneity	4	437.4	1.73	0.115
Canopy cover	4	437.6	1.93	0.104
Compositional heterogeneity	4	438.1	2.48	0.079
Global	8	440.7	5.03	0.022
(c) Number of minutes foraging				
Grass biomass	4	721.8	0	0.672
Null	3	725.6	3.85	0.098
Compositional heterogeneity	4	726.1	4.38	0.075
Configurational heterogeneity	4	726.4	4.68	0.065
Shrub cover	4	727.4	5.63	0.040
Canopy cover	4	727.4	5.66	0.040
Global	8	730.1	8.32	0.010

Models for each seed species included individual fixed variables, a global model with all variables, and a null model.

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[1] http://www.silverhillseeds.co.za/

criterion (AICc) corrected for small sample size. We considered models with AICc scores lower than the null model and within four AICc units of the best model to be competing models (Burnham and Anderson, 2002). We considered parameters from competing models to be significant if their 95% CIs did not include zero.

Rodent Activity

To link rodent activity to overall seed removal (i.e., both species), we related the proportion of seeds removed during each trial to the total number of minutes that rodents foraged at each tray. Using both species, we modeled the proportion of seeds removed during each trial as a function of rodent activity with a mixed effects model fitted to a binomial distribution with seed station as random effect. In addition to examining 95% CIs, we evaluated the strength of the relationship by calculating the marginal pseudo-R^2 using the *sjstats* package (Lüdecke, 2021). Next, to determine if activity varied as a function of the species of seed, we modeled the foraging activity during each trial (i.e., total number of minutes of rodent activity). We correlated these count data with the seed species used during the trial using a generalized Poisson distribution and seed station as the random effect. Finally, to determine if rodent activity varied with environmental factors in a manner that reflected variation in measures of seed removal, we fitted generalized linear mixed models to rodent activity using a generalized Poisson distribution and site as a random effect to the same seven models (**Table 1**) and assessed model parsimony and significance as described above.

RESULTS

We recorded 1,065 foraging events by seven species of granivorous rodents during seed experiments that were conducted from June 23–July 26, 2018 (**Supplementary Table 2**). The rodents most frequently detected at the seed stations were the seed predators *M. natalensis* (39.0%, *n* = 415), *A. ineptus*/*M. namaquensis* (25.4%, *n* = 270), and *L. rosalia* (25.1%, *n* = 267). Rodents with the potential for secondary seed dispersal accounted for only 10.6% of the foraging events. The diminutive *M. minutoides* accounted for 10.1% (*n* = 108) of the activity and we only recorded five foraging events by *S. pratensis* (0.3%, *n* = 3), and *S. campestris* (0.2%, *n* = 2). Of the 64 seed stations used in the experiment, one had no sign of seed removal or rodent activity and two were incorrectly set up; hence, all three were removed from further analysis (*n* = 61).

Comparing the proportion of seeds removed by species, we found that rodents removed a greater proportion of *D. cinerea* than *S. nigrescens* (β = −1.30, 95% CI −2.52 to −0.26, reference = *D. cinerea*). Model predicted estimates suggested that rodents removed 32.6% more *D. cinerea* seeds ($\bar{x}$ = 0.87, SE = 0.06) than *S. nigrescens* seeds ($\bar{x}$ = 0.66, SE = 0.10).

Examining the influence of the surrounding environment on the number of seeds removed, for both seed species, we found a model with only the fixed effect of grass biomass was the best model with no competing models (**Table 1**). Grass biomass had a significant negative relationship with the number of *D. cinerea* seeds remaining in trays (β = −0.76, 95% CI −1.26 to −0.26), where the number of *D. cinerea* seeds remaining decreased from 31 to 1 as grass biomass increased from a minimal 1,000 with a maximum of 4,500 kg/ha (**Figure 2**). The relationship between grass biomass and the number of *S. nigrescens* remaining was not significant (β = −0.478, 95% CI −1.07 to 0.12), suggesting a weaker relationship. We found little evidence that seed removal was affected by the broader landscape context (i.e., composition and configuration; **Table 1**).

Of the 61 seed stations used to understand seed removal, six had camera failures. Using the seed stations with operational cameras (*n* = 55), we found a strong positive relationship between the proportion of seeds removed and rodent activity (β = 3.19, 95% CI 1.75–4.65, pseudo R^2 = 0.76). However, we found no indication that activity varied with the seed species used during the trial (β = 1.15, 95% CI −0.24 to 0.19, reference = *D. cinerea*). Similar to our investigation of seed removal, we found the best model, with no competing models, to explain variation in rodent activity was a model that included only the fixed effect of grass biomass (**Table 1**). Rodents spent more time foraging in areas with more grass biomass (β = 0.46, 95% CI 0.13–0.80). The total number of minutes increased from approximately 96 to 450 over the range of grass biomass recorded at our sites (**Figure 3**).

DISCUSSION

We found a strong linkage between the removal of seeds and rodent activity, suggesting a potentially important role for rodents in shaping the composition and structure of woody vegetation in savannas. With only a small percentage of rodent activity from rodents with the known ability to cache seeds, we assumed the majority of rodent-seed interactions ended with seed predation. This was particularly true for rodents' interactions with the seeds of the woody encroaching shrub *D. cinerea*. Despite spending similar amounts of time with both seed species, rodents removed 33% more of the seeds from *D. cinerea*.

Rodents' selection of *D. cinerea* may be based on seed properties (e.g., morphology, nutrition, and palatability). The larger *S. nigrescens* seeds may provide rodents with a greater volume of food, but *D. cinerea* likely has a higher nutritional value (Janzen, 1984; Tiffney, 2004). This difference has been documented in the seed pods and may extend to the seeds (Tsopito and Adogla-Bessa, 1998; Aganga and Motshewa, 2007). Additionally, optimal foraging theory predicts that animals select seeds that provide the most nutritional gain for the least amount of energy expended (Charnov, 1976; Brown et al., 1999). The larger *S. nigrescens* seeds may require more energy to handle or increase the rodent's vigilance behavior during foraging (Quenette, 1990). Accordingly, rodents may have selected the smaller seeds of *D. cinerea* to consume food with minimal effort while remaining vigilant.

We also found that the number of seeds removed by rodents and the amount of time rodents spent foraging increased with increases in grass biomass (**Figures 2**, **3**). This supports our prediction that rodents are more strongly influenced by localized vegetation than the surrounding landscape. Thick grass cover is

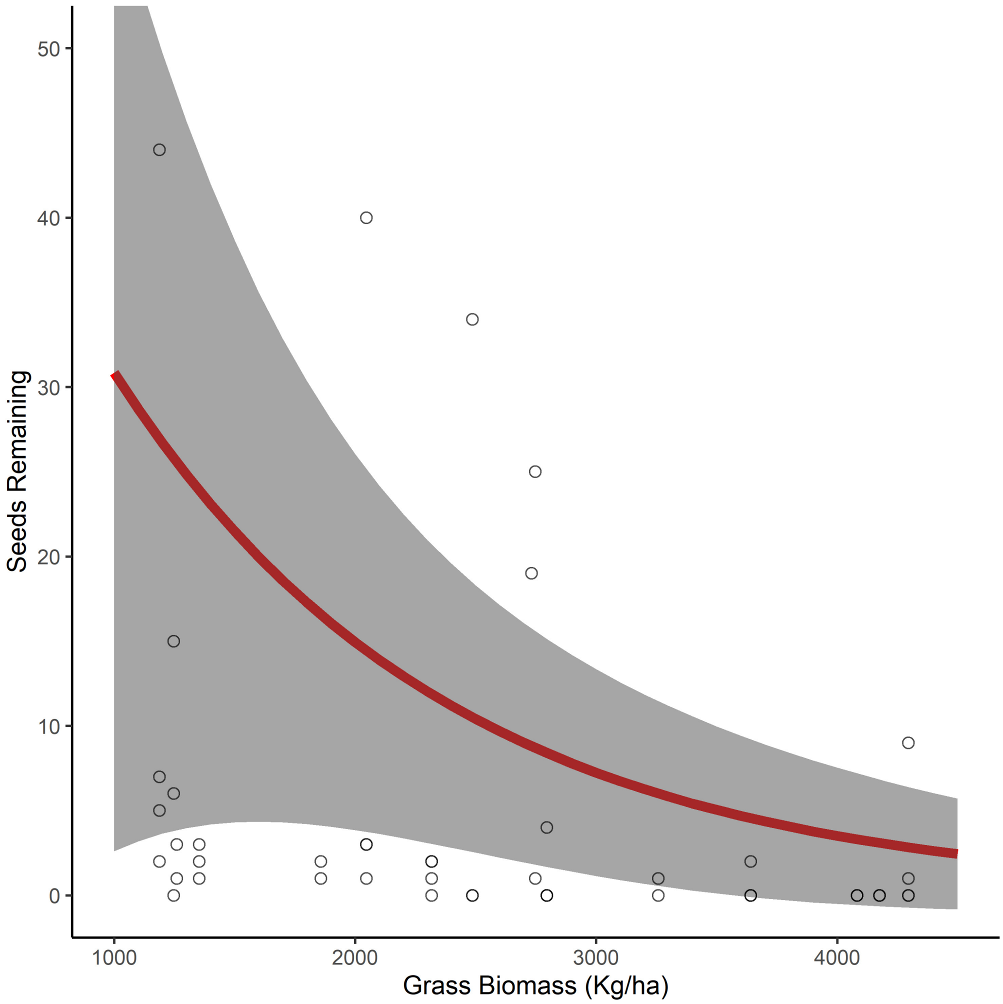

FIGURE 2 | The predicted number of *Dichrostachys cinerea* seeds remaining in seed trays (95% confidence interval in gray) as a function of grass biomass (kg/ha) in the surrounding environment (0.25 ha).

likely to provide rodents with ample food resources and reduce their perception of fear (Banasiak and Shrader, 2016). These findings are consistent with the "landscape of fear" framework (Laundré et al., 2014), where animals alter their movements and behaviors to minimize predation risk while maximizing benefits (e.g., foraging on seeds) (Lima and Dill, 1990; Brown, 1999; Bleicher, 2017).

In savannas, grasses and shrubs compete for resources (e.g., water and light) and areas with a thick grass layer have lower rates of seedling survival, reducing the chances of shrub establishment (Köchy and Wilson, 2000; Rinella et al., 2015; Pierce et al., 2018). Additionally, rodent predation of seeds of encroaching shrubs in areas with thick grass may create a feedback loop, where high grass biomass limits shrub establishment and facilitates rodent seed predation which helps to maintain the dominance of grassy vegetation. This feedback loop may be more pronounced for plants that are herbivore-dispersed such as *D. cinerea*, which rodents appear to select. Nonetheless, the role of rodents may be substantially reduced if the system switches from an open grassy savanna to an encroached savanna with minimal grassy cover.

Through the removal of seeds, rodents can decrease seedling recruitment (Ostfeld et al., 1997; Nuñez et al., 2008; Yu et al., 2014) and the density of adult plants (Maron and Kauffman, 2006; Larios et al., 2017), altering composition (Louda, 1982; Pearson et al., 2012, 2013) and shaping vegetation (Brown and Heske, 1990; Edwards and Crawley, 1999; Moorhead, 2017). In our savanna system, rodents have the potential to reduce the recruitment of woody encroaching plants; however, we did not consider the role of other herbivores. The nutritious seeds and seed pods of woody encroachers are often consumed and deposited in the dung of non-rodent herbivores, where they can germinate rapidly (Campos-Arceiz and Blake, 2011). This mechanism of dispersal may protect seeds from rodent predation and enhance secondary dispersal (Vander Wall et al., 2005; Enders and Vander Wall, 2011). Additionally, it is plausible that the root suckering version of *D. cinerea* and other encroaching species may be more important than seed

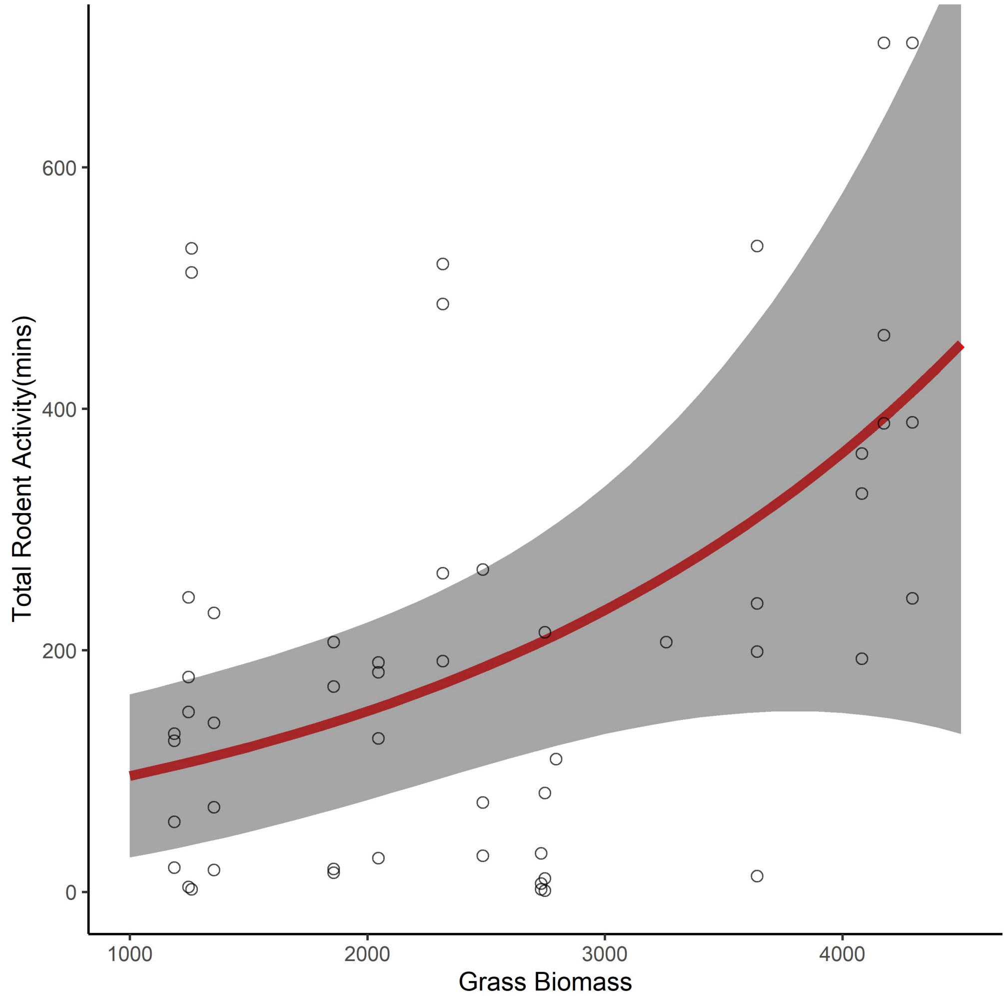

FIGURE 3 | The predicted number of minutes that rodents foraged at seed trays (95% confidence interval in gray) as a function of grass biomass (kg/ha) in the surrounding environment (0.25 ha).

dispersal in the establishment of *D. cinerea* and other encroachers (Wakeling and Bond, 2007).

Shrub encroachment is altering tropical savannas (Stevens et al., 2016a,b) and our results suggest a potential role for rodents in mitigating their spread. However, rodent-shrub interactions will need to be evaluated on more ecologically relevant scales, while accounting for variability in the placement and relative abundance of seeds (Lichti et al., 2014; Yi and Wang, 2015) before we can interpret the role of rodents in limiting the encroachment of woody plants. Future work should explicitly examine rodent and seed interactions (Forget and Wenny, 2005; Wróbel and Zwolak, 2013), instead of assuming seed predation or dispersal based on previous research, laboratory studies, and natural history accounts. If rodents provide this critical service, it highlights the consequences of the loss and decline of seed-eating mammals (Hurst et al., 2014; Mills et al., 2018) and the need to maintain savannas' thick grassy-layer that facilities seed predation, which is threatened by chronic overutilization by domestic and wild ungulates.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of Florida's Institutional Animal Care and Use Committee (#201509045).

AUTHOR CONTRIBUTIONS

ST collected the data and wrote the initial draft of the manuscript. RM and ST conducted the data analysis. All authors helped design the study and contributed to the writing and review of the manuscript.

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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.2021.676572/full#supplementary-material

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REVIEW
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Necromys lasiurus: Lessons From a 38-Year Study in an Amazonian Savanna

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Amazonian savannas are isolated patches of open habitats within an array of extensive tropical forest. The mammal fauna of the savannas in the Alter do Chão region (Santarém Municipality), is dominated by *Necromys lasiurus*, whose populations have been studied by researchers of the National Institute of Amazonian Research since 1983. Here, we summarize the studies and advances made so far to better understand aspects related to population dynamics and ecology of savanna rodents and the strategies they use to persist in an environment with frequent fires subject to global climatic influences. In the Amazonian savannas the species acts as a seed disperser and population fluctuations are related to invertebrate availability, but not with fire or vegetation structure. Global climate appears to affect *N. lasiurus* population dynamics at local scale (i.e., plot scale) but not at the regional scale of the Alter do Chão savannas. The long-term studies in Alter do Chão generated many advances about *Necromys lasiurus* population dynamics and ecology, including aspects relating to feeding, home range, animal-plant interactions, the effects of fire and climate change.

Keywords: long-term studies, population dynamics, Rodent ecology, savanna mice, Tropical savanna

INTRODUCTION

Necromys lasiurus (Rodentia: Cricetidae) is a small (approximately 60 g, with males being slightly larger than females, Cangussu et al., 2002), terrestrial and diurnal rodent widely distributed in open habitats with seasonally dry and arid climates in South America (Paglia et al., 2012). It has been intensively studied in many open formations in South America, especially in the Brazilian Cerrado. It is a generalist species that eats roots, seeds, leaves, and invertebrates (Talamoni et al., 2008). The species is a major food source for predators, such as snakes and owls (Bueno and Motta-Júnior, 2015). In the Cerrado, *Necromys lasiurus* is terrestrial, with a mean displacement of 42 m in a 24-h period (Vieira et al., 2005), and males move greater distances than females between successive captures (Pires et al., 2010). The mean home range of males is larger than that of females (Pires et al., 2010). The species constructs nests on the ground, and sometimes uses armadillo burrows as nest sites (Vieira et al., 2005).

In Brazil, *N. lasiurus* is common in open habitats of the Cerrado, Pantanal and Caatinga (Souza and Alho, 1980; Becker et al., 2007), but also occurs in open patches within Amazonian and

Atlantic forests (Gheler-Costa et al., 2012; Magnusson et al., 2021). In the Cerrado, *N. lasiurus* is usually the most abundant rodent within its area of occurrence and predominates in most vegetation physiognomies (Becker et al., 2007; Pires et al., 2010). In Amazonia, the species is found in savanna vegetation (Ghizoni et al., 2005) and in the Atlantic Forest it is often found in agroecosystems (Gheler-Costa et al., 2012). Santos et al. (2018) and Malange et al. (2016) noted that crops and pastures have favored the expansion of the species in the Atlantic Forest, and human-modified environments are associated with the occurrence of the species in all Brazilian domains (Santos et al., 2017).

Necromys lasiurus is considered to be one of the main hantavirus reservoirs in Brazil (Oliveira et al., 2013; Santos et al., 2017), and hence surveillance of its populations is of important. This species shows abrupt density fluctuations, and changes from extremely common to rare between seasons or years (Souza and Alho, 1980). Although *N. lasiurus* is a common and well-studied species, especially in Cerrado domain, there are few studies of the population dynamics of *N. lasiurus* in Amazonian savannas (e.g., Francisco et al., 1995; Magnusson et al., 2021).

Amazonian savannas are found as islands of vegetation between forest patches of varying size and are considered one of the most threatened Amazonian habitats because many of the savanna patches are being transformed by large-scale agriculture, increases in infrastructure, and uncontrolled fires, all of which are interlinked (Diniz and Santos, 2005).

Most of the studies carried out in Amazonian savannas have focused on plants, with only occasional studies of reptiles, birds, mammals, and invertebrates (De Carvalho and Mustin, 2017), suggesting that Amazonian-savanna biodiversity is underestimated. In 2004, the Brazilian Ministry for the Environment recognized the Amazonian savanna complexes as conservation priorities for the country (Ministério do Meio Ambiente [MMA], 2004), resulting in an increase of more than 60% in the number of protected areas in Amazonian savannas in Brazilian territory. Today, 36.8% of Brazilian Amazonian savannas are under some degree of protection, almost half of which are in indigenous lands (De Carvalho and Mustin, 2017). Despite the Brazilian policies to protect Amazonian savannas during the last 20 years, savannas are often the first environments lost, since major international attention has been focused on forests (Ratter et al., 1997). One exception to the paucity of knowledge of areas covered by Amazonian savannas is the Amazon savanna of Alter do Chão, located in the Brazilian state of Pará. Studied since 1983, the cumulative knowledge provided by the studies at Alter do Chão have turned the region into a laboratory for scientific investigation of ecological processes of savannas and fragmented tropical areas. An iconic example is comprised by the long-term studies carried out on *Necromys lasiurus* populations in the Alter do Chão savannas.

In this paper, we present the advances in knowledge of the biology of *N. lasiurus* and how the species has been used to study ecological and climate-change process in the Alter do Chão region since 1983. *Necromys lasiurusis* relatively abundant in the savannas of Alter do Chão and the installation of standardized plots and subsequent funding from diverse sources, allowed a program to study the abiotic and biotic factors that influence the long-term dynamics of populations of the species in Amazonian savannas.

History of Sampling Design of *Necromys lasiurus* Populations

Our study was conducted near Alter do Chão, a village in the Santarém municipality, Pará. The Alter do Chão region has supported typical savanna tree species for about 1.49 Ma (Buzatti et al., 2018), with a local landscape relatively stable for at least the last 7,000 to 6,000 years (Sanaiotti et al., 2002). The area is a project within the International Long-Term Ecological Research (LTER) Network (Mirtl et al., 2018) that seeks to investigate the local and global drivers of biodiversity change, such as fire and global warming, in savanna and forested environments.

Sampling of *Necromys lasiurus* began in 1983 in a single plot of approximately 4 ha using baited (Brazil nuts and peanut butter mixed with oats) Sherman traps (10 cm × 10 cm × 30 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) that were checked once daily, during the morning. The plot originally had a 150 m × 200 m size with a minimum spacing between capture points of 10 m. Traps were set on 25% of the plot intersections during 3 or 4 days and then advanced one trap position so that the whole plot was covered. In 1986, the plot size was increased to 200 m × 200 m, and in 1988 the plot was extended to 300 m × 340 m. However, researchers realized that the 200 m × 200 m plot was sufficient to have a good sample and, in 1997, the plot decreased to 200 m × 200 m. After this, the traps were placed every 20 m for 2 days, then moved 10 m to cover the intermediate positions for another 2 days. On that plot, 100 Sherman traps were used simultaneously and this plot has been sampled with this protocol since 1997. Temporal variation in abundance of *N. lasiurus* on this plot was obtained from 1985 to 1989, from 1997 to 1998, and 2000 to 2020, giving data in 23 of the 38 years. Details of the methods are given in Francisco et al. (1995); Magnusson et al. (1995), and Magnusson et al. (2010).

In 1999, 40 sampling plots were installed in the savannas across Alter do Chão, allowing studies on a regional scale to evaluate short and long-term patterns of biodiversity change and its drivers (Magnusson et al., 2013). Plots were sampled along four parallel 250-m-long transects that are 50 m apart (**Figure 1**). This standardized protocol has been repeated till now and can be used to evaluate fluctuations of *Necromys lasiurus* populations. In the first studies (Francisco et al., 1995; Magnusson et al., 1995), animals were marked by toe clipping. Already in 1999, the first year of sampling, many individuals were recaptured in each session and it became obvious that 4 days was more time than necessary, and the mice were becoming trap happy. Therefore, the effort in the 40 standardized plots was reduced to 2 days, allowing, in the following years, the sampling of the plots in a shorter time. Since 1999, in each of the regional plots, 50 Sherman live traps are set at 20-m intervals on four 250-m parallel transects spaced 50 m apart that covers the plot (**Figure 1**). To distribute the 50 traps into the four transects, we standardized the installation of 13 traps in the first and third transects and 12 traps in the second and fourth transects. Traps remained open for

2 days in each capture session and were checked each morning. Detailed descriptions of the methods are provided in Layme et al. (2004); Ghizoni et al. (2005), and Magnusson et al. (2021).

In summary, two long-term studies with comparable protocols were carried out in the Alter do Chão savanna simultaneously. One study used a single 4-ha plot, with an effort of 4 days and 100 traps placed simultaneously (e.g., Francisco et al., 1995; Magnusson et al., 1995, 2010), and the other study used up to 40 plots (at present 35) with a sampling effort of 2 days and 50 traps placed simultaneously for each plot (e.g., Layme et al., 2004; Ghizoni et al., 2005; Magnusson et al., 2021). Between 2005 and 2020, five plots were deactivated because of illegal land clearing, resulting in 35 active plots today.

Natural History of *Necromys lasiurus* in the Alter Do Chão Savanna

During the two decades of sampling, *N. lasiurus* was the only rodent trapped regularly in the savanna in our study region. Individuals of *Proechimys sp.* and *Didelphis marsupialis* were occasionally caught in the traps, but were never recaptured and probably use the savanna only in transit, since both species are common in neighboring forest patches (Magnusson et al., 1995; Borges-Matos et al., 2016). In contrast, despite extensive trapping, only one individual of *N. lasiurus* has been captured in neighboring forest patches (Magnusson et al., 1995).

The first published paper about *N. lasiurus* near Alter do Chão by Magnusson and Sanaiotti (1987) found many *Miconia albicans* seeds in the feces of these mice. *Miconia albicans* is a common shrub in Amazonian savanna near Alter do Chão and, although its fruits are rarely eaten by birds or lizards, they are often consumed by *N. lasiurus*. The seeds can germinate after passing through the digestive tract of the mice, indicating that they may be important dispersal agents for this plant and, to the best of our knowledge, the study by Magnusson and Sanaiotti (1987) was the first to document seed dispersal through the digestive tract of a small rodent.

In addition to *M. albicans* seeds, Francisco et al. (1995) showed that the diet of *N. lasiurus* is composed of vegetable material and invertebrates (mostly centipedes, beetles, and termites). Fire at the end of the dry season appeared to affect the diet of the mice, causing increased consumption of invertebrates during the following wet season (Francisco et al., 1995). This consumption pattern is consistent with observations made for *N. lasiurus* in the Cerrado (Talamoni et al., 2008), and for *Mastomys natalensis*, a small rodent common in savannas of South Africa (Monadjem, 1998). In both cases, rodents consumed more invertebrates during the rainy season, and less during the dry season when there was an increase in vegetable items. These studies indicate that small rodents living in savanna environments are opportunistic, varying their diets depending on the abundance of food resources.

To determine the proportions of food sources that came from food chains based on grasses or bushes, Magnusson et al. (1999) measured the stable isotopes of carbon extracted from tissue samples. Although the mice spent most of their time among the grasses, where they would be protected from predators, such as raptors, the stable isotopes indicated that most of their food (∼60%) came from chains that originated in bushes and trees (Magnusson et al., 1999). A comparable pattern is found in African savanna rodent communities, where rodent activity and amount of food removed is greater under shrubs than under grasses, as an answer to the perception of low predation risk under shrubs (Loggings et al., 2019). Therefore, the balance between tree-bush clumps for nutrition and grasses for protection is likely to affect the densities of *N. lasiurus* and other rodents in savanna environments.

Near Alter do Chão, *N. lasiurus* has a mean home-range size that varies among years and between sexes. Mean home-range size for males varied from 4,138 to 21,880 m^2 (one male, whose home range overlapped the perimeter of the study area, used 51,000 m^2 within the plot) and for females varied from 1,317 to 5,480 m^2 (Magnusson et al., 1995). The home-range sizes in Amazonian savanna reported by Magnusson et al. (1995) were higher than those reported in studies in the Cerrado vegetation in central Brazil (Souza and Alho, 1980; Alho and Pereira, 1985) and grassland among Atlantic-coastal-forest fragments in south-eastern Brazil (Pires et al., 2010).

In the Alter do Chão savanna, females have smaller, largely exclusive, home ranges, indicating that they are strongly territorial, and male home ranges are larger and overlapping (Magnusson et al., 1995). Because of a perpetual cycle of gestation and lactation, adult females probably need more food, so they defend their territories against potential intruders. In contrast, adult males probably have enough food resources, so they can spend more energy to find receptive females to reproduce (Magnusson et al., 1995). Males of *N. lasiurus* also had larger home ranges than females in the study by Pires et al. (2010) in grassland among Atlantic-coastal-forest fragments, but home-range sizes did not vary significantly between seasons for either sex.

In our study region, *Necromys lasiurus* has a short life cycle (a little over a year) and consequently the species has a fast rate of replacement of individuals in its populations (Francisco et al., 1995; Magnusson et al., 1995). Francisco et al. (1995) found a proportion of males and females of 1:1, with a quarter of the individuals being juveniles (weighing less than 30 g) and the remainder adults (weighing above 30 g). Reproduction and growth of *N. lasiurus* are strongly seasonal, with an increase in the rainy season (January to May), which may be related to the availability of fruits and invertebrates, which are the main food resources of *N. lasiurus* (Francisco et al., 1995; Layme et al., 2004). This pattern was also observed in a 6-year study in a savanna in central Brazil in which the captures of reproductive individuals of *N. lasiurus* were significantly higher in the rainy season (Rocha et al., 2017).

Necromys lasiurus as an Indicator of Ecological Process and Climate Change in the Savanna

The first studies showed that the species was relatively common in the Alter do Chão savanna and easily captured (Francisco et al., 1995; Magnusson et al., 1995; Layme et al., 2004), which

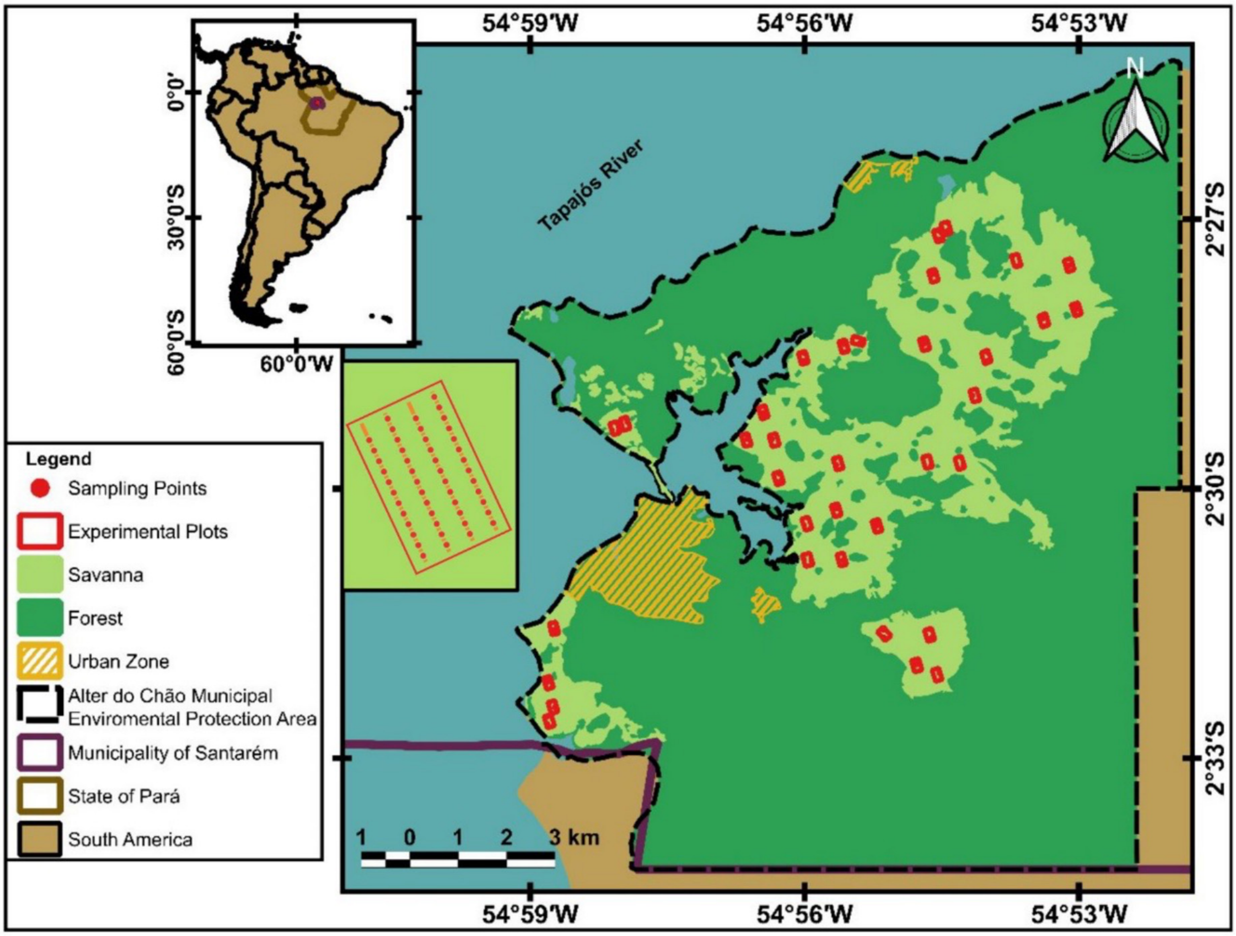

FIGURE 1 | Sampling areas used to study *Necromys lasiurus* near Alter do Chão, Santarém, Pará.

appeared to make *N. lasiurus* an excellent study organism. The studies by Layme et al. (2004) and Ghizoni et al. (2005) carried out in the 40 sampling plots of the Alter do Chão savanna, investigated the densities and rates of increase of *N. lasiurus* in relation to food availability (invertebrates), fire, and vegetation structure. Densities of *N. lasiurus* were not influenced by vegetation structure or fire, but were strongly related to invertebrate availability (Layme et al., 2004). Rates of increase of *N. lasiurus* among years indicated that the mice were generally decreasing throughout the study area, but the degree and sometimes the direction of density changes varied among plots (Ghizoni et al., 2005). Reductions in density were smaller in plots where the availability of invertebrates increased and was also related to vegetation structure (proportion of shrubs, tall-grass species, shortgrass species, and open soil along the central line of each plot). The study of Layme et al. (2004), showed that, at large scale, there was a slight tendency to capture more individuals in areas with higher cover of tall-grass, and the densities of *N. Lasiurus* were not associated with short-grass or shrubs. At scales of tens of meters, more individuals were associated with areas that had a combination of short-grass and shrubs. However, Ghizoni et al. (2005) showed that the hypothesis of Layme et al. (2004) that densities of *N. lasiurus* are associated with tall grasses was not supported. Density and population growth rates were more associated with tree, shrub, and small grass, an effect that had not been detected when only density, and not density change, had been studied (Ghizoni et al., 2005). Fire appeared to have little direct effect on the densities or rates of increase of *N. Lasiurus* (Layme et al., 2004; Ghizoni et al., 2005). Also, fire did not influence reproduction or growth of *N. lasiurus* in a single 4 ha plot (Francisco et al., 1995), which is consistent with studies conducted in Cerrado areas of Central Brazil (Vieira and Marinho-Filho, 1998).

Previous studies in the Cerrado indicate that, although the species is captured frequently, populations fluctuate markedly and may disappear from trapping grids (e.g., Souza and Alho, 1980; Valle et al., 1982). However, during the first 6 years of sampling in the late 1980s and early 1990s in a single 4 ha plot, the number of mice captured in the Alter do Chão savanna was relatively constant and zero density was not registered in any trapping session (Francisco et al., 1995; Magnusson et al., 1995). Nevertheless, subsequent studies carried out in the early

2000s showed that the density of *N. lasiurus* was declining (Layme et al., 2004; Ghizoni et al., 2005) and the species disappeared from the plot previously sampled (Magnusson et al., 2010). Fluctuations in the population size of *N. lasiurus* over 22 years in a single plot were associated with local rainfall (Magnusson et al., 2010), which was largely controlled by the Southern Oscillation Index (SOI), which gives an indication of the development and intensity of El Niño or La Niña events in the Pacific Ocean by measuring the periodic interannual variation in global patterns of atmospheric and oceanic circulation that are correlated with variations in global climate patterns (Ropelewski and Halpert, 1987). Densities of *N. lasiurus* increased with the intensity of SOI and the extent of fire in the region. SOI affected rainfall and reduced the extent of fire. Nevertheless, the amount of rain had no measurable direct effect on mouse densities (Magnusson et al., 2010). The study by Magnusson et al. (2010) was carried out in a single plot of 4 ha, which is insufficient to capture regional fluctuations of the species, although studies on the population dynamics of rodents are often carried out in plots of similar or smaller size (e.g., Vieira, 2003; Rocha et al., 2011; Ribeiro et al., 2019). The studies by Layme et al. (2004); Ghizoni et al. (2005), and Magnusson et al. (2010) carried out in the Alter do Chão savanna suggested that the drivers of the population dynamics of the species can vary spatially and temporally.

To better understand the potential of climate change to impact the species, studies by Layme et al. (2004); Ghizoni et al. (2005), and Magnusson et al. (2010) were extended for another 9 years in eight permanent plots distributed over an area of approximately 16,000 ha (Magnusson et al., 2021). The aim of this study was to determine whether fluctuations in different areas were correlated, and whether these local fluctuations were related to climatic variables, such as local rainfall and SOI. The results showed that, considering all plots together, there was no effect of SOI or local rainfall. Overall, the density tended to decrease during the study period, with peaks in 2000, 2004, and 2013. However, a video of the density fluctuations throughout the period (Magnusson et al., 2021: supplement) indicated that there were three distinct clusters of plots in terms of geographic distribution and coordinated rates of change. *Necromys lasiurus* in individual plots do not form a population, and are influenced by immigration from neighboring plots. Grouping the data from each cluster, resulted in different conclusions. Density variations in one cluster were related to SOI, but those in the other clusters were not (Magnusson et al., 2021).

Since most studies of small mammals are carried out in a single plot of four hectares or less (e.g., Francisco et al., 1995; Magnusson et al., 2010; Rocha et al., 2011; Ribeiro et al., 2019), they might not reflect the regional population dynamics of small rodents. We are also wary of conclusions from studies undertaken when a species has very high densities. This facilitates field work and statistical analyses. Nevertheless, many species of rodents are at low density most of the time and what regulates densities of a species in the system may differ from the factors that affect its population dynamics when at high densities (Magnusson et al., 2021). Although our data clearly indicate that *N. lasiurus* at Alter do Chão is limited by invertebrate availability when at high densities, that might not explain most of the fluctuations in density. Global effects, such as SOI, and local rainfall may affect some areas, but much of the fluctuations in density seem to be unrelated to these phenomena. We suspect that the metapopulation dynamics of the mice are mainly affected by other factors, and a prime candidate for future studies is the effect of disease on local populations.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Corrigendum: *Necromys lasiurus*: Lessons From a 38-Year Study in an Amazonian Savanna

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A Corrigendum on

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There is an error in the Funding statement. The correct Name of one of the Funders is **Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brazil (CAPES)—PROEX n. 0742/2020**.

The correct Funding section is below:

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An author name was incorrectly spelled as ****Clarisa Alves Rosa****. The correct spelling is ****Clarissa Alves da Rosa****.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

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A Hollow Argument: Understory Vegetation and Disturbance Determine Abundance of Hollow-Dependent Mammals in an Australian Tropical Savanna

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Native mammals are suffering widespread and ongoing population declines across northern Australia. These declines are likely driven by multiple, interacting factors including altered fire regimes, predation by feral cats, and grazing by feral herbivores. In addition, the loss of tree hollows due to frequent, intense fires may also be contributing to the decline of hollow-dependent mammals. We currently have little understanding of how the availability of tree hollows influences populations of hollow-dependent mammals in northern Australian savannas. Here, we test the hypothesis that the abundance of hollow-dependent mammals is higher in areas with a greater availability of tree hollows. We used camera-trap data from 82 sites across the savannas of Melville Island, the largest island in monsoonal northern Australia. Royle–Nichols abundance-induced heterogeneity models were used to investigate the biophysical correlates of the abundance of three threatened mammals: northern brushtail possum (*Trichosurus vulpecula arnhemensis*), black-footed tree-rat (*Mesembriomys gouldii*), and brush-tailed rabbit-rat (*Conilurus penicillatus*). Our analyses included two variables that reflect the availability of tree hollows: the density of tree hollows, estimated from the ground, and the density of large eucalypt trees (*Eucalyptus* and *Corymbia* spp.). We found no evidence that the abundance of the three hollow-dependent mammals is positively associated with the availability of tree hollows on Melville Island. Despite their reliance on hollow-bearing trees for denning, the abundance of these mammals appears to be more strongly associated with other factors, such as the characteristics of the understory (i.e., shrub density), which affords protection from predators (including feral cats) and access to food resources. Future conservation management should aim to maintain a dense, diverse understory by managing fire and feral herbivores to facilitate the persistence of hollow-dependent mammals across northern Australia.

Keywords: cavity-bearing trees, eucalypts, fire management, land management, mammal decline, marsupials, tropical savanna, rodents

INTRODUCTION

Australia has lost around 10% of its native terrestrial mammal species since the arrival of Europeans almost 250 years ago (Short and Hide, 2012; Woinarski et al., 2015). Introduced predators and/or habitat modification have been implicated in the majority of mammal declines and extinctions in Australia (Woinarski et al., 2014, 2019). Mammal declines and extinctions have been pervasive and severe among species with a body size in the so-called "critical weight range" (35–5,500 g; Cardillo and Bromham, 2001; Johnson and Isaac, 2009). Whereas most mammal extinctions occurred in central and southern Australia before the mid-20th Century, there are now severe declines occurring across the vast, uncleared savanna landscapes of northern Australia (Woinarski et al., 2010, 2011). Drivers of these declines have been difficult to identify, despite being one of Australia's most pressing biodiversity conservation challenges. However, a recent conceptual model postulates that the decline of native mammals across northern Australia reflects the interaction between habitat degradation (through overgrazing by feral herbivores and livestock and altered fire regimes) and predation processes (Stobo-Wilson et al., 2020a).

A disproportionate number of mammals in northern Australian savannas that have experienced severe declines are arboreal and semi-arboreal species that are reliant on tree-hollows for denning (Taylor et al., 2003; Woinarski et al., 2011). Once common across the savannas, hollow-dependent mammals have typically contracted to the higher rainfall, higher productivity parts of their ranges (Woinarski et al., 2014; von Takach et al., 2020), where large trees and hollows are most abundant (Woolley et al., 2018). Existing studies have noted the importance of eucalypts as den trees for northern Australian arboreal rodents and marsupials (Griffiths et al., 2001; Firth, 2003; Hohnen et al., 2015; Penton et al., 2020b; Stobo-Wilson et al., 2021). Stobo-Wilson et al. (2021) demonstrated den tree selection by the savanna glider (*Petaurus ariel*) differed based on hollow availability, highlighting the influence of hollow limitation in lower rainfall areas of the tropical savannas.

It has been suggested that an increase in the frequency of high-intensity fires in recent decades has reduced the abundance of large hollow-bearing trees in northern Australia's savannas (Woolley et al., 2018), which likely has had a negative impact on hollow-dependent mammals (Firth et al., 2010; Woinarski et al., 2011). Studies from temperate forests in Australia and overseas show a loss in hollow-bearing trees is typically associated with a decline in hollow-dependent fauna (Lindenmayer and Cunningham, 1997; Aitken and Martin, 2008; Cockle et al., 2010). As such, there may be a direct link between the decline of hollow-dependent mammals in northern Australian savannas and fire-driven loss of tree hollows.

To investigate whether the availability of tree hollows limits populations of hollow-dependent mammals in a high-rainfall tropical savanna, we analyzed camera-trap data on Melville Island, the largest island in monsoonal northern Australia (**Figure 1**). We hypothesized that the availability of tree hollows would be strongly correlated with the abundance of hollow-dependent mammals on Melville Island, while the attributes of the understory, such as shrub density, would be of secondary importance.

MATERIALS AND METHODS

Study Site

Melville Island is situated approximately 25 km off the central coast of northern Australia, and is Australia's second-largest island (5,786 km^2) (**Figure 1**). Melville Island is the larger of the two main Tiwi Islands, a critical refuge for numerous mammal species that are in severe decline on the northern Australian mainland. However, recent evidence shows that mammals have declined on Melville Island over the last two decades (Davies et al., 2018). Although the declines have not progressed to the same extent as the mainland, the same processes are likely impacting the island populations (Stobo-Wilson et al., 2020a).

Melville Island experiences a tropical monsoonal climate, with over 90% of rainfall occurring in the wet season (Australian Bureau of Meteorology, 2020a). There is a substantial gradient in mean annual rainfall across the island, from 1,400 mm in the east to 2,000 mm in the north-west. Tropical savanna, dominated by tall eucalypts (predominantly *Eucalyptus miniata*, *Eucalyptus tetrodonta*, and *Corymbia nesophila*), covers 75% of the island (Woinarski et al., 2003). The understory is predominantly grassy, and shrub density is highly variable. Due to the high density of large trees, Melville Island generally supports a higher tree hollow densities than the adjacent mainland (Woolley et al., 2018; Penton et al., 2020a). Although hollow densities increase with mean annual rainfall across Melville Island, there is still substantial localized variability, driven by disturbance, such as tropical cyclones, fire, termite activity (Woolley et al., 2018). These forms of disturbance are particularly important drivers of hollow availability on Melville Island because the region is frequently exposed to severe tropical cyclones (Cook, 2001; Cook and Goyens, 2008), experiences very high fire frequencies (Richards et al., 2012), and has particularly high abundance and species richness of termites (Abensperg-Traun and Steven, 1997).

Study Species

We focused on three hollow-dependent, semi-arboreal mammals that once occurred across vast areas of northern Australia at the time of European arrival but are now in various stages of decline (Woinarski et al., 2011, 2014). All three are endemic to the tropical savannas. The northern brushtail possum (*Trichosurus vulpecula arnhemensis*) has declined severely (Stobo-Wilson et al., 2019), and remains abundant only in the highest-rainfall parts of its former range (von Takach et al., 2020), including the Tiwi Islands (Davies et al., 2018, 2021). The black-footed tree-rat (*Mesembriomys gouldii*) is one of Australia's largest rodents and has declined severely in both the Kimberley and mainland Northern Territory (Firth et al., 2010; von Takach et al., 2020), while the Melville Island subspecies (*M. g. melvillensis*) has also shown considerable decline (Davies et al., 2018). Finally, the brush-tailed rabbit-rat (*Conilurus penicillatus*) has experienced a very severe decline (Firth et al., 2010), and the Tiwi Islands subspecies (*C. p. melibius*) has displayed the same rapid pattern

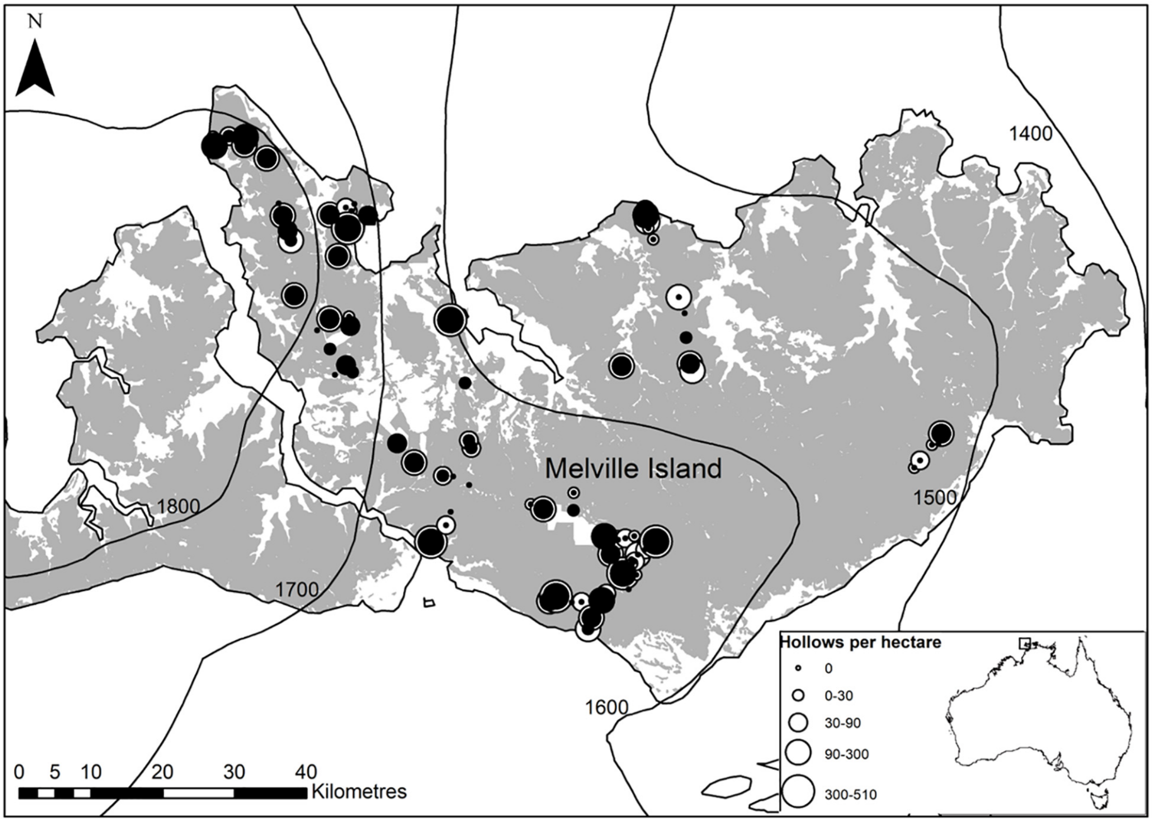

FIGURE 1 | Camera trap locations (Davies et al., 2018) and hollow surveyed sites (Penton et al., 2020a) across Melville Island, Northern Territory, Australia. Gray shading indicates eucalypt savanna and isohyets show the gradient in mean annual rainfall across the island. The diameter of the circles is proportional to the densities of hollows ≥5 cm entrance diameter in white and ≥10 cm entrance diameter in black at each site.

of decline on Melville Island (Davies et al., 2017). All three species (or subspecies in the case of the northern brushtail possum) are listed as Vulnerable under Australia's Environment Protection and Biodiversity Conservation Act (1999). Both rodents are listed as Vulnerable on the IUCN Red List (Burbidge and Woinarski, 2016; Woinarski and Burbidge, 2016).

Penton et al. (2020b) recently identified that the brush-tailed rabbit-rat, black-footed tree-rat, and northern brushtail possum predominantly den in large hollows (≥10 cm entrance diameter), which are generally found in large eucalypt trees [≥30 cm diameter at breast height (DBH), 1.3 m]. Large hollows are relatively scarce in northern Australia's tropical savannas (estimated as only 10% of all hollows in the landscape), and trees with large hollows are particularly vulnerable to disturbance (Murphy and Legge, 2007; Woolley et al., 2018).

Data Collection of Hollow-Dependent Mammal Abundance

In 2015, camera trap surveys were conducted at 88 sites across the lowland savannas of Melville Island (Davies et al., 2017), which had been selected from previous surveys in 2000–2002 (see Firth et al., 2006a). Davies et al. (2017) selected the subset of sites located within savanna woodland, stratified by fire frequency and rainfall, separated by a minimum distance of 1 km. Each site was surveyed with five horizontally facing motion-sensor cameras deployed in a square formation around a central camera, with 50 m between the central and outermost cameras. A bait station consisting of peanut butter, oats, and honey was placed 1.5 m from two of the five cameras, whereas the remaining three cameras at each site had a bait station placed 2.5 m from the camera (Gillespie et al., 2015). Vegetation within each camera's field of view was cleared to create a fire break and reduce the chance of false triggers, extending battery life. Of the five cameras deployed at each site, two were HC550 Hyperfire white-flash cameras, whereas the remaining three cameras PC800 Hyperfire Professional infra-red flash cameras (Reconyx, Inc., Holmen, WI, United States). Cameras could be triggered at any time of day and were set to a high sensitivity, with cameras programmed to take three images per trigger, with a 1-s interval between images. The cameras were deployed for at least 35 consecutive days (range 35–53 days).

This dataset has been analyzed previously by Davies et al. (2017, 2018), to investigate environmental correlates of the site-occupancy of mammals on Melville Island. However, due to very high site-occupancy rates for both the black-footed tree-rat and northern brushtail possum (Davies et al., 2018), occurring at most sites across the island, and gregarious social structure of the brush-tailed rabbit-rat (i.e., strong spatial clustering of populations; Firth et al., 2006b; Penton et al., 2020b), we considered that abundance was a more appropriate response variable (cf., site occupancy) to test our hypothesis. Hence, we used Royle–Nichols abundance-induced heterogeneity models, which assume that heterogeneity in detection frequency is indicative of variability in a species' abundance (Royle and Nichols, 2003).

Tree Hollow Availability and Other Environmental Variables

Davies et al. (2017, 2018) investigated a range of environmental correlates of site-occupancy of the brush-tailed rabbit-rat, black-footed tree-rat, and northern brushtail possum. We used similar environmental variables, but to evaluate the influence of the availability of tree hollows and hollow-bearing trees on the abundance of hollow-dependent mammals, we revisited the mammal survey sites in 2017, 2 years after the original survey, and measured two additional variables: (1) hollow density and (2) density of large eucalypts (which are more likely to contain numerous hollows; Woolley et al., 2018; **Table 1**). Six of the sites surveyed in 2015 could not be resurveyed in 2017 and were excluded from the analysis, leaving 82 sites (**Figure 1**).

At each site, a random central reference point was selected following the plotless "point centered quarter" method (Krebs, 1999). To increase number of points sampled up to 12 trees (alive or dead) with a DBH of ≥15 cm closest to the central point, equally represented in each quadrant were selected for hollow surveys, which produced a total sample of 963 trees across 82 sites. The hollows in the selected trees were counted from the ground using binoculars. A hollow was defined as having an entrance diameter of ≥5 cm. All ground-based surveys were performed by one individual (CP) and were conducted in good light and weather conditions for optimal visibility (e.g., no rain or mist). A minimum of 2 min was spent surveying each tree for hollows from all available vantage points. We recorded the total number of hollows in two entrance diameter classes (5–10 cm and ≥10 cm) for each tree. Due to the high frequency of termitaria blocking hollows <10 cm entrance diameter, we calibrated 5–10 cm hollows before calculating total hollow counts (≥5 cm and ≥10 cm entrance diameter) using a subset of trees that were double sampled with climbing surveys (Penton et al., 2020a).

We also recorded calculated large eucalypts (dead or alive) ≥30 cm DBH at each site from the original tree dataset, which produced a sub-sample of 465 trees across the 82 sites. We calculated hollow and large eucalypt densities using the plotless "point-centered quarter" method where the area around the random point is divided into four quadrants, and the distance to the nearest tree is measured in each quadrant:

$$\mathit{Estimated}\ \text{density}\ \left(h\mathrm{a}^{-1}\right)\ = \frac{4\ \left(4\left(n\right)-1\right)}{\pi\,\Sigma\left(r_{ij}2\right)}$$

Where n is the number of samples and r_{ij} is the distance (m) from random point i to the closest individual in quarter j (Krebs, 1999; Jamali et al., 2020).

TABLE 1 | Description of the variables used in the analyses to assess the correlates of Melville Island arboreal mammal distribution in 2015.

Environmental variable	Coding	Measurement
Mean annual rainfall	Continuous, centered, and standardized	Mean annual rainfall (mm per annum) (Australian Bureau of Meteorology, 2020b)
Distance to watercourse	Continuous, centered, and standardized	The distance (m) from each site to the closest watercourse derived from Geoscience Australia DEM SRTM 1 Second Hydrologically Enforced Map
Dingoes	Categorical	Presence/absence of dingoes. If a dingo was recorded once at the site, it was recorded as present
Large feral herbivores	Categorical	Presence/absence of large feral herbivores. If a feral herbivore was recorded once at the site, it was recorded as present. Feral herbivores included water buffalo (*Bubalus bubalis*) and horse (*Equus caballus*)
Feral cat activity	Continuous, centered, and standardized	As an index of feral cat activity. We used the predicted probability of detecting feral cats at each site, derived from spatially explicit generalized linear models (Murphy et al., 2010)
Fire frequency	Continuous, centered, and standardized	The number of times a site had been burned in the previous 5-year period (Lawes et al., 2015) immediately before the faunal survey (2015) from the Northern Australia Fire Information (NAFI) dataset (www.firenorth.org.au)
Coarse woody debris	Continuous, centered, and standardized	A count of the number of logs with a diameter of >5 cm that crossed a 200 m long transect at each site
Shrub density	Continuous, centered, and standardized	A count of the number of shrubs in a 1 m × 100 m quadrat at each site. Shrubs were defined as anything taller than 20 cm but shorter than 1.3 m or taller than 1.3 m with a diameter at breast height of <5 cm. Shrubs with multiple stems were counted as a single individual
*Large eucalypt density**	Continuous, centered, and standardized	Plotless PCQ method surveying eucalypts ≥30 cm DBH (dead or alive) at each site
*Hollow density**	Continuous, centered, and standardized	Plotless PCQ method surveying trees ≥15 cm DBH for hollows 5–10 cm and ≥10 cm entrance diameter. Hollows 5–10 cm were calibrated before calculating total hollows ≥5 cm entrance diameter for the brush-tailed rabbit-rat and ≥10 cm entrance diameter for the larger bodied species at each site

**Between the faunal surveys and commencement of tree surveys Melville Island did not experience any major disturbances at the study sites (i.e., tropical cyclones or late dry season high-intensity wildfires). Six sites were burned between 31/07/2016 and 08/08/2016 (NAFI) just after the carbon abatement cut-off date, though this was not a high-intensity burn.*

Penton et al. (2020b) found that den tree selection was significantly correlated with the presence of a large hollow (i.e., ≥10 cm entrance diameter) in that tree. They found that the brush-tailed rabbit-rat used tree hollows with an entrance diameter ≥5 cm. Hence, for this species, we calculated hollow density using hollows with an entrance diameter ≥5 cm (Penton et al., 2020b). For the larger-bodied species (black-footed tree-rat and northern brushtail possum), which tend to use larger hollows, we calculated hollow density using only hollows with an entrance diameter ≥10 cm.

Data Analysis

All analyses were undertaken in the statistical program R (R Core Team, 2020). To examine the relationship between the abundance of three hollow-dependent species and our ten environmental variables (**Table 1**), we used Royle–Nichols abundance-induced heterogeneity models (Royle and Nichols, 2003) in the R package "unmarked" (Fiske and Chandler, 2011).

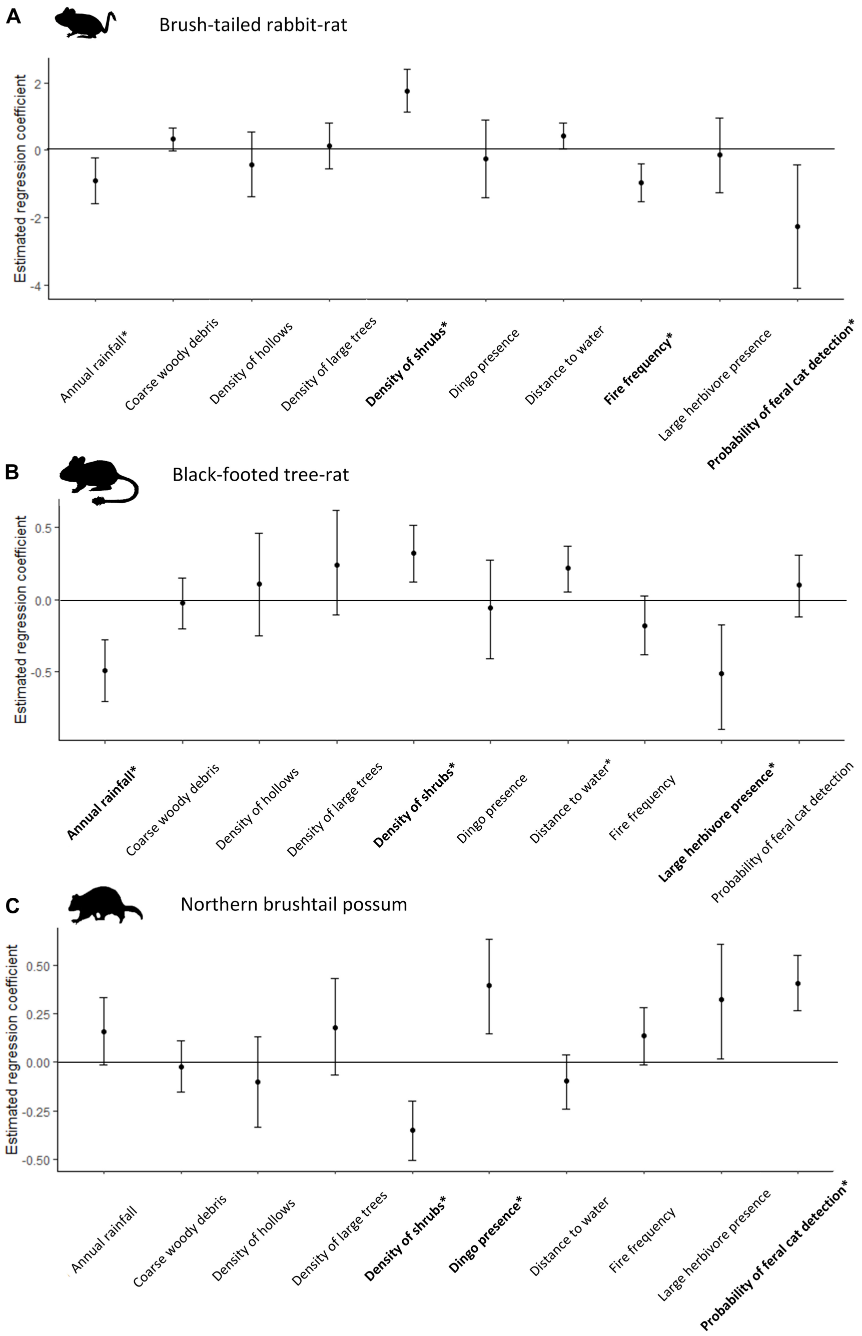

FIGURE 2 | Coefficient estimates for **(A)** brush-tailed rabbit-rat; **(B)** black-footed tree-rat; and **(C)** northern brushtail possum from the global model. Error bars indicate 95% confidence intervals; asterisks indicate where they do not overlap zero, i.e., a statistically significant effect and covariates in bold are for which there was clear evidence of a relationship from the Royle–Nichols models (**Table 2**).

This model assumes that heterogeneity in detection frequency is indicative of variability in a species' abundance by assuming there is a constant probability of detecting each individual, and detections are independent. We created nightly detection histories for each of the three mammal species at each site by dividing the camera surveys into 24-h sampling occasions. Mammal detections were combined for all cameras at each site.

We developed a set of 1,024 candidate models to explain variation in the abundance of each mammal species. This represented all combinations of the ten environmental variables, with no interactions. Models were ranked and evaluated using Akaike's Information Criterion (AIC). All continuous environmental variables were log-transformed, then centered and standardized by deducting the mean and then dividing by twice the standard deviation (Gelman, 2008). We confirmed that there was not excessive collinearity among environmental variables by examining the variance inflation factor (VIF). Following Zuur et al. (2010), we used a conservative VIF threshold of 3; if a variable had VIF > 3 we removed it. We further screened collinearity of variables with known associations (e.g., feral cat activity and fire frequency) with Pearson's correlation coefficient, r, to confirm all variables had a weak or negligible correlation (i.e., $r < 0.45$). We checked for spatial autocorrelation in the residuals of the global model by visually examining variograms of the model residuals and conducted a Moran's I test on the residuals of a linear regression global model with a response variable of total nights the species was recorded at a site in R package "ape" (Paradis and Schliep, 2019); brush-tailed rabbit-rat Moran's $I = 0.08$, $p < 0.001$; black-footed tree-rat Moran's $I = 0.05$, $p = 0.05$; northern brushtail possum Moran's $I = 0.08$, $p = 0.002$ indicating very weak spatial autocorrelation (Moran, 1950).

The abundance of arboreal mammals has been shown to have a "humped response" to hollow availability (Wormington et al., 2002). Thus, we initially considered a quadratic function (i.e., humped relationship) between the abundance of the three mammal species and each of hollow density and large eucalypt density. However, there was no evidence that quadratic relationships were more suitable than linear relationships. We also examined interactions between shrub density and large eucalypt density, the inclusion of the interaction terms did not substantially improve the best models (i.e., AIC reduced by ≥ 2).

We created a global model, including all ten environmental variables, and plotted the standardized coefficients to evaluate the relative effect sizes of each variable (**Figure 2**). Variables that occurred in all of the well-supported models ($\Delta \text{AIC} \leq 2$; **Table 2**) were considered important environmental variables.

RESULTS

There was significant variability in the density of tree hollows and large eucalypts across Melville Island (**Figure 1** and **Table 3**). Across all sites sampled, the mean density of hollows (entrance diameter ≥ 5 cm) was 91 ha^{-1} (±12 SE), ranging from 0 to 503 ha^{-1}. Of this, larger hollows (entrance diameter ≥ 10 cm) contributed 37 ha^{-1} (±7 SE), ranging from 0 to 286 ha^{-1}. Larger hollows were present at only half of the sites surveyed. The mean density of large eucalypts was 66 ha^{-1} (±7 SE), ranging from 0 to 336 (**Table 3**).

We found no evidence that the abundance of the three hollow-dependent mammals was correlated with the density of tree hollows or large eucalypts. Neither hollow density nor large eucalypt density consistently appeared in well-supported models (**Table 2**).

The abundance of all three hollow-dependent mammals was strongly correlated with shrub density. This variable appeared in all well-supported models (**Table 2**). However, the direction of the relationship varied between species, being positive for the brush-tailed rabbit-rat and black-footed tree-rat, which were more abundant at shrubby sites (**Figures 2A,B**), but negative for the northern brushtail possum, which was less abundant at shrubby sites (**Figure 2C**).

Brush-tailed rabbit-rat abundance was strongly negatively correlated with cat activity and fire frequency (**Table 2A** and **Figure 2A**). Black-footed tree-rat abundance was negatively correlated with mean annual rainfall and feral herbivore presence (**Table 2B** and **Figure 2B**). Northern brushtail possum abundance was positively correlated with dingo presence and cat activity (**Table 2C** and **Figure 2C**).

Overall detectability from the best model ranged from 0.86 for the brush-tailed rabbit-rat to 0.99 for both the black-footed tree-rat and northern brushtail possum (**Appendix 1**).

DISCUSSION

We investigated the hypothesis that the availability of tree hollows strongly limits the abundance of hollow-dependent mammals. Despite significant variation in tree hollow availability across Melville Island, we found no evidence to support this hypothesis. We found that factors relating to the quality of the understory (i.e., shrub density, fire frequency, large herbivore presence) and predator assemblages (i.e., predicted cat activity, dingo presence) were stronger correlates of hollow-dependent mammal abundance on Melville Island, than were arboreal habitat features (i.e., hollow density, density of large eucalypts). Our study suggests that a disturbance-driven reduction in the availability of tree hollows has not played a significant role in driving the decline of hollow-dependent mammals on Melville Island, indicating that hollows are not limiting at this region. Rather, patterns of abundance are more strongly influenced by other factors associated with understory habitat quality and ground-based threats (i.e., shrub density and impacts of feral animals). This finding is consistent with recent studies of patterns of the abundance of small mammals across northern Australia more broadly (Davies et al., 2018; Legge et al., 2019; Stobo-Wilson et al., 2019, 2020a).

Although large hollows occur at varying densities across northern Australia's tropical savannas (Woolley et al., 2018), denning behaviors may compensate for variable availability of

TABLE 2 | Model ranking table for the abundance three arboreal mammal species examined on Melville Island 2015: **(A)** brush-tailed rabbit-rat; **(B)** black-footed tree-rat; **(C)** northern brushtail possum.

Response	Mean annual rainfall	Distance to water	Dingo presence/ absence	Feral cat detection probability	Large herbivore presence/ absence	Fire frequency	CWD	Density of shrubs	Density of large eucalypt trees	Hollow density	ΔAIC	wi	Nagelkerke R-squared index
(A) Brush-tailed rabbit-rat Null model; AIC = 624.7, logLik = −308.3	•	•		•		•	•	•			0.0	0.08	0.59
	•			•		•	•	•			0.7	0.13	0.59
	•	•		•		•	•	•		•	1.3	0.17	0.58
				•		•	•	•			1.4	0.20	0.60
	•	•		•		•		•			1.5	0.24	0.57
	•	•	•	•		•	•	•			1.7	0.27	0.58
	•	•		•	•	•	•	•			1.8	0.30	0.60
	•	•		•		•	•	•	•		1.9	0.33	0.60
(B) Black-footed tree-rat Null model = 2134.3, logLik = −1063.1	•	•			•	•		•			0.0	0.03	0.29
	•	•			•			•			0.4	0.06	0.27
	•	•			•			•	•		0.5	0.08	0.29
	•	•			•	•		•	•		0.6	0.11	0.30
	•	•			•			•		•	0.7	0.13	0.29
	•	•		•	•	•		•			1.0	0.15	0.30
	•	•			•	•		•		•	1.3	0.17	0.30
	•	•			•			•	•	•	1.5	0.18	0.30
	•	•		•	•	•		•	•		1.6	0.20	0.31
	•	•	•		•	•		•			1.7	0.21	0.30
	•	•			•	•	•	•			1.9	0.22	0.30
	•				•	•		•			2.0	0.24	0.26
(C) Northern brushtail possum Null model; AIC = 3522.1, logLik = −1757.0	•		•	•	•	•		•			0.00	0.04	0.57
			•	•	•	•		•			0.2	0.07	0.56
			•	•	•			•			0.5	0.10	0.54
	•	•	•	•	•	•		•			0.8	0.12	0.57
	•		•	•	•	•		•	•		1.0	0.15	0.57
		•	•	•	•	•		•			1.0	0.18	0.56
	•		•	•	•			•			1.0	0.19	0.55

(Continued)

TABLE 2 | (Continued)

Response	Mean annual rainfall	Distance to water	Dingo presence/ absence	Feral cat detection probability	Large herbivore presence/ absence	Fire frequency	CWD	Density of shrubs	Density of large eucalypt trees	Hollow density	ΔAIC	wi	Nagelkerke R-squared index
		●	●	●	●			●			1.1	0.21	0.55
			●	●	●	●		●	●		1.6	0.23	0.56
	●	●	●	●	●			●			1.6	0.25	0.56
	●	●	●	●	●	●		●	●		1.7	0.26	0.58
	●	●	●	●	●	●		●	●		1.7	0.26	0.57
	●		●	●	●	●		●		●	1.7	0.28	0.55
			●	●	●			●	●		1.8	0.30	0.56
	●	●	●	●		●		●			1.8	0.31	0.57
		●	●	●	●	●		●	●		1.9	0.32	0.56
			●	●	●	●		●		●	1.9	0.34	0.55
			●	●	●			●		●	2.0	0.35	0.57

*Royle–Nichols models were ranked according to ΔAIC and w_i is the Akaike weight. The set of candidate models (n = 1,023 models per species) included all combinations of explanatory variables (**Table 1**), but only models with an ΔAIC ≤ 2 are shown. The AIC and logLik are included for the null model of each species. ● is the cumulative AIC weight. Pseudo R-squared is Nagelkerke's (1991) index. The shading indicates variables for which there is clear evidence of a relationship (i.e., the variable appears in all models with ΔAIC ≤ 2).*

TABLE 3 | The density of hollows and large eucalypts across the 82 sites surveyed on Melville Island.

Variables	Mean (±SE)	Median (range)	Proportion of sites present (%)
≥5 cm hollow density	91 (±12) ha^{-1}	55 (0–503) ha^{-1}	85
≥10 hollow density	37 (±7) ha^{-1}	3 (0–286) ha^{-1}	50
Large eucalypt density	66 (±7) ha^{-1}	54 (0–336) ha^{-1}	93

The mean density, standard error, median and range of each variable. The percentage of total sites surveyed where hollows (≥5 cm and ≥10 cm) and large eucalypts were recorded present.

hollows in mesic savannas on Melville Island. The hollow-dependent mammals we studied have been shown to use 2–6 dens in a fortnightly period, overlap in home range, and often use hollows of similar attributes (Penton et al., 2020b, 2021). Northern Australian arboreal mammals may also be more socially tolerant (Kerle, 1998), allowing them to adapt their denning behavior (e.g., increase their propensity to share dens) in areas where hollows are limiting (Banks et al., 2011). All three species use dens other than tree hollows, including hollow logs on the ground, the canopy of the arborescent monocotyledon *Pandanus spiralis*, and dreys (nests of dried leaves and twigs; Griffiths et al., 2001; Firth et al., 2006b; Penton et al., 2020b). Anecdotal evidence suggests that arboreal mammals were in higher abundance prior to European arrival across northern Australian savannas (Woinarski et al., 2011). In areas containing lower densities of hollow-bearing trees, it is likely that alternative den sites may have been used more frequently or at higher rates than recorded more recently. Current threats may be amplified where alternative den uptake is higher (i.e., in areas where hollow densities are lower) as there may be a higher risk of predation or exposure to disturbances such as high intensity fires when denning at or near ground level (Leahy et al., 2016). Therefore, hollow densities below a certain threshold may limit and impact the persistence of populations of hollow-dependent mammals.

The three hollow-dependent mammal species we studied demonstrate varying levels of arboreal behavior, spending time foraging and traveling across the savanna floor due to the open canopy structure of tropical savannas (Friend, 1987; Kerle, 1998; Griffiths et al., 2001; Firth et al., 2006b). The brush-tailed rabbit-rat dens close to the ground or in hollow logs on the ground and spends much of its time foraging for grass seeds (Firth et al., 2005, 2006b; Penton et al., 2020b). Though the black-footed tree-rat dens higher in the canopy (Penton et al., 2021), its reliance on fruiting shrubs, and its large home range (Friend, 1987; Pittman, 2003; Rankmore, 2006) suggests that this species frequently moves across the savanna floor. In comparison, the northern brushtail possum likely spends less time on the savanna floor as it has a smaller home range and does not exhibit large movements across the savanna (Kerle, 1998; Woinarski, 2004; Rankmore, 2006). Irrespective, all three species spend significant amounts of time on the ground foraging and moving across the savanna floor. The amount of time these species spend on the ground, and their reliance on understory and midstory resources, supports why we found the strongest correlates of abundance to be related to the quality of understory and predator assemblage, rather than the availability of tree hollows.

Despite having undergone a severe decline elsewhere in northern Australia (Woinarski et al., 2010; Stobo-Wilson et al., 2019), it appears that the northern brushtail possum is stable on Melville Island (Davies et al., 2018) even in disturbed areas (i.e., high cat activity and large herbivore presence). This may indicate that the northern brushtail possum is more resilient to these ground-based threats than the two rodent species examined in our study. The northern brushtail possum may spend a greater amount of time in the sub-canopy, as it preferentially feeds on flowers and fruits from *Acacia difficilis*, *Grevillea pteridifolia, Acacia bivenosa*, and *Ficus* spp. (Kerle and Burgman, 1984; Cruz et al., 2012). Historically, the distribution of the northern brushtail possum included areas of relatively low productivity. Although in more recent decades the contraction to higher rainfall areas of northern Australia and patchy distribution of northern brushtail possum populations has been attributed to a reliance on less disturbed areas that support dense and diverse foliage (Kerle and Burgman, 1984; Stobo-Wilson et al., 2019). Thus, while the decline of the northern brushtail possum on the mainland has been less severe than that of the rodents, it seems to be negatively affected by similar threats – most likely cat predation and reduction in habitat complexity – in the long-term.

The two rodent species in our study (black-footed tree-rat and brush-tailed rabbit-rat) may be particularly vulnerable across northern Australia because they are reliant on multiple vegetation strata, namely a shrubby understory and overstorey of hollow-bearing trees (Friend, 1987; Firth et al., 2006b; Penton et al., 2020b), and because they respond negatively to ground-layer disturbances including fire (Davies et al., 2017) and large herbivores. This habitat use will limit these species to areas with little disturbance to access adequate food resources and shelter. Simplification of understory habitat by overgrazing and frequent high-intensity fires likely reduces the availability of food resources while increasing the exposure of mammals to predation (Leahy et al., 2016; Legge et al., 2019). Native rodents may be more susceptible to feral cat predation as they represent the majority of native mammals killed Australia-wide, with this offtake strongly concentrated in northern Australia (Pearre and Maass, 1998; Murphy et al., 2019). Disturbances such as high-intensity fire and heavy grazing by feral herbivores can offer significant advantages to feral cats by simplifying the understory, increasing hunting efficiency (Davies et al., 2020; Stobo-Wilson et al., 2020a,b). Feral herbivores may also create "game trails," which facilitate the movement of cats and dingoes through the savanna (Leahy et al., 2016; McGregor et al., 2016; Davies et al., 2020). The question of why semi-arboreal and arboreal mammals have been disproportionally represented among declining mammals in northern Australia has not yet been resolved by this study. It is clear from our results that simply maintaining high densities of hollows in places such as Melville Island may not be sufficient to prevent further decline of hollow-dependent mammals.

Implications for Future Research and Management

Due to the higher densities of hollow-bearing trees on Melville Island compared to the mainland (Woolley et al., 2018), we are unable to speculate as to whether the depletion of tree hollows has contributed to the broad-scale decline of arboreal mammals in northern Australia. Frequent late dry-season fires have been shown to impact the density of suitable hollows for the threatened Gouldian finch (*Erythrura gouldiae*) in northern Australia (Radford et al., 2021). In habitats with low hollow densities, the frequent utilization of alternative dens (e.g., hollow logs, *Pandanus spiralis*) may expose individuals to greater predation risk and impact breeding success, particularly after fire (Leahy et al., 2016; Penton et al., 2020b). Future research should evaluate how mammal abundance varies with hollow availability across larger spatiotemporal scales to address whether frequent high-intensity fires have contributed to the dramatic decline of hollow-dependent arboreal species in northern Australia. Manipulative experiments using nest boxes could also provide insights into whether an increase in denning resources leads to an increase in native mammal abundance.

It is essential that the conservation management of native mammals in tropical savannas focuses on maintaining a complex and diverse understory. Studies on the northern Australian mainland have shown shrub density is strongly influenced by fire regimes, with frequent, high-intensity fires tending to reduce shrub density (Edwards et al., 2003, 2018; Russell-Smith et al., 2003). The impacts of which are also likely exacerbated by high feral herbivore densities (Legge et al., 2019). There needs to be a greater exploration of how frequent fires, even those of low intensity, influence vegetation structure and diversity, especially in relation to the shrub and grass layers, which provide critical shelter from predators and also provide food resources (e.g., fruits, flowers, and seeds; Bowman, 1988; Fensham, 1990; Paramjyothi et al., 2020). In the relatively intact savannas of northern Australia, such as Melville Island, management should aim to conserve hollow-bearing trees while retaining dense and complex under-and mid-story vegetation, which appears to be essential for the conservation of hollow-dependent arboreal mammal species.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by permission for animal use was authorized by the Charles Darwin University Animal Ethics Committee (A16002) and the Northern Territory Department of Flora and Fauna (Permit to Interfere with Protected Wildlife No. 58472).

AUTHOR CONTRIBUTIONS

CP, BM, IR, L-AW, and HD conceived the idea for this chapter. TR, HD, and CP collected all the data for this chapter. CP completed all the analyses with support from HD and wrote the draft of the chapter. HD, L-AW, IR, and BM provided the editorial comments on the chapter. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: TR was employed by company Tiwi Resources Pty., Ltd., Casuarina, NT, Australia.

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

APPENDIX

Appendix 1 | Comparison of the nightly probability of detection and the overall probability of detection (over 36–53 nights) for the null model (where relative abundance and detectability parameters are assumed to be constant across all survey sites) and the most parsimonious Royle–Nichols occupancy model.

Species	Model	Night detection probability (P) (±SE)	Overall detection probability
Brush-tailed rabbit-rat	Null model	0.10 (±0.02)	0.99
	Best model	0.04 (±0.04)	0.86
Black-footed tree-rat	Null model	0.11 (±0.01)	0.99
	Best model	0.10 (±0.01)	0.99
Northern brushtail possum	Null model	0.13 (±0.01)	0.99
	Best model	0.10 (±0.01)	0.99

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Landscape-Scale Effects of Fire, Cats, and Feral Livestock on Threatened Savanna Mammals: Unburnt Habitat Matters More Than Pyrodiversity

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Northern Australia has undergone significant declines among threatened small and medium-sized mammals in recent decades. Conceptual models postulate that predation by feral cats is the primary driver, with changed disturbance regimes from fire and feral livestock in recent decades reducing habitat cover and exacerbating declines. However, there is little guidance on what scale habitat and disturbance attributes are most important for threatened mammals, and what elements and scale of fire mosaics actually support mammals. In this study, we test a series of hypotheses regarding the influence of site-scale (50 × 50 m) habitat and disturbance attributes, as well as local-scale (1 km radius), meta-local scale (3 km), landscape-scale (5 km) and meta-landscape scale (10 km) fire mosaic attributes on mammal abundance and richness. We found that habitat cover (rock, perennial grass, and shrub cover) at the site-scale had a positive effect, and disturbance factors (feral cats, fire, feral livestock) had a negative influence on mammal abundance and richness. Models supported site-scale habitat and disturbance factors as more important for mammals than broader-scale (local up to meta-landscape scale) fire mosaic attributes. Finally, we found that increasing the extent of $\geq$ 4 year unburnt habitat, and having an intermediate percentage (ca. 25%) of recently burnt (1-year burnt) habitat within the mosaic, were the most important functional elements of the fire mosaic at broad scales for mammals. Contrary to expectations, diversity of post-fire ages ('pyrodiversity') was negatively associated with mammal abundance and richness. These results highlight the need for management to promote retention of longer unburnt vegetation in sufficient patches across savanna landscapes (particularly of shrub and fruiting trees), maintain low-intensity patchy fire regimes, reduce the extent of intense late dry season wildfires, and to reduce the impact of feral livestock. This study provides further evidence for the role of feral cats in northern Australian mammal declines, and highlights the need for increased research into the efficacy of cat control methodologies in reducing biodiversity impacts in these extensive landscapes.

Keywords: critical weight range mammals, conceptual models, feral cats, fire mosaics, feral livestock, explanatory variables, population dynamics

INTRODUCTION

Australia has the dubious distinction during the previous two centuries of having the highest number of mammalian extinctions; 21 out of the 230 non-volant mammals present at European colonization are now gone, and another 23 have disappeared from most of their former range (Woinarski et al., 2014). While many of these extinctions occurred in the early years of European colonization in southern and arid Australia (Johnson, 2006), more recent declines in the tropical savannas of northern Australia have occurred in areas that had relatively intact mammal assemblages right up until the 1990's and early 2000's, up to a century after many of the previous declines occurred (Braithwaite and Muller, 1997; Woinarski et al., 2001, 2010).

In Northern Australia it has been unclear what the primary mechanisms behind declines might be, and a range of hypotheses have been raised (Woinarski et al., 2001, 2010, 2011; Andersen et al., 2005; Ziembicki et al., 2015). These include predation by feral cats (Frank et al., 2014; McGregor et al., 2016), changes in the influence of dingoes, either directly on mammals, or via impacts on feral cats (Kennedy et al., 2012), changed fire regimes and management (Woinarski et al., 2010; Lawes et al., 2015; Radford et al., 2015, Radford et al., 2020a), pastoralism and feral livestock (Legge et al., 2011, 2019; Radford et al., 2015), cane toad invasion (Ziembicki et al., 2015; Radford et al., 2020b), declining ecosystem productivity due to changed disturbance regimes (McKenzie et al., 2007), disease or pathogens (Ziembicki et al., 2015) and climate change (Braithwaite and Muller, 1997; Ziembicki et al., 2015). However, no single mechanism explains mammal declines across northern Australia.

Australia wide, mammalian extinctions and declines have primarily been attributed to introduced predators, particularly the feral cat (*Felis catus*) and the red fox (*Vulpes vulpes*) based on the historical coincidence of arrival of predators with mammal declines and extinctions (Dickman, 1996; Johnson, 2006) and also on fenced cat exclosure experiments (Moseby et al., 2009; Frank et al., 2014; Tuft et al., 2021). The most parsimonious explanation for mammal declines in northern Australia is that cats are driving this decline too (though not foxes as they do not persist in the tropics). However, cats have co-existed in northern Australia with intact mammal faunas for ca. a century since they first established in the 1890's (Abbott, 2002).

What then could have led to increased predation impacts of feral cats in northern Australia leading to the most recent savanna mammals declines? Recent studies have shown that cats preferentially hunt (McGregor et al., 2014, 2015), have higher kill rates (McGregor et al., 2016) and have greater impacts on small mammal prey in open, recently burnt savannas, or in habitats heavily disturbed by feral livestock (McGregor et al., 2015; Leahy et al., 2016; Shaw et al., 2021). Feral cat activity is thus greatest in areas under severe disturbance regimes, such as frequent high severity fires and/or high feral livestock activity; which is mechanistically linked to repeated removal of ground-layer vegetation and suppression of plant regrowth (McGregor et al., 2015; Legge et al., 2019; Davies et al., 2020). Conceptual models explaining northern Australian mammal declines now postulate predation by feral cats as the primary driver, but that changed disturbance regimes in recent decades (e.g., fire regimes and feral livestock grazing pressure) have reduced habitat cover and productivity, thereby exacerbating predation impacts on small mammals (Johnson, 2006; McKenzie et al., 2007; Radford et al., 2014; Ziembicki et al., 2015; Legge et al., 2019; Stobo-Wilson et al., 2020a).

Studies have now linked regional patterns of mammal abundance and richness with cat occupancy, disturbance regimes and vegetation cover, providing some support for these conceptual models (Davies et al., 2017, 2020; Radford et al., 2020a; Stobo-Wilson et al., 2020a; Penton et al., 2021). However from a management perspective, it is still unclear what site-scale habitat or disturbance features support or threaten mammal assemblages. Although we know that applying low intensity prescribed burning mosaics to savannas can lead to declines in the extent of damaging late dry season wildfires, and benefits to savanna mammals (Radford et al., 2020a), it is unclear which fire mosaic attributes specifically are important (or *functional* as per Parr and Andersen, 2006) in supporting local population increases or decreases. Moreover, it is unclear at what scale (local, landscape, regional) these functional mosaic attributes are essential for savanna mammals. Such questions are crucially important if conservation managers are to design the most appropriate interventions for threatened species at the local, landscape and regional scale across vast savanna landscapes in northern Australia.

In this study we use repeated measures analysis to test for the relative importance of site-linked habitat and disturbance attributes, and landscape-scale fire mosaics, in driving site-based mammal abundance and richness in north-west Australia. Uniquely, this longitudinal study spans nine years (2011–2019) and includes study sites stratified between rocky and non-rocky savannas, due to previously described compositional differences between mammal communities in these habitats (Radford et al., 2014; Radford et al., 2020a). Repeated measures analysis allows us to assess the importance of dynamic habitat and disturbance factors, including episodic fire events, in driving mammal population trends at the site scale. This contrasts with recent single time-step analyses (Radford et al., 2015; Davies et al., 2017; Stobo-Wilson et al., 2020a). By examining site-level fixed and dynamic habitat and disturbance factors, we can further scrutinize fine-scale vegetation and disturbance dynamics most relevant to on-ground management for improving mammal abundance and richness. Additionally, by testing for the relationship between fire regime attributes from local up to landscape and sub-regional scales, we can elucidate the most important functional components of fire mosaics for threatened savanna mammals.

Here, we test the following hypotheses: (1) That mammal abundance and richness is highest with increasing site-scale ground layer habitat cover/complexity (Radford et al., 2015, Radford et al., 2020a; Davies et al., 2017, 2020; Stobo-Wilson et al., 2020a); (2) that mammal abundance and richness is highest at sites where predator (feral cat and dingo), fire and cattle 'disturbance' is least prevalent or abundant (McGregor et al., 2014, 2015, 2016; Lawes et al., 2015; Radford et al., 2015; Leahy et al., 2016; Stobo-Wilson et al., 2020a,b; Shaw et al., 2021); (3) that site- and local-scale fire mosaic attributes will be more influential on mammal abundance and richness than broader landscape- or subregional-scale mosaic attributes due to recolonization/dispersal limitations for some mammal species (Leahy et al., 2016; Shaw et al., 2021); and (4) the most important attributes of local and landscape fire mosaics will be presence of longer unburnt habitat based on previous observations (e.g., Legge et al., 2008; Radford et al., 2015, Radford et al., 2020a) and that pyrodiversity (diversity of post-fire habitat age) will be positively associated with mammal abundance and richness based on patch mosaic burning theory (critiques by Parr and Andersen, 2006; Jones and Tingley, 2021).

MATERIALS AND METHODS

Study Area

The study area is the Northern Kimberley biogeographic region of north-western Western Australia (**Figure 1**). The region experiences a tropical monsoonal climate, with high temperatures year-round (daily mean maximum 29.6–36.0°C) and high rainfall (900–1550 mm) occurring predominantly during the warmer months (i.e., November to April). Savanna vegetation is characteristic of this region, with *Eucalypt* species making up the tree canopy in most areas and C4 grasses dominating the understory. Vegetation ranges from savanna forest (30–50% tree cover) through to woodland and open woodland (10–30% cover) and shrubland (<10% cover) depending on substrates. Tussock and hummock grass cover ranges from 5 to almost 100%. Small patches of rainforest and riparian gallery forest with closed canopies (>70% cover) and zero grass cover occur within the savanna matrix. Substrates range from relatively fertile clay soil on igneous rock, through laterite derived loam and gravel substrates, to sandy or skeletal soils on rugged sandstone. Due to the annual cycle of a wet season followed by an extended dry season (>6 months) in which grasses cure, savannas in the region are subject to annual grass fueled fire regimes (Russell-Smith et al., 2003b). The Northern Kimberley region has not been subject to extensive vegetation clearing; however, fire regimes changed to high-intensity wildfire dominated fire regimes during the 20th century with the breakdown of traditional Indigenous fire management (Russell-Smith et al., 2003b; Connor et al., 2018). Introduced herds of cattle, horses, and donkeys are widespread throughout the region as an additional critical disturbance factor.

Survey Design

Survey sites were distributed across 11 subregions within the Northern Kimberley (**Figure 1** and **Table 1**). Study sites were stratified between two major geological landscapes: sandstone and volcanic (**Figure 1**), based on previous analyses which show that mammal assemblages diverge strongly between these habitats (Bradley et al., 1987; Start et al., 2007, 2012; Radford et al., 2014; Radford et al., 2020a). Habitat structure in sandstone landscapes was characterized by abundant rock cover and crevices due to the rugged rocky sandstone substrate, with vegetation ranging from hummock grassland to shrubland, woodland, and vine thicket. Volcanic landscapes had relatively few rock crevices, though sometimes with high rock cover, and vegetation ranging from open woodland on basalt to open forest on lateritic substrates. Location of survey sites was based primarily on the presence of historical survey sites (Bradley et al., 1987; Start et al., 2007, 2012; Radford et al., 2014). However, where historical sites were not available, additional survey sites were added in suitable habitats. Sites were located both inside and outside National Parks to account for the possible influences of differing tenure, management and disturbance factors within the region. Despite close proximity of some sites due to remote access constraints (ca. within 100 m in some areas) sites are considered independent due to the relatively few occasions (6%) where recaptures occurred among nearby sites.

In order to account for inherent variation among sites this study used repeated surveys to account for fixed site differences. In total, 407 surveys were undertaken at 94 sites between 2011 and 2019; 44 sites on sandstone and 50 in volcanic habitats (**Table 1**). Most sites were surveyed five times (n = 47), 18 sites were surveyed six times, while another 16 sites were surveyed three times. Ten sites were surveyed only once. Due to logistical constraints, selecting and surveying sites was a staged process, with not all sites surveyed every year (**Table 1**). Trap effort varied between the first and all other years of the study and is included as an offset within our analyses. Site trap effort was either 72 or 144 trap nights in 2011 (24 traps open for 3 or 6 nights) and was standardized from 2012 onward at 120 trap nights (24 traps open 5 nights).

Mammal Data

Mammal data were collected from 50 × 50 m quadrats (*survey site*) similar to those used as a standard monitoring plot in other areas of northern Australia (Woinarski et al., 2010; Legge et al., 2011; Radford et al., 2015). A total of 20 large (15 × 15.5 × 46 cm) and medium (9 × 10 × 33 cm) metal box traps (Elliotts), were alternately placed around the perimeter of each quadrat. Four larger wire cage traps (25 × 30 × 73 cm) were placed at the corners. Traps were baited with a mixture of peanut butter and

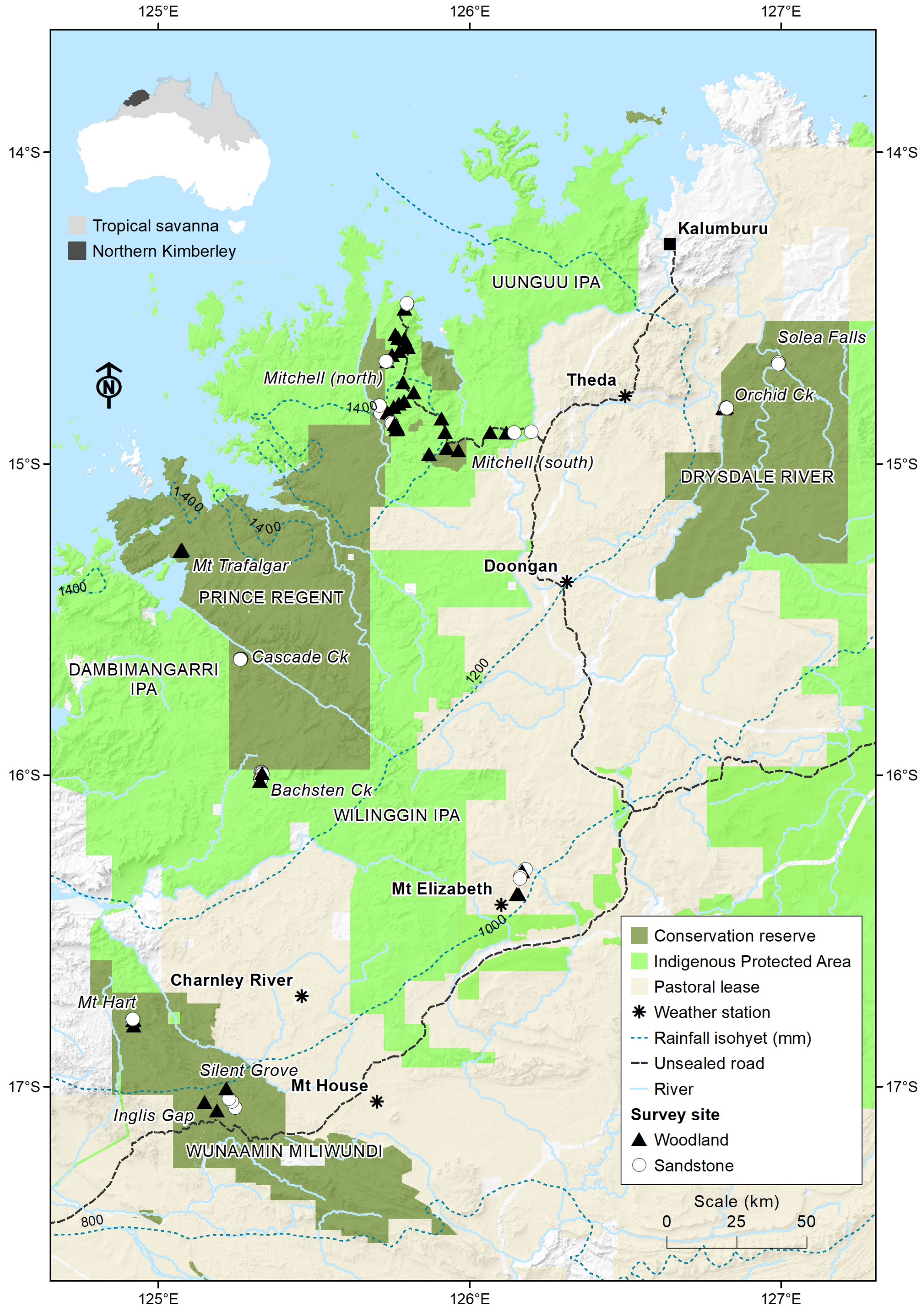

FIGURE 1 | Locations of survey sites and locations in the Northern Kimberley region of northern Western Australia.

rolled oats. Traps were shaded using grass, leaves or hessian sacks and checked early each morning to prevent overheating. Mammals were identified to species and marked using ISO FDX-B Microchips (Mychip) for larger species or permanent marker pens on small rodents' ears. Site mammal data were described in terms of abundance (total number of individuals

TABLE 1 | Summary of survey sites, tenure, and survey frequency and Bureau of Meteorological Stations used for rainfall data.

Subregions	Tenure	Number of sites	Years surveyed	n	Nearest Bureau of Meteorology station
Orchid Creek	Conservation reserve	8	2013, 2015, 2018	3	Doongan station
Solea Falls	Conservation reserve	6	2015, 2017, 2019	3	Doongan station
Mitchell (north)	Conservation reserve, Indigenous Protected Area	21	2011, 2012, 2013, 2014, 2016	5	Theda station
Mitchell (south)	Conservation reserve, Indigenous Protected Area	17	2011, 2012, 2013, 2014, 2015, 2016	6	Theda station
Mount Elizabeth	Pastoral	9	2013, 2015, 2016, 2017, 2018	5	Mount Elizabeth station
Bachsten Creek	Indigenous Protected Area	8	2013, 2015, 2016, 2017, 2018	5	Theda station
Cascade Creek	Conservation reserve	7	2012, 2014, 2015, 2016, 2017, 2019	6	Theda station
Mount Trafalgar	Conservation reserve	6	2012, 2014, 2015, 2016, 2017	5	Theda station
Inglis Gap	Conservation reserve	2	2011, 2012, 2014, 2015, 2016, 2019	6	Mount House station
Mount Hart	Conservation reserve	6	2011, 2013, 2015, 2016, 2017, 2019	6	Charnley River
Silent Grove	Conservation reserve	4	2011, 2012, 2014, 2015, 2016, 2019	6	Mount House station
	Total	94			

'n' total number of subregion surveys.

captured not including recaptures) and species richness (total number of species captured). Sandstone and volcanic habitat mean (±se) mammal captures per site were 9.5 (±1.1) and 7.2 (±1.0) respectively and site species richness was 2.7 (±0.1) and 2.1 (±0.1) respectively.

Survey Site Habitat and Productivity Attributes

Each survey site (50 × 50 m) was assessed for both fixed and dynamic habitat structural attributes during the mammal surveys (**Table 2**). Tree (height > 4 m) and shrub (height < 4 m) projected canopy cover was estimated using a 1% Bitterlich gauge (Lindsey et al., 1958). Each plant canopy was assessed as 1% cover if the 10 cm cross-bar, held 50 cm from the observer's eye, was narrower than the canopy width when standing at the quadrat's central point (37 m along the diagonal from the quadrat corner post). Assessing each canopy in a 360° arc from the central point gives a total percentage value for canopy cover. Separate canopy cover was estimated for trees which produced fleshy fruits eaten by arboreal savanna mammals as an index of habitat suitability for these species. Tree basal area was estimated using a Basal Area Factor 1 Metric Wedge Prism (CruiseMaster). Ground vegetation cover attributes were assessed using a 50 m transect run diagonally from the corner post through the survey site. The accumulated distance under the transect tape was used to estimate percentage cover of perennial grasses (tussock or hummock), annual grass (*Sorghum* spp.), herbaceous forbes (non-grasses) and leaf/branch litter. The fixed percentage of exposed rock and/or gravel cover was estimated using the same transect method. Combined introduced plant cover 'weeds' was estimated as a combined percentage projected ground cover of exotic tree, shrub and ground-layer vegetation cover.

Productivity is directly linked to rainfall in seasonal tropical savannas of northern Australia (McKenzie et al., 2007; Radford et al., 2014). Wet season rainfall (July–June) was calculated for survey sites within each sub-region (**Table 1** and **Figure 1**) based on monthly rainfall totals from the nearest weather station within the same rainfall isohyet with a complete monthly rainfall data set during the study period (**Table 1** and **Figure 1**).

Disturbance Attributes

Predator Activity

Predator trap success data was recorded at survey sites through the use of remote infrared cameras at each site during live-trapping surveys (see above). Single cameras were placed out for five nights per survey. In addition, each site was trapped once using a 5-camera array (as per Einoder et al., 2018; Stobo-Wilson et al., 2020a) over a 30–50 days period. Reconyx PC900 Hyperfire Professional Infra-red (IR) or PC950 Hyperfire Security IR cameras were used in camera surveys, both of which are successful in detecting mammals > 1 kg. Cameras were baited using universal bait (peanut butter and oats). The presence of predators cannot, therefore, be attributed primarily to the bait. Rather the presence of predators is likely to reflect natural visitation of sites in savanna landscapes, with the omnivorous bait providing a short distance cue to encourage the predator to come close to the camera. Dingoes were frequently detected at many survey sites during the study period and trap success (number of detections per 100 trap nights) was recorded for each site during each year of survey. Cats were not detected at the majority of survey sites despite multiple surveys over a 9 years study period. However, cats were detected at some sites and at these sites were sometimes frequently recorded. This suggests that cats had a preference for some sites over others despite all sites being equally available to cats as they are ubiquitous throughout the region. To account for this site-specific preference (possibly related to local disturbance regimes), cat trap success (number of detections per 100 trap nights) was calculated as a fixed variable accounting for the relative preference cats had of visiting each monitoring site.

Fire Mosaics at Survey Site Up to Landscape Scales

Fire mosaics were measured at multiple pre-defined scales within and around survey sites to test for the effects of

TABLE 2 | Explanatory variables measured at and around survey sites, their definitions and summary statistics.

Variable	Abbreviation	Description	Range	Mean
Site habitat attributes				
Perennial grass cover (%)	PG	Percentage cover of perennial tussock and hummock grasses along 50 m plot transect	0–98	22.2
Annual grass cover (%)	AG	Percentage of cover of annual spear grass (*Sorghum stipoideum*) along 50 m plot transect	0–62	2.4
Litter cover (%)	litter	Percentage of ground covered by leaf and woody litter along 50 m plot transect	0–97	26.9
Rock cover (%)	rock	Percentage ground cover of rocks and gravel along 50 m plot transect	0–90	24.7
Shrub cover (%)	shrub	Percentage shrub cover along 50 m plot transect	0–79	86.9
Tree canopy cover (%)	trcov	Projected tree canopy cover as a percentage using bitterlich gauge at 50 × 50 m plot	0–96	25.8
Tree basal area	BA	Basal area of timber per hectare (m^2ha^{-1}) within 50 × 50 m plot using factor 1 prism	0–25	6.9
Fleshy fruit tree cover (%)	fruittree	Cover of fleshy fruited trees (i.e., *Buchanania obovata, Gardenia* spp., *Livistona eastoni, Planchonia careya, Pandanus spiralis, Owenia vernicosa,* and *Terminalia hadleyana*) within 50 × 50 m plot	0–45	5.2
Percentage weed cover (%)	weeds	Percentage of projected ground cover of introduced plant species within 50 × 50 m plot	0–50	0.9
Site disturbance processes				
Cat activity	cats	Number of nights cats detected per 100 camera trap nights per site (averaged among all years)	0–23	0.5
Dingo activity	dingoes	Number of nights dingoes detected per 100 camera trap nights per survey	0–100	3.1
Cattle index	cattleindex	Sum of cattle disturbance indices including cattle sighted, trampling, dung and grazing impacts (scale 0–4) within 50 × 50 m plot	0–11	1.7
Site fire attributes				
Fire frequency	FF	Number of times site was burnt in the previous 10 years	1.3–8.0	4.7
Fire intensity	FI	Fire intensity at 50 × 50 m plot; 1 – patchy, 2 – low (<2 m scorch), 3 – moderate (scorch 2–5 m), 4 – high (canopy scorch), 5 – extreme (canopy charred) (as per Russell-Smith and Edwards, 2006)	0–4	1.4
Distance to unburnt (m)	Dist > 20haUB	Linear distance (m) from site to the nearest unburnt vegetation > 20 ha in previous year (**Figure 2A**)	0–3827	387
Percentage site burnt	% burnt	The estimated percentage of 50 × 50 m plot burnt during most recent fire	0–100	30.1
Landscape fire mosaic attributes				
Burnt previous year (%)	1yrB	Percentage of area around site (1, 3, 5, and 10 km radius) burnt in previous year (**Figure 2A**)	0–100	41.0
Area of longer unburnt (≥4 years) vegetation (%)	>4yrB	Percentage of area around site (1, 3, 5, 10 km radius) where vegetation is ≥4 years unburnt (**Figure 2B**)	0–100	21.0
Fire age diversity (pyrodiversity)	FADiv	Number of post-fire vegetation ages (>5% area) within 1, 3, 5, and 10 km radius of survey site (**Figure 2C**)	1–8	3.0
Ratio of Late Dry Season burns to total burns	LDSBratio	Ratio of the LDS area burnt to the total area burnt in previous 3 years (within 1, 3, 5, and 10 km radius from site)	0–1	0.3
Landscape productivity				
Wet season rainfall (mm)	rain	Wet season rainfall (July–June) from nearest representative rainfall station (see **Figure 1**)	287–2577	1203

disturbance attributes from survey site up to broad landscape scales (**Figure 2**). Mosaic scales were defined as *site* (50 × 50 m), *local* (1 km radius from survey site; total area of 3 km^2), *meta-local* (3 km radius; total area of 28 km^2), *landscape* (5 km radius; total area of 79 km^2), and *meta-landscape* scales (10 km radius; total area of 314 km^2).

Site-scale mosaic attributes included fire intensity (based on leaf scorch height as per Russell-Smith and Edwards, 2006) and percentage of site burnt in the current year were estimated at the time of each survey (**Table 2**). Remote sensing data were used to derive other fire mosaic attributes (**Table 2**). Analyses are based on fire scars derived from Moderate Resolution Imaging Spectroradiometer (MODIS) imagery at 250 m resolution[1]. MODIS data for each year were obtained from the North Australia and Rangelands Fire Information (NAFI) website[2]. Site scale fire frequency was calculated over the previous 10 years based on fire scars intersecting with site locations during each year of the study period and also based on direct observations during the study period. As an indication of fire size at the site scale (year previous to survey), raster analysis was used to determine the distance from each survey site to the nearest unburnt vegetation patch > 20 ha. This size patch was chosen to represent the minimum size an unburnt patch could be to support a single home range for savanna mammal species (e.g., Cook, 2010; Hohnen et al., 2015, 2016a; Penton et al., 2020).

Local up to meta-landscape scale mosaic attributes within radial areas included percentage of area burnt in the previous year, the area unburnt for ≥ 4 years, fire age diversity

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[1] http://modis.gsfc.nasa.gov/

[2] https://firenorth.org.au/nafi3/

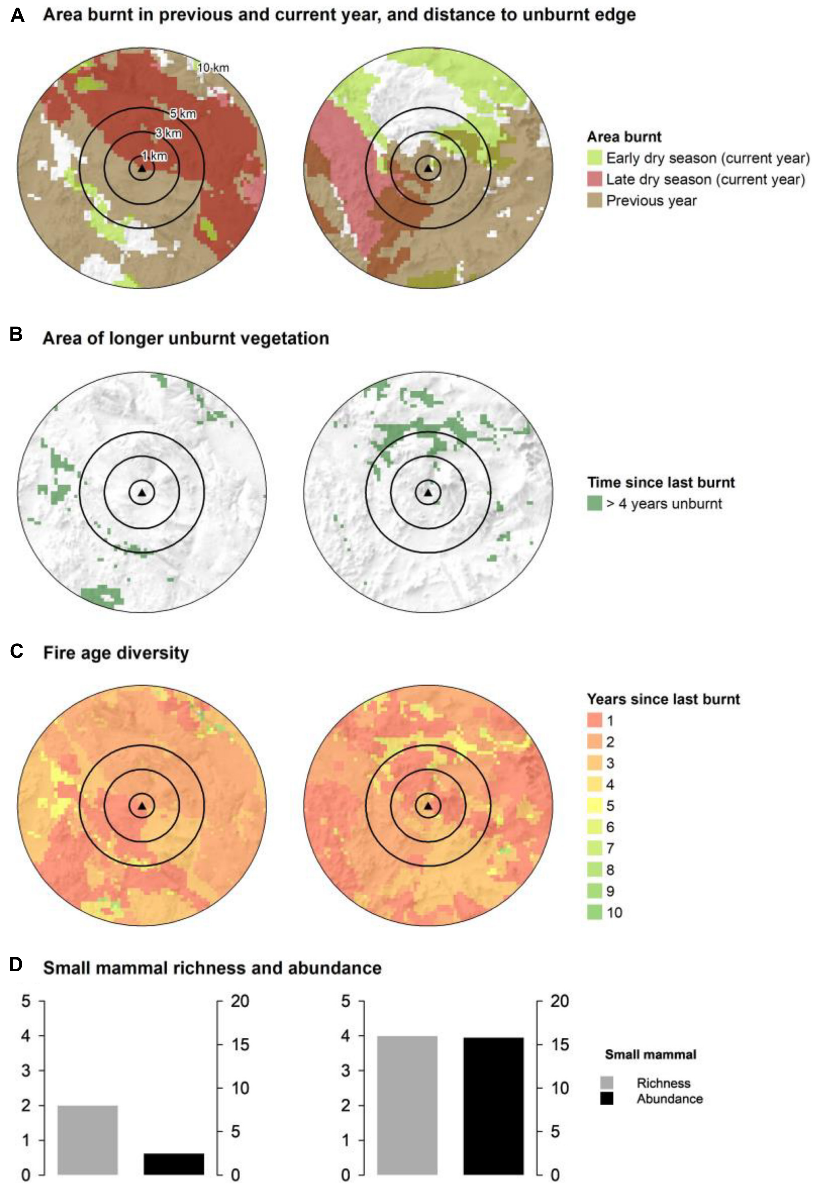

FIGURE 2 | Fire mosaic elements within the landscape context of two of the mammal survey sites, LCI 205 at Inglis Gap (left) and LCI 210 at Mt Hart (right). The graphs show concentric spatial areas around sites defined by rings at 1, 3, 5, and 10 km from the center of the location of the survey site and provides a partial view of the fire mosaic context within which these sites are placed. **(A)** Shows the spatial extent of early (March–July) and late dry season fires (August–December) during the year of the survey and the total extent of fire in the previous year. **(B)** Shows the spatial extent of habitat unburnt for four or more years. **(C)** Shows the patterns of 'pyrodiversity,' here defined as the number of post-fire habitat ages, within the landscape context of the survey sites. **(D)** Shows a histogram of mammal abundance (black; number of individuals per 100 trap nights) and richness (grey; number of different species) for the two sites, with the Mt Hart site LCI 210 supporting much greater mammal abundance and richness (right) than the Inglis Gap site LCI 205 (left).

(pyrodiversity) and the ratio of late dry season burning (**Table 2** and **Figure 2**). All spatial analyses were carried out in ArcMap 10.1 using tools in the Spatial Analyst extension.

Survey Site Feral Herbivore Disturbance

Feral livestock disturbance (mainly cattle) was qualified as cattle sighted [none (0), single individual (1), several (2), groups (3)], grazing level and evidence of tracks/trampling [no evidence (0), light (1), moderate (2), heavy (3)] and cattle dung [none (0), some sighted (1), scattered (2), extensive (3)]. These four herbivore disturbance attributes were added together to give an index of cattle disturbance impact at the site.

Data Analysis

To examine the relationship between mammal richness or mammal abundance and potential predictor variables (**Table 1**), we fitted generalized linear mixed models (GLMM) (R package glmmTMB: Brooks et al., 2017) with Poisson or negative binomial distribution and log-link, offset for trap effort, and with site included as a random effect using statistical software program R (R Core Team, 2021). All continuous variables were centered and standardized (Gelman, 2008) and included as quadratic polynomial terms where non-linear trends were detected during data exploration. Collinearity between variables was tested using Variance Inflation Factors (VIF) with cutoff for inclusion of 3 and Pearson's correlations with cutoff for inclusion of 0.7 (Zuur et al., 2010). Due to collinearity (VIF > 3), fire frequency was dropped from analyses for volcanic habitat.

Because mammal species assemblages differ between habitats (Radford et al., 2014; Radford et al., 2020a), separate analyses were conducted for each habitat type, i.e., sandstone and volcanic. These analyses were structured according to three main hypotheses being tested (1) site-level habitat, (2) site-level disturbance and (3) pyrodiversity at 1, 3, 5, and 10 km radii around a particular site (**Table 1** and **Figure 2**). To identify highly influential predictors in each of these models, we used an information-theoretic model-averaging approach (Burnham and Anderson, 2002). A top (95% confidence) model set was selected according to AICc (Akaike Information Criterion corrected for small sample size), i.e., the top models with cumulative sum of Akaike weights less than 0.95 (R package MuMIn: Barton, 2020). The best models included only highly influential variables from the top model set. These variables are defined as having a relative variable importance (sum of Akaike weights for all models containing a given predictor variable) ≤ 0.73, which is equivalent to an AICc difference of <2 (Richards, 2005). Model assumptions were verified by normal probability plots (QQ-plots) of fixed versus random effects, plotting residual versus fitted values versus each covariate in the model, and versus each covariate not in the model. We tested for overdispersion, zero-inflation, temporal autocorrelation (based on Durbin-Watson test) and spatial autocorrelation (based on Moran's I) (R package DHARMa: Hartig, 2021). Model validation indicated no problems.

RESULTS

Mammal Abundance

In sandstone habitats, the site-scale attributes (50 × 50 m) most strongly associated with increased mammal abundance were (1) habitat (positive relationship): rock cover and tree canopy cover, (2) disturbance (negative relationship): cat activity, fire frequency and proportion of the site burnt in the current year (**Table 2**). Mosaic attributes, including fire age diversity, proportion of the site burnt in the previous year (negative relationships), and proportion of ≥4-year old unburnt vegetation (positive relationship) were associated with increased mammal abundance at the local and meta-local scales (≤3 km) around a site (**Table 3** and **Figure 3**). Previous wet season rainfall within sub-regions (≥5 km) was also a strong predictor of increased mammal abundance (**Table 3**).

At the local/meta-local scale (≤3 km) around a site, the disturbance + mosaic model, together with the fixed habitat attribute of rock cover, was the best model for mammal abundance in sandstone habitats (**Table 3** and **Figure 3**). At the landscape and meta-landscape scale (≥5 km), mosaic attributes were less important and the disturbance model, together with habitat attribute rock cover, and sub-regional rainfall was the best model of mammal abundance in sandstone habitats (**Table 3**).

In volcanic habitats, the site-scale attributes most strongly associated with increased mammal abundance were (1) habitat (positive relationships): rock cover, shrub cover, perennial grass cover, and negatively with annual grass (*Sorghum stipoideum*) cover; (2) site-scale disturbance (negative relationships): distance to the nearest unburnt patch > 20 ha and proportion of the site burnt in the current year (**Table 3**). Mosaic attribute (proportion of ≥ 4-year old unburnt vegetation) was associated with increased mammal abundance at the landscape and meta-landscape scale (≥5 km; **Table 3** and **Figure 4**).

At the site-scale, the local-scale and at the meta-local scales (≤3 km), disturbance attributes were less important and the habitat model, was the best model of mammal abundance in volcanic habitats (**Table 3**). At the landscape- and meta-landscape-scales, the habitat model and mosaic attribute, the proportion of ≥4 years old unburnt vegetation, was the best model for mammal abundance in volcanic habitats (**Table 3** and **Figure 4**).

Mammal Richness

In sandstone habitats, the site-scale attributes most strongly associated with increased mammal richness were (1) habitat: rock cover, and (2) disturbance (negative relationship): cat activity, cattle index and distance to the nearest unburnt patch > 20 ha (**Table 3**). Mosaic attribute, fire age diversity was associated with decreased mammal richness at the local- and meta-local scales (<3 km; **Table 3**). Previous wet season rainfall within sub-regions was a strong predictor of increased mammal richness (**Table 3**). The site-scale disturbance model, together with sub-regional rainfall, was the best model of mammal richness in sandstone habitats (**Table 3** and **Figure 5**).

In volcanic habitats, the site-scale attributes most strongly associated with increased mammal richness were (1) habitat: rock cover, shrub cover, perennial grass cover, and negatively with annual grass (*Sorghum stipoideum*) cover (2) disturbance (negative relationships): proportion of the site burnt in the current year (**Table 3**). Fire mosaic attributes were not strong predictors of mammal richness at any scale (**Table 3**). The habitat model was the best model of mammal richness in volcanic habitats (**Table 3** and **Figure 6**).

DISCUSSION

Our study supports the hypotheses that habitat values, both fixed (rock cover) and dynamic (perennial grass and shrub cover), disturbance (site-based feral cat activity, percentage of recently burnt habitat, feral livestock) are fundamentally significant in determining savanna mammal abundance and richness at the site scale. This supports previous work showing relationships between mammals and vegetation productivity (Stobo-Wilson et al., 2020a), shrub and grass cover

TABLE 3 | The relative importance of habitat, disturbance, pyrodiversity, and productivity variables derived from general linear mixed models (GLMM) modeling the effect of these variables on mammal abundance or richness.

Response variable and spatial scale	**Hypothesis tested**	**Predictor variables**																					**R^2**	
		Site-scale habitat attributes									**Site-scale disturbance attributes**							**Scaled fire mosaic attributes**				**Productivity attribute**	**Marginal**	**Conditional**
		Perennial grass	**Annual grass**	**Litter**	**Rock**	**Shrub**	**Tree canopy cover**	**Tree basal area**	**Fruiting tree cover**	**Weeds**	**Cats**	**Dingoes**	**Cattle**	**Fire frequency**	**Fire intensity**	**Distance to unburnt**	**Burnt in current year**	**Burnt in previous year**	**Burnt ≥ 4 years ago**	**Pyrodiversity (Fire age diversity)**	**LDS ratio**	**Wet season rainfall**		
Sandstone																								
Mammal abundance																								
Site	Habitat	0.68 (114)	0.28 (87)	0.26 (85)	**0.99** **(194)**	0.27 (82)	**0.74** **(117)**	0.34 (93)	**0.83** **(128)**	0.26 (83)													0.17	0.81
Site	Disturbance										**0.99** **(55)**	0.25 (24)	0.48 (30)	**0.73** **(31)**	0.37 (24)	0.60 (32)	**0.77** **(33)**						0.24	0.77
Site + 1 km	Habitat + Disturbance + Mosaic + Productivity				**0.98** **(181)**		0.58 (111)		0.58 (101)		**0.96** **(160)**			0.26 (76)			**1.00** **(202)**	**0.95** **(167)**	**0.85** **(153)**	0.47 (94)	0.67 (119)	0.69 (130)	0.32	0.82
Site + 3 km	Habitat + Disturbance + Mosaic + Productivity				**0.97** **(132)**		0.60 (87)		0.44 (76)		**0.98** **(136)**			**0.78** **(103)**			**0.93** **(115)**	**1.00** **(52)**	0.27 (61)	**0.98** **(143)**	0.61 (85)	**0.83** **(113)**	0.35	0.81
Site + 5 km	Habitat + Disturbance + Mosaic + Productivity				**0.98** **(460)**		0.41 (251)		0.45 (265)		**0.96** **(432)**			**0.90** **(385)**			**0.97** **(446)**	0.63 (291)	0.25 (185)	0.47 (246)	0.28 (203)	**0.96** **(450)**	0.32	0.80
Site + 10 km	Habitat + Disturbance + Mosaic + Productivity				**0.98** **(525)**		0.46 (304)		0.44 (294)		**0.96** **(483)**			**0.86** **(413)**			**0.97** **(505)**	0.59 (310)	0.29 (250)	0.25 (215)	0.30 (243)	**0.94** **(482)**	0.30	0.81
Mammal richness																								
Site	Habitat	0.30 (118)	0.28 (121)	0.29 (130)	**0.79** **(191)**	0.24 (112)	0.25 (116)	0.27 (118)	0.32 (132)	0.24 (113)													0.06	0.69
Site	Disturbance										**0.90** **(42)**	0.24 (22)	**0.93** **(46)**	0.24 (21)	0.31 (23)	**0.73** **(42)**	0.31 (22)						0.30	0.63
Site + 1 km	Habitat + Disturbance + Mosaic + Productivity				0.50 (110)						**0.86** **(132)**		**0.98** **(186)**			0.39 (93)		0.51 (107)	0.72 (125)	0.50 (100)	0.29 (83)	**0.74** **(130)**	0.36	0.63
Site + 10 km	Habitat + Disturbance + Mosaic + Productivity				0.48 (110)						**0.85** **(144)**		**0.96** **(178)**			0.51 (106)		0.46 (103)	0.29 (91)	0.38 (96)	0.56 (108)	**0.92** **(158)**	0.34	0.62
Volcanic																								
Mammal abundance																								
Site + 3 km	Habitat + Disturbance + Mosaic + Productivity				0.45 (104)						**0.86** **(135)**		**0.96** **(169)**			0.49 (100)		0.53 (96)	0.27 (78)	**0.77** **(130)**	0.34 (87)	**0.85** **(140)**	0.36	0.62
Site + 5 km	Habitat + Disturbance + Mosaic + Productivity				0.49 (104)						**0.85** **(136)**		**0.94** **(157)**			0.53 (105)		0.42 (92)	0.27 (78)	0.39 (94)	0.58 (99)	**0.96** **(165)**	0.34	0.62

(Continued)

TABLE 3 | (Continued)

Response variable and spatial scale	Hypothesis tested	Predictor variables																					R^2	
		Site-scale habitat attributes									Site-scale disturbance attributes							Scaled fire mosaic attributes				Productivity attribute	Marginal	Conditional
		Perennial grass	**Annual grass**	**Litter**	**Rock**	**Shrub**	**Tree canopy cover**	**Tree basal area**	**Fruiting tree cover**	**Weeds**	**Cats**	**Dingoes**	**Cattle**	**Fire frequency**	**Fire intensity**	**Distance to unburnt**	**Burnt in current year**	**Burnt in previous year**	**Burnt ≥ 4 years ago**	**Pyrodiversity (Fire age diversity)**	**LDS ratio**	**Wet season rainfall**		
Site	Habitat	**0.98 (106)**	**0.82 (70)**	0.24 (47)	**1.00 (113)**	**0.80 (67)**	0.30 (48)	0.26 (46)	0.65 (63)	0.63 (63)													0.31	0.64
Site	Disturbance										0.47 (19)	0.28 (17)	0.61 (22)	*N/A*	0.29 (17)	**0.92 (31)**	**0.73 (22)**						0.14	0.66
Site + 1 km	Habitat + Disturbance + Mosaic + Productivity	**0.79 (379)**	**0.85 (356)**		**1.00 (522)**	0.43 (249)										0.65 (288)	**0.77 (353)**	0.32 (233)	0.48 (268)	0.38 (230)	0.30 (222)	0.32 (232)	0.25	0.68
Site + 3 km	Habitat + Disturbance + Mosaic + Productivity	**0.84 (366)**	**0.83 (325)**		**1.00 (483)**	0.44 (233)										0.66 (280)	0.71 (321)	0.30 (220)	0.65 (287)	0.49 (225)	0.24 (190)	0.29 (206)	0.25	0.68
Site + 5 km	Habitat + Disturbance + Mosaic + Productivity	**0.85 (352)**	**0.83 (316)**		**1.00 (467)**	0.46 (222)										0.51 (249)	0.67 (309)	0.31 (210)	**0.74 (288)**	0.25 (183)	0.25 (186)	0.27 (192)	0.24	0.69
Site + 10 km	Habitat + Disturbance + Mosaic + Productivity	**0.90 (355)**	**0.83 (301)**		**1.00 (454)**	0.51 (222)										0.38 (220)	0.56 (287)	0.40 (232)	**0.85 (309)**	0.40 (209)	0.32 (190)	0.26 (191)	0.30	0.66
Mammal richness																								
Site	Habitat	**0.98 (108)**	**0.73 (78)**	0.25 (46)	**0.92 (88)**	**0.97 (101)**	0.24 (43)	0.26 (44)	0.63 (69)	0.60 (72)													0.26	0.50
Site	Disturbance										0.51 (25)	0.38 (22)	0.37 (22)	NA	0.38 (28)	0.66 (29)	**0.77 (30)**						0.13	0.52
Site + 1 km	Habitat + Disturbance + Mosaic + Productivity	**0.93 (282)**	**0.78 (249)**		**0.94 (281)**	**0.86 (241)**											0.40 (197)	0.31 (155)	0.65 (206)	0.41 (177)	0.31 (152)	0.53 (213)	0.23	0.51
Site + 3 km	Habitat + Disturbance + Mosaic + Productivity	**0.96 (272)**	**0.77 (217)**		**0.95 (269)**	**0.88 (218)**											0.37 (177)	0.32 (145)	0.66 (185)	0.41 (151)	0.25 (129)	0.42 (169)	0.22	0.51
Site + 5 km	Habitat + Disturbance + Mosaic + Productivity	**0.96 (255)**	**0.78 (207)**		**0.96 (258)**	**0.89 (210)**											0.38 (163)	0.30 (133)	0.66 (171)	0.30 (122)	0.26 (123)	0.39 (157)	0.22	0.52
Site + 10 km	Habitat + Disturbance + Mosaic + Productivity	**0.97 (262)**	**0.78 (202)**		**0.96 (252)**	**0.90 (203)**											0.35 (160)	0.37 (146)	0.59 (157)	0.48 (138)	0.27 (120)	0.38 (153)	0.24	0.49

Relative variable importance values (w+) and the number of models containing the variable (N, in brackets) derived from the 95% confidence model set generated from model-averaging are shown. Highly influential variables (w + ≥ 0.73) are indicated in bold.

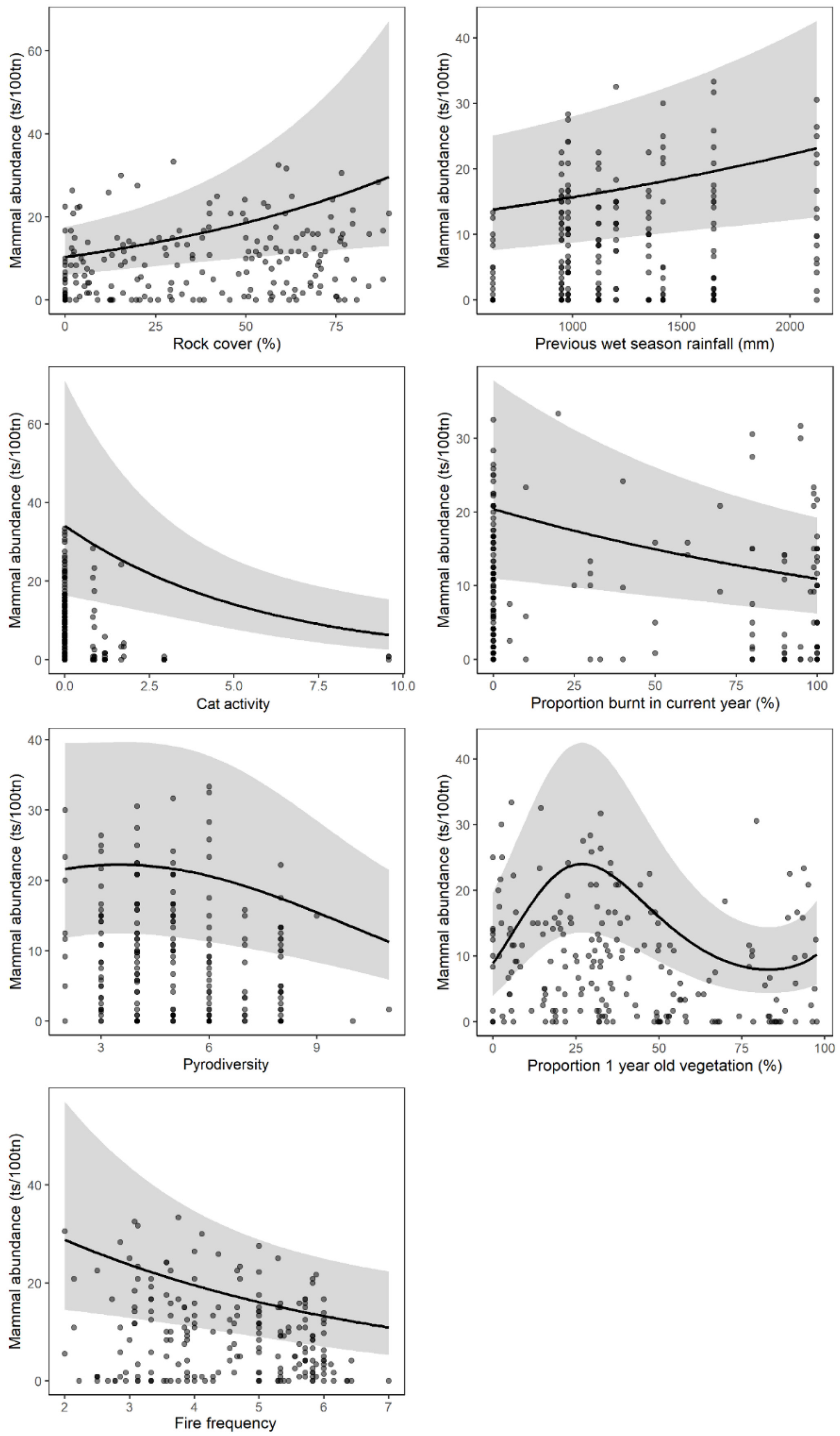

FIGURE 3 | Mammal abundance [trap success per 100 trap nights (ts/100 tn)] in sandstone habitat shown only for highly influential predictor variables sampled at the 3 km scale around each site (see **Table 2**). Relationships for each variable were derived from GLMM predictions while holding other explanatory variables constant at their median level. Model fit is shown by a black line and the gray band represents the 95% confidence interval. Gray circles indicate observed data values and are darker when repeated observations occur at the same point. Cat activity is cat detections per 100 camera trap nights, pyrodiversity is the number of post fire vegetation ages within 3 km of the site, fire frequency is the number of times the site was burnt in the previous 10 years.

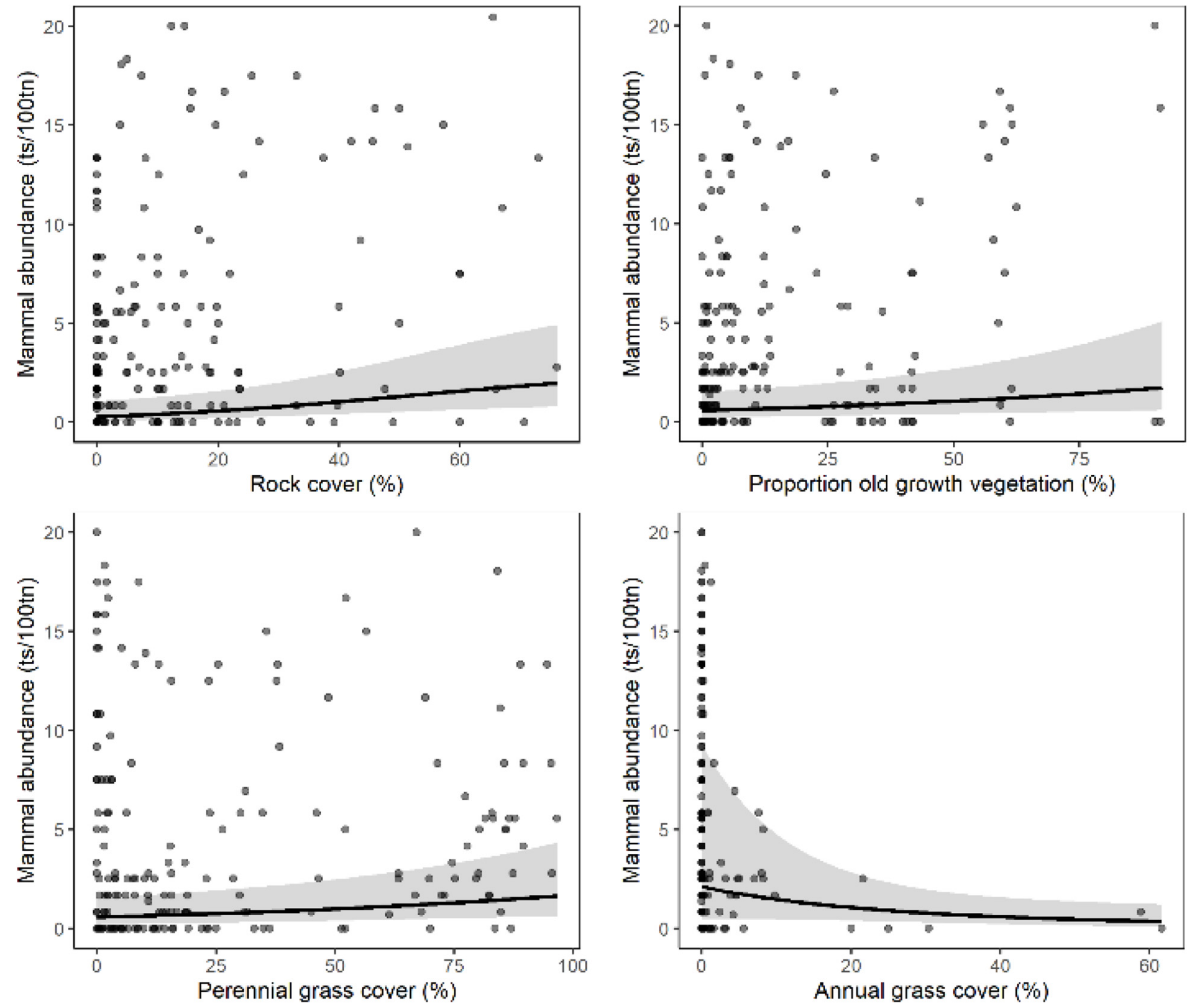

FIGURE 4 | Mammal abundance [trap success per 100 trap nights (ts/100tn)] in volcanic habitat shown only for highly influential predictor variables sampled at the 3 km scale around each site (see **Table 2**). Relationships for each variable were derived from GLMM predictions while holding other explanatory variables constant at their median level. Model fit is shown by a black line and the gray band represents the 95% confidence interval. Gray circles indicate observed data values and are darker when repeated observations occur at the same point.

(Radford et al., 2015; Davies et al., 2017; Penton et al., 2021), cat occupancy (Davies et al., 2017; Stobo-Wilson et al., 2020a), fire 'activity' or extent (Lawes et al., 2015; Radford et al., 2015; Stobo-Wilson et al., 2020a) and the presence of feral livestock (Legge et al., 2019). Our study also supported the hypothesis that site-scale disturbance and habitat features are more directly important to local mammal populations than broader landscape-scale (see above) or regional-scale (as per Radford et al., 2020a; Stobo-Wilson et al., 2020a) fire mosaic attributes. As far as we are aware this is the first study published in northern Australia which has explicitly tested for the importance of fire mosaic attributes at different spatial scales on threatened mammal assemblages. Finally our study identifies ≥ 4 years old unburnt habitat as the most important functional element (as per Parr and Andersen, 2006) of both site-scale and broad-scale fire mosaics for savanna mammals, not pyrodiversity *per se*. Such information has significant implications on how prescribed burning and other management actions should be applied at multiple spatial scales across northern Australian savanna landscapes.

The Positive Influence of Site-Scale Habitat Cover

Habitat cover at the site-scale was the most consistently identified attribute supporting mammal abundance and richness. The fixed mosaic habitat element, rock cover, was strongly supported in habitat and combined models for rocky sandstone habitats, and the abundance and richness of mammals in volcanic habitats. Rocks and rock crevices have been identified as critical habitat features supporting persistence of savanna mammals (Ibbett et al., 2017; Stobo-Wilson et al., 2020a) not least because feral cats have lower occupancy and hunt less effectively in rock habitats (McGregor et al., 2015; Hohnen et al., 2016b). Our study supports the importance of rocks as a key habitat attribute for

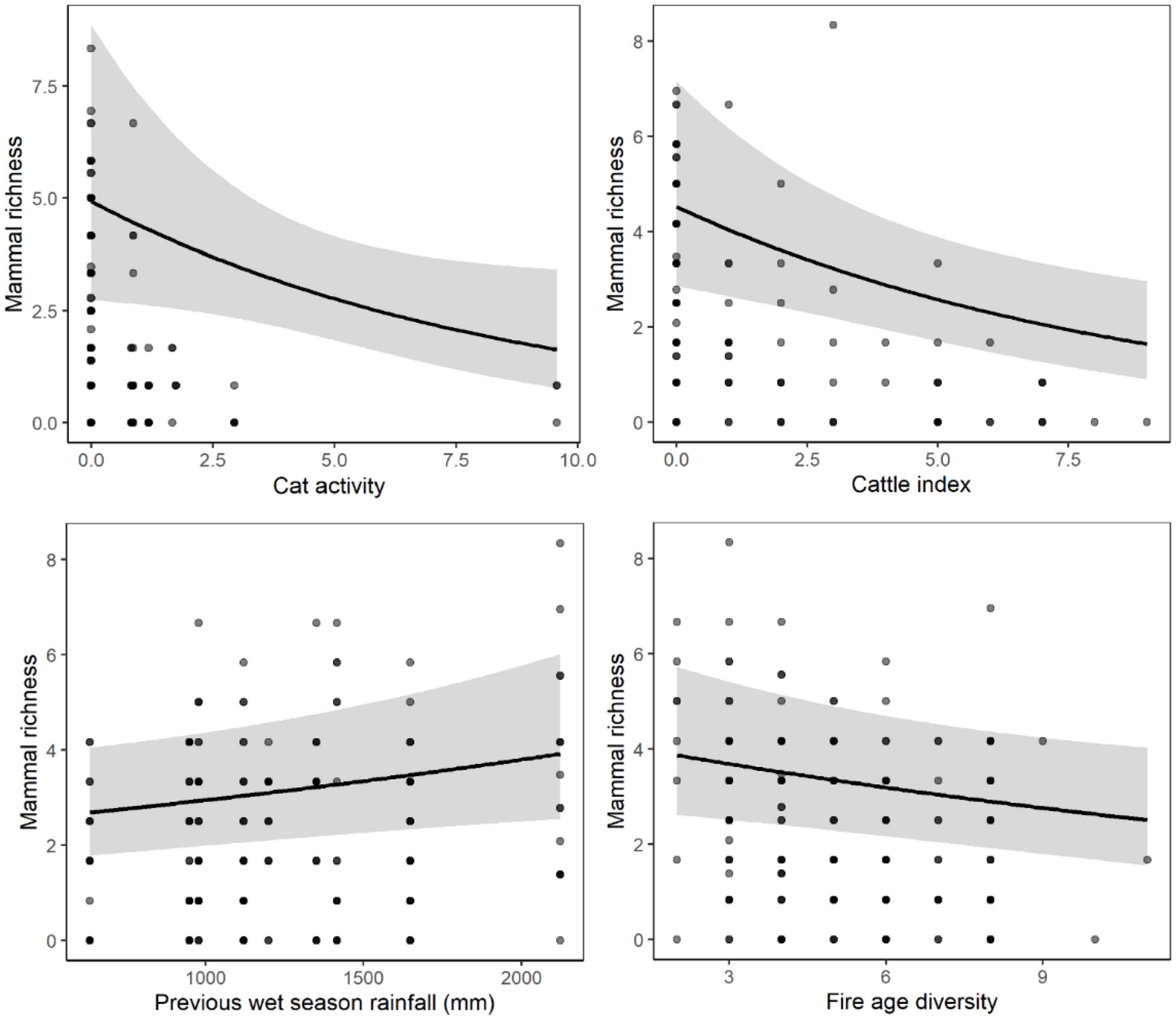

FIGURE 5 | Mammal richness [species per 100 trap nights (tn)] in sandstone habitat shown only for highly influential predictor variables sampled at the 1, 5, and 10 km scale around each site (see **Table 2**). Relationships for each variable were derived from GLMM predictions while holding other explanatory variables constant at their median level. Model fit is shown by a black line and the gray band represents the 95% confidence interval. Gray circles indicate observed data values and are darker when repeated observations occur at the same point.

threatened savanna mammals. Dynamic ground layer vegetation cover attributes (vegetation cover, perennial grass, and shrub cover) were also strongly supported in models for mammal richness and abundance in non-rocky, but high productivity, volcanic savannas. This corroborates Stobo-Wilson et al. (2020a) in finding that vegetation productivity was positively associated with mammal richness at broad scales except for when fires removed the cover. The importance of shrub cover as a model attribute for volcanic habitats also support previous findings for the threatened mammal *Conilurus penicillatus* in Melville Island savannas (Davies et al., 2017; Penton et al., 2021). The dynamic nature of ground layer vegetation highlights a key implied threat to savanna mammals in these open habitats. Total consumption of ground-layer vegetation after high intensity, extensive fires, has been shown to increase feral cat visits and hunting activity to burnt areas (McGregor et al., 2014, 2016), and result in elevated predation related mortality (Leahy et al., 2016), and the need for mammals to disperse and recolonize from remote refuge habitats in order to re-establish local populations (Shaw et al., 2021). A key feature of sites that retained mammal populations after fire were that they had been burnt in lower intensity, more patchy fires which retained local vegetation cover (Shaw et al., 2021). Such areas act as refugia for local mammals after extensive fires (Legge et al., 2008). As such it is crucial that prescribed burning for conservation outcomes in savannas retain frequent unburnt patches (ca. 2–20 ha), equivalent of threatened mammal home ranges (e.g., Oakwood, 2002; Pardon et al., 2003; Cook, 2010; Hohnen et al., 2015, 2016a; Leahy et al., 2016; Penton et al., 2020) throughout the burnt landscape if mammal populations are to persist at the local scale.

One dynamic ground layer vegetation attribute that had a negative relationship with savanna mammals was annual *Sorghum* grass cover. Unlike perennial grass, which spreads out and provides ground layer cover, annual *Sorghum* grass mostly

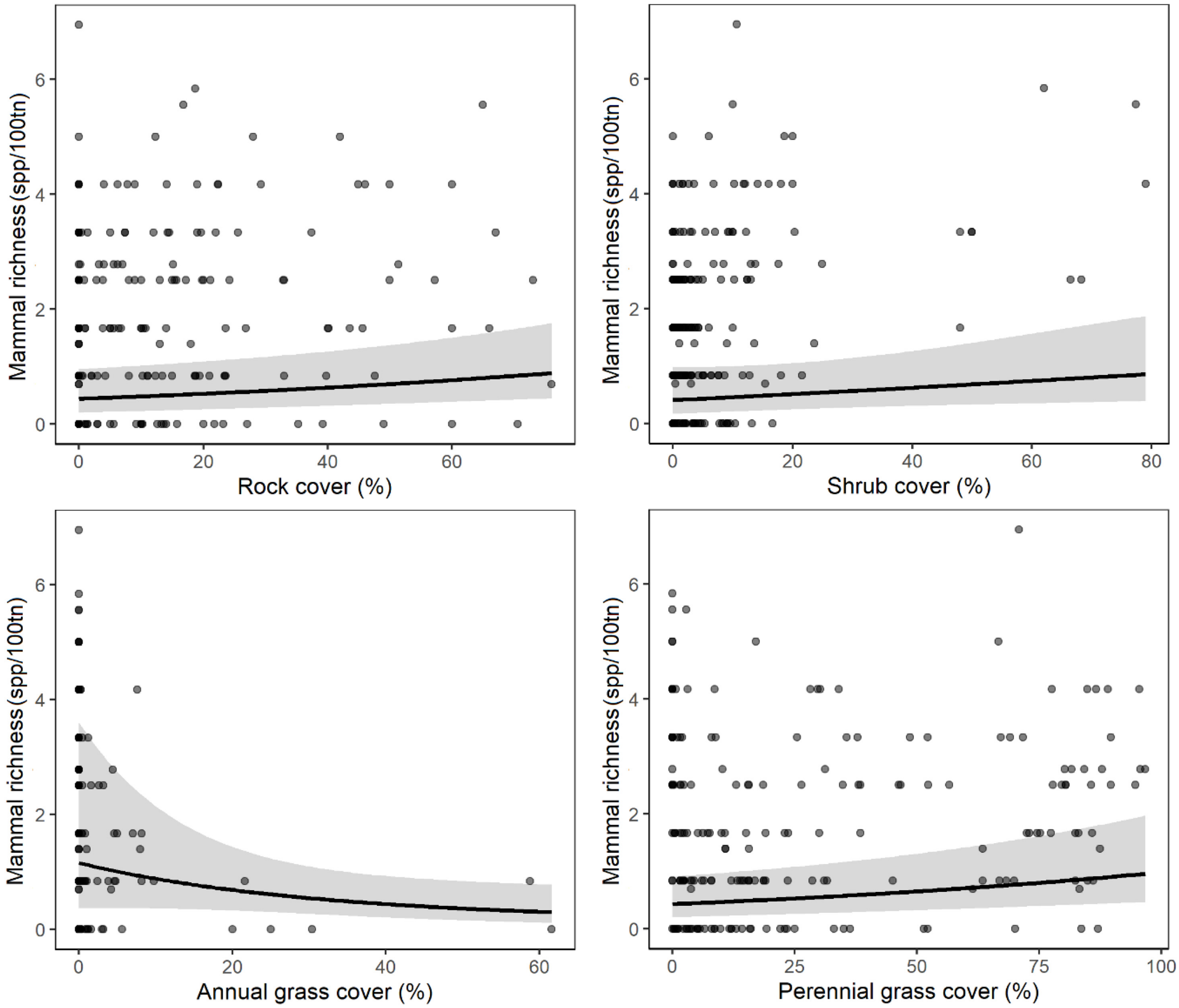

FIGURE 6 | Mammal richness [species per 100 trap nights (tn)] in volcanic habitat shown only for highly influential predictor variables sampled at all scales around each site (see **Table 2**). Relationships for each variable were derived from GLMM predictions while holding other explanatory variables constant at their median level. Model fit is shown by a black line and the gray band represents the 95% confidence interval. Gray circles indicate observed data values and are darker when repeated observations occur at the same point.

grows vertically as a single very tall tiller (Weier et al., 2016) with very few leaves at ground level to provide cover. In this study, sites with high *Sorghum* cover (>10% projected canopy cover) had low mammal abundance and richness. Luckily Northern Kimberley savannas generally have relatively low *Sorghum* cover. Among our study sites, the mean annual *Sorghum* grass cover was 2% while perennial grass cover was 22% (**Table 1**). However, in other regions of northern Australia, savannas often have much greater annual *Sorghum* dominance (Russell-Smith et al., 2003a; Scott et al., 2010). *Sorghum* not only provides little cover for mammals, but it is also highly flammable once cured, leading to low patchiness and extensive fires even under milder fire weather conditions in the early dry season (Miles, 2020). Fire management which can reduce local fire frequency, will potentially also reduce *Sorghum* dominance (biomass, cover, seed set) and thereby benefit savanna mammals, through increasing competition from resprouting perennial grasses, shrubs and tree canopies (Radford and Fairman, 2015; Weier et al., 2018; Radford et al., 2021).

The Negative Influence of Site-Scale Disturbance – Feral Cats, Fires, and Cattle

Mammal abundance and richness was greatest where cats, fire extent and livestock disturbance was least. Cats are putatively the primary threat to savanna mammals in northern Australia (Johnson, 2006; Frank et al., 2014; Ziembicki et al., 2015; McGregor et al., 2016; Tuft et al., 2021). While feral cats are ubiquitous across the entire study region (Legge et al., 2017), the few survey sites where cats were recorded all had very low mammal abundance and richness compared to sites where cats were not recorded. This suggests a strong local influence of cat activity on mammal populations where cat activity is high. Stobo-Wilson et al. (2020b) found a negative relationship between vegetation productivity and cat occupancy, and these results are mirrored in our study with cat activity levels higher at low productivity (lower rainfall) sites (e.g., Mount Elizabeth, Solea Falls, Orchid Creek; **Figure 1**). High feral cat activity in savannas has also been linked with disturbance of ground layer vegetation either through frequent fire or extensive grazing (Davies et al., 2020; Penton et al., 2021). This is also reflected in this study, with feral cats more active at sites on one pastoral station (Mount Elizabeth) and sites subject to extensive wildfires during the study period (Solea Falls, Orchid Creek). Despite the failure of camera trapping to detect feral cats at most volcanic savanna sites, it is also likely that the overriding influence of habitat cover in these savannas relates directly to risk of predation by feral cats. Cats are known to have higher occupancy rates in open non-rocky savannas compared to rugged rocky savanna habitats (Hohnen et al., 2016b). Removal of vegetation ground cover in non-rocky savannas, through frequent fires or cattle disturbance, leads to much greater cat predation related mortality for savanna mammal species (McGregor et al., 2015; Leahy et al., 2016; Stobo-Wilson et al., 2020a,b).

Our study supports a predominantly negative relationship at the site-scale of fire disturbance on mammal abundance and richness. This is despite the positive influence of increased early dry season prescribed burning at regional scales in the same region (Radford et al., 2020a). The current study showed that at the site-scale, mammals were negatively associated with the extent of fire in the current year, with distance to unburnt habitat, and also with increased site fire frequency. These results mirror a number of previous studies from northern Australia showing predominantly negative influences of fires on savanna mammals (Andersen et al., 2005; Woinarski et al., 2010; Lawes et al., 2015; Radford et al., 2015; Stobo-Wilson et al., 2020a). However, the influence of early dry season prescribed burning at regional scales in modifying fire intensity, patchiness and extent at landscape and local scales may also allow greater site-scale vegetation cover to be maintained than under a late dry season wildfire regime dominated by high intensity, high consumption fires. Possibly the mechanism underlying mammal improvements at the regional-scale in the previous study (Radford et al., 2020a) was increased retention of habitat cover at the site-scale under managed compared to unmanaged fire regimes.

Despite previous studies reporting negative influences of cattle on savanna mammals in northern Australia (Legge et al., 2011, 2019; Radford et al., 2015; Davies et al., 2020; Mihailou and Massaro, 2021), cattle disturbance was associated with negative impacts in this study only for mammal richness in sandstone habitats. Surprisingly, the influence of cattle is detected only in sandstone habitats when these are known to have low carrying capacity for cattle in the Kimberley region (Speck et al., 1960). Volcanic woodlands are the only habitats considered suitable for cattle production in the Northern Kimberley (Speck et al., 1960). However, throughout much of the study period a cattle culling program was being undertaken which probably reduced cattle impacts on grass layer vegetation (Reid et al., 2020). One thing these results also highlight, however, is that despite cattle being at relatively low abundance in much of the study region, their impacts can still be high in low productivity sandstone sites where ground layer vegetation cover may take longer to recover. As shown in previous studies (Legge et al., 2011, 2019; Radford et al., 2015), our study highlights the need for ongoing cattle management if threatened mammal conservation is a priority for land owners.

Functional Local-Scale Up to Meta-Landscape-Scale Elements of Fire Mosaics

Combined models with both site- and broader-scale fire mosaic attributes emphasize that site-scale habitat and disturbance features are much more influential for savanna mammals than broader-scale fire mosaic elements. Site-scale attributes were strongly supported in all 16 combined habitat-disturbance-mosaic models. In contrast, only five models had broad-scaled mosaic attributes supported (**Table 3**). This emphasizes the importance of local-scale ecological processes in shaping savannas mammal population dynamics (Legge et al., 2008; Radford, 2012; Radford et al., 2015; Leahy et al., 2016; Shaw et al., 2021) over and above the over-arching influences of broader scale fire mosaic patterns from local up to landscape and regional scales (Lawes et al., 2015; Radford et al., 2020a; Stobo-Wilson et al., 2020a). The finding that site-scale, over broader landscape-scale factors, are more important for *in situ* persistence of mammal populations is also supported by recent studies from other biomes (Hale et al., 2021).

Nonetheless the results of this study highlight a number of key functional attributes of broader scale fire mosaics (as per Parr and Andersen, 2006) which do influence savanna mammal patterns. An important beneficial functional attribute of broader-scale fire mosaics verified in this study was the extent of ≥4-year old unburnt habitat (**Table 2** and **Figures 3**, **5**). Increasing unburnt habitat was beneficial for savanna mammals within 1 km of a site (local scale) in sandstone habitats and within 5–10 km of sites in volcanic savanna habitats (landscape and meta-landscape scales). The benefits of the presence within a fire mosaic of unburnt refuge habitat through multiple years at both local and landscape scales is likely to result from the ability of mammal populations to persist in association with unburnt habitat. Many mammal species use unburnt refugia in the short term following a fire (Legge et al., 2008). In addition, these refugia within broader frequently burnt landscapes facilitates lower predator related mortality (Leahy et al., 2016), local persistence of population and therefore greater population stability at the site- and local- and landscape-scales (Shaw et al., 2021). This result emphasizes further the importance of achieving persistence of longer unburnt vegetation (≥4 years) patches within savanna landscapes for the benefit of threatened mammal in northern Australia.

Mammal abundance in savannas on rocky sandstone was greatest after years with intermediate fire extent (ca. 25%) the previous year at both local and meta-local scales (≤3 km) within broader fire mosaics (**Table 3** and **Figure 3**). This suggests that some burning at local/meta-local scales is beneficial for savanna mammals within sandstone habitats. However, given the benefits of unburnt habitat highlighted above, these benefits are probably derived through reduced total fire extent and retention of ground-layer vegetation cover at the site-scale due to protective networks of burnt patches, rather than due to the direct benefits of burnt habitat *per se* (though see Radford, 2012 for an example of benefits of burnt habitats for carnivous mammals). This suggests that benefits from prescribed burning mosaics (Radford et al., 2020a) might result more from the unburnt patches achieved at the site- and local/meta-local scale through low intensity burning, rather than some resource or habitat feature of the burnt habitat itself.

In their critique of the patch mosaic burning paradigm, Parr and Andersen (2006) and Andersen et al. (2014), emphasized the importance of functional elements within fire mosaics, rather than pyrodiversity (diversity of post-fire habitat age and fire frequency) *per se*. They argued that focus on diversity alone may cause conservation managers to miss crucial elements of mosaics needed by target biodiversity while focusing on superfluous (non-functional) mosaic elements. For instance, major variations in fire frequency within mosaics were found not to influence savanna ant assemblages, only very long unburnt habitat (>6 years) (Andersen et al., 2014). Our study provides another example, where pyrodiversity (diversity of post-fire age) at the local and meta-local scales (≤3 km from survey site) was negatively related to savanna mammal abundance and richness in sandstone habitats (**Table 3** and **Figure 4**). This is likely related to pyrodiversity being directly correlated in this context with larger fire extent and therefore to less unburnt habitat. Either way, this finding is crucially important for conservation managers in showing that pyrodiversity *per se* (diversity of post-fire fuel ages) is not a useful target when applying prescribed burning management for target biodiversity – in this case because of a negative association with threatened savanna mammals. Instead, it is much more important for fire managers to focus on the establishment and deliberate retention of patches ≥ 4 years unburnt habitat through multiple years. The benefits therefore of establishing an intermediate extent (25%) of recent fire within mosaics, is in maintaining longer unburnt habitat refugia within the savanna matrix. Our study joins an increasing number of ecological studies which do NOT support a general finding that 'pyrodiversity begets biodiversity' (Jones and Tingley, 2021). Future studies need to move beyond simplistic ideas concerning pyrodiversity and biodiversity, and focus more on the key functional elements within fire mosaics which mechanistically support target species with particular ecological traits, if progress is to be made in use of prescribed fire mosaics for threatened species conservation.

Explanatory Habitat, Disturbance and Mosaic Features Not Supported

Dingoes have been postulated to have both positive and negative impacts on threatened savanna mammals in northern Australia. Stobo-Wilson et al. (2020a) found negative associations between savanna mammals and dingoes (postulated predation impacts). However there is also some evidence of positive effects of dingoes on savanna mammals via reductions in meso-predatory cat activity/occupancy (Kennedy et al., 2012; Leo et al., 2019). Our study provides no support for any influence of dingoes in our study area despite them being common throughout the region. The relative rockiness of Kimberley savanna could explain this as dingoes are negatively associated with increasing rockiness (Stobo-Wilson et al., 2020b).

Another hypothesis raised in some studies is that late dry season wildfires are much more damaging to savanna biodiversity and habitat, particularly mammals, and that low intensity prescribed burning in the early dry season can benefit mammals (Andersen et al., 2005; Lawes et al., 2015; Radford et al., 2020a, Radford et al., 2021). Despite this there was little support in our study for additional impacts of late dry season fires compared to early dry season fires. Neither fire intensity observed at the site-scale (which correlates with fire season) nor the proportion of late dry season fires within our broader-scale mosaics were supported in our models. Instead it was simply the extent of fire at site-scale and broader mosaic scales that influenced mammal abundance and richness. Late dry season fires may only be detrimental to savanna mammals (as per Radford et al., 2020a) because of their large extent and lack of patchiness compared to early dry season prescribed burns, rather than because of any inherent difference in the impacts of these fires on habitat/vegetation structure (Andersen, 2020). These findings emphasize the importance of prescribed fire in NOT removing key habitat cover values, rather than in any inherent value of the early dry season burnt habitat itself.

Management Implications

To implement fire management for explicit biodiversity conservation, we recommend the following:

Reduce fire extent via the application of judicious and strategic low-intensity prescribed burns (Andersen et al., 2005), which provide barriers to wildfires but maintains shrub and fruiting tree cover. This approach requires burning in the months where conditions (e.g., Fire Weather Index) is conducive to producing smaller, less intense fires (Perry et al., 2019).

Maintain more and larger patches (up to 5 km^2) of longer unburnt vegetation (>4 years) across the landscape (Radford et al., 2020a) through the strategic application of prescribed fire (as above).

Reduce fire frequency by minimizing prescribed burning in areas that are naturally less fire-prone (Andersen et al., 2005). When implementing prescribed burning, use landscape features that maximize the stopping power of strategic fire scars (Fisher et al., 2021). Satellite-mapped fire histories, available from the North Australia and Rangelands Fire Information (see footnote 2) and Savanna Monitoring and Evaluation Framework[3] websites, are particularly useful for identifying less fire-prone areas.

Finally, managers must implement concurrent conservation actions that reduce the impacts of feral livestock, cats and weeds to increase landscape productivity and maximize the benefits of fire management (Legge et al., 2019; Stobo-Wilson et al., 2020a).

We realize that such an approach across northern Australia's vast and remote landscapes is both a formidable and expensive challenge. We note that significant fire regime benefits have been realized across some areas in the last ten years (e.g., Radford et al., 2020a; Edwards et al., 2021), but that further improvements are also required (e.g., Russell-Smith et al., 2017; Evans and Russell-Smith, 2019; Edwards et al., 2021).

Many of these improvements are being driven by emissions reductions schemes ('savanna burning') that incentivize the reduction of wildfires, and can provide the quantum of money needed to resource fire management for biodiversity conservation (Edwards et al., 2021). However, it is imperative that adequate and targeted monitoring, evaluation- and reporting are embedded within fire programs in an adaptive management context (see Corey et al., 2020) to better understand the biodiversity implications of fire management. Furthermore, fire management programs should have increasing patches of longer unburnt vegetation throughout the landscape as an explicit target for their management performance. Our results suggest that longer unburnt vegetation is more important than fire seasonality *per se* for threatened savanna mammals.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://naturemap.dbca.wa.gov.au.

ETHICS STATEMENT

The animal study was reviewed and approved by Department of Biodiversity, Conservation and Attractions Animal Ethics Committee.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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[3] https://smerf.net.au/

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Winners and Losers: How Woody Encroachment Is Changing the Small Mammal Community Structure in a Neotropical Savanna

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Years of fire suppression, decreases in herbivores, and global climate change have led to shifts in savannas worldwide. Natural open vegetation such as grasslands and shrublands is increasing in wood density, but the effects for small mammals are not well understood. While most of the mammal studies from the Brazilian Cerrado are concentrated in the core area of this large Neotropical savanna, its southern portions are suffering from biome shifting through woody encroachment. Herein, we surveyed a small mammal community from the southeastern boundary of Cerrado (Santa Bárbara Ecological Station) and evaluated the micro and macro environmental variables shaping community structure in order to investigate how the woody encroachment in the last 15 years may have influenced this assemblage. We recorded 17 species of marsupials and rodents along five distinct habitats in a gradient from grasslands to woodlands. Although richness was not affected by microhabitat variables, total and relative abundance varied according to habitat type and in relation to herbaceous, shrub, and tree density. Rodents such as *Calomys tener* and *Clyomys laticeps* were positively affected by increasing herb cover, *Cerradomys scotti* and *Oligoryzomys nigripes* by shrub cover, while the marsupial *Didelphis albiventris* had higher association with increasing tree cover. We detected an increase of 27.4% in vegetation density (EVI) between 2003 and 2018 in our study site, and this woody encroachment negatively affected the abundance of some small mammals. The open-area specialists *Cryptonanus chacoensis* and *C. scotti* had a decrease in abundance, while *D. albiventris* and *O. nigripes* were favored by woody encroachment. Our data suggest that woody encroachment is shifting community composition: small mammals often associated with grasslands and open savannas are likely to be negatively affected by woody encroachment; while species that rely on tree-covered habitats are likely to benefit from an increasing woody landscape. Therefore, forest-dwellers are gradually replacing open-vegetation inhabitants. Active management of open formations (e.g., with prescribed burning) may be needed to maintain Cerrado biodiversity, especially considering the open-area endemics.

Keywords: Cerrado (Brazilian savanna), Didelphimorphia, EVI, microhabitat selectivity, habitat use, Rodentia, fire suppression, grasslands

INTRODUCTION

Savannas worldwide have faced an increase in woody plant cover in the last century (Stevens et al., 2016a; Archer et al., 2017; García Criado et al., 2020). Changes in savannas natural landscapes due to tree encroachment have been described in Africa (e.g., Mitchard and Flintrop, 2013; Blaser et al., 2014; Stevens et al., 2016b), Australia (e.g., Fensham et al., 2005; Price and Morgan, 2008), North America (e.g., Archer, 1994; Van Auken, 2009; Ratajczak et al., 2012), and South America (e.g., Honda and Durigan, 2016; Passos et al., 2018; Rosan et al., 2019). The fast increase in woody biomass, stem density, woody cover, and/or woody density in an ecosystem defines woody encroachment, which leads to the conversion of natural open habitats into woodlands (Stevens et al., 2016a; Rosan et al., 2019; Eldridge and Ding, 2021). This increase in forest formations across savanna landscapes often leads to a decrease in herbaceous cover and changes in associated biodiversity, primarily at the expense of savanna specialists (Van Auken, 2009; Abreu et al., 2017; Archer et al., 2017). The main causes of woody encroachment vary regionally as different and complex mechanisms act across savanna ecoregions, differing in ecological, climatic, evolutionary, and social aspects (Archer, 1994; Archer et al., 2017). Changes in natural fire regime, herbivory, climate (temperature and precipitation), land use, and higher atmospheric CO_2 are suggested as the main causes for this phenomenon and are often associated with human disturbance in these ecosystems (Bond and Midgley, 2000; Stevens et al., 2016a; García Criado et al., 2020).

South American savannas showed the highest mean of woody cover increase (7.4% per decade) across tropical savannas (Stevens et al., 2016a). Moreover, 19% of the remaining Brazilian Cerrado areas are under woody encroachment, probably induced by fire suppression and agricultural land abandonment, intensified by the increase in atmospheric CO_2 (Moreira, 2000; Roitman et al., 2008; Passos et al., 2018; Rosan et al., 2019). Fire is a determinant driver for savanna dynamics, which has a historical evolution modeled by fire and herbivory processes, along with other fire-prone ecosystems (Bond and Keeley, 2005; Parr et al., 2014; Fidelis, 2020). The Cerrado high biodiversity is a result of these processes, with a rich mosaic of habitats (from open grasslands to woodland savannas) and endemic species adapted and often dependent on frequent fire events to maintain their populations (Simon et al., 2009; Fidelis and Blanco, 2014; Pilon et al., 2018, 2020). Brazilian Cerrado already lost about half of its natural vegetation due to extensive agriculture, especially soybean monoculture, and human occupation, leading to a high level of fragmentation (Motta et al., 2002; Sano et al., 2010; Alencar et al., 2020). Changes in the natural balance of the local fire regime (such as frequency and intensity) can lead to declines in local populations or even local extinction, particularly for savanna specialists (Bowman et al., 2020). For instance, the Santa Bárbara Ecological Station (SBES), located in southeastern Brazil, has been under almost complete fire suppression for about 30 years, and recently (since 2015) fire management was introduced (Durigan et al., 2020). Over three decades (1985–2015), this remnant of Cerrado experienced woody encroachment and decreases in plant (especially herbs and shrubs) and ant species typical of open habitats (Abreu et al., 2017, 2021).

Most studies on the consequences of woody encroachment are focused on plants and biogeochemical cycles (e.g., Moreira, 2000; Huxman et al., 2005; Price and Morgan, 2008; Van Auken, 2009; Ratajczak et al., 2012; Blaser et al., 2014; Honda and Durigan, 2016; García Criado et al., 2020) with few dedicated to the responses of animal communities (e.g., Eldridge et al., 2011; Abreu et al., 2017; Stanton et al., 2017; Andersen and Steidl, 2019). Stanton et al. (2017) highlight a minor research effort about shrub encroachment impacts on vertebrates in all continents, with a higher number of studies on bird communities (almost twice those on mammals and herpetofauna, individually). For mammals, studies show a decrease in diversity and abundance with shrub encroachment in Africa (Stanton et al., 2017). Thus, it is urgent to study the possible impacts of woody encroachment on mammals from Cerrado, the richest savanna for mammal species, most of which composed of small mammals (Paglia et al., 2012; Mendonça et al., 2018). About 20% of the Cerrado non-flying small mammals (rodents and marsupials) are endemic and present high habitat selectivity and low dispersal capacity, which makes them highly vulnerable to changes in their habitat remnants (Pardini et al., 2010; Carmignotto et al., 2012; Gutiérrez and Marinho-Filho, 2017; Carmignotto, 2019).

Habitat structure modifications unleashed by the increase in tree density include a decrease in the area covered by the herbaceous layer due to competition for resources such as soil moisture, nutrients, and light, and intolerance to high canopy shading (Archer, 1994; Van Auken, 2009; Parr et al., 2014). This modified ecosystem will probably impact animal communities of savanna specialists, for instance, through changes in macro and microhabitat variables, such as the amount of sunlight that reaches the soil, microclimate, water, food, and refuge availability, and vegetation structure (Abreu et al., 2017; Loggins et al., 2019). As small mammals exhibit high habitat selectivity and have a heterogeneous distribution associated with the mosaic of habitats in the Cerrado, these changes in habitat structure can lead to a shift in the composition of local small mammal communities (Carmignotto et al., 2012, 2014). Although the microhabitat perspective has been explored by small mammal ecologists since the 60s (e.g., Morris, 1987; Stancampiano and Schnell, 2004; Melo et al., 2013; Corrêa et al., 2017), the definition and clarity of which variables and scale define it vary among studies [see review by Jorgensen (2004)]. There are few studies evaluating microhabitat effects on the density of Cerrado small mammals (e.g., Vieira, 2003; Rocha et al., 2011), a topic that is broadly explored for the neighbor Atlantic Forest (e.g., Püttker et al., 2008; Melo et al., 2013). In this study, we evaluated habitat selectivity from both the macro and microhabitat perspectives, aiming to contribute to the understanding of which factors, at different scales, shape a small mammal community at the southeastern Cerrado boundary. We also aimed to evaluate how the woody encroachment in the last 15 years may have influenced community structure. We expect a notable change in the small mammal community of Cerrado sites under woody encroachment, with forest-dwellers gradually replacing open-vegetation inhabitants, partially due to differential habitat and microhabitat preferences.

MATERIALS AND METHODS

Study Area

Our study was conducted in the Santa Bárbara Ecological Station (hereafter SBES; 22°46′–22°51′S/49°10′–49°16′ W, 600–680 m above sea level, Águas de Santa Bárbara municipality, São Paulo, Brazil), one of the few protected areas that preserves open savannas in the southern Brazilian Cerrado (Durigan et al., 2020). SBES is characterized by a mosaic of savannas and Atlantic Forest patches (Melo and Durigan, 2011), comprising 2,715 ha. Currently, SBES vegetation is mostly represented by native Cerrado formations, from grasslands ("*campo sujo*" and "*campo cerrado*") and savannas ("*cerrado sensu stricto*") to woodlands ("*cerradão*") (Oliveira-Filho and Ratter, 2002; Araujo et al., 2010; Melo and Durigan, 2011). The SBES was under a fire suppression policy for 30 years (1985–2015; Abreu et al., 2017; Durigan et al., 2020). The grasslands that we studied here are among the few ones that had some accidental fire events more recently. The 2003 "*campo limpo*" ("*campo sujo*" in the 2017–2018 survey) patch had at least four fire events before 2008, when the last one was registered. One "*campo cerrado*" patch had only one fire event recorded in the last 30 years, in 2001, and the other patch in 2011, and both have been under fire suppression since then. The other plots that were sampled, burned for the last time before 1985 (Melo and Durigan, 2011; Conciani et al., 2021). Although these sparse fire events contributed to the grasslands maintenance in the area, SBES have been suffering under woody encroachment across this period (Melo and Durigan, 2011; Abreu et al., 2017, 2021). The study site also holds stands of exotic timber plantations, including *Eucalyptus* sp. and *Pinus* sp. Dry/cold (April to September) and wet/warm (October to March) seasons are strongly marked. The climate is classified as Köppen Cwa-type, with annual rainfall between 1010 and 2051 mm and an average of 1454 mm (Alvares et al., 2013; CIIAGRO, 2016). The mean temperature of the coldest months is 17°C and for the hottest months, 24°C, with a maximum of 35.2°C and a minimum of 3.4°C. These data correspond to the period from 1995–2014 and come from the weather station in the municipality of Manduri, São Paulo, Brazil, 20 km from our study area (CIIAGRO, 2016). SBES soils are characterized as deep oxisols with low nutrient and high sand content, high saturation of aluminum, and low capacity of holding water (Melo and Durigan, 2011).

Data Sampling

Small Mammal Surveys

To characterize the habitat and microhabitat preferences in order to investigate the role of woody encroachment in the small mammal community (rodents and marsupials), we used data from two temporally spaced surveys: (1) the 2003 survey carried out during January and February 2003, in four Cerrado habitats of SBES including open grasslands ("*campo limpo*" and "*campo sujo*"), savanna ("*cerrado sensu stricto*"), and woodland ("*cerradão*"), comprising a 10-day field-trip and a capture effort of 1,365 live trap nights and 1,680 pitfall trap nights [more details about the sampling design of the 2003 survey can be found in Carmignotto (2005)]; and (2) the 2017–2018 survey, from August 2017 to July 2018, with 12 monthly 10-day field trips, also in four Cerrado habitats, from grassland to woodland ("*campo sujo*," "*campo cerrado*," "*cerrado sensu stricto,*" and "*cerradão*"), comprising 2,880 live trap nights and 2,880 pitfall trap nights in each habitat surveyed (three sampling points by habitat), totaling 11,520 live trap nights and 11,520 pitfall trap nights across the 12 sampling points. Each sampling point had eight live traps: four Sherman traps (25 cm × 8 cm × 9 cm, Sherman^{TM}) and four-wire mesh traps (two of 30 cm × 16 cm × 18 cm and two of 32 cm × 20 cm × 20 cm, Metal Miranda), alternated and 15 m apart. Traps were distributed in two arrays (A and B, each with two Shermans and two-wire mesh traps) 60 m apart. At the beginning of each field trip, the live traps were set on the ground and baited with a mix of peanut butter, cornmeal, and canned sardines. This bait was fixed on pieces of sweet potatoes in the wire mesh traps. Each sampling point was also composed of two lines of pitfall traps, 60 m apart, each with four 100-L buckets, 10 m apart, connected by a 60–70 cm high and ∼10 cm buried plastic drift fence. The pitfall trap arrays were 60 m apart from the live trap lines, and the buckets were opened and closed at the beginning and ending of each field trip.

The individuals captured were identified at species level (Voss and Jansa, 2009, and Fegies et al., 2021, for marsupials; and Patton et al., 2015, for rodents), weighted, and sexed. Other information about age (juvenile, subadult, and adult), behavior, and reproduction was taken when possible. We collected tissue samples from the ear of all individuals for taxonomic identification through molecular analysis. This small cut also served as recapture recognition for individuals weighing less than 30 g (although not allowing recognition at the individual level). We used numbered ear tags (ZT 900 by Zootech) for individual identification of animals weighing over 30 g. Some individuals were collected for morphological taxonomic identity and subjected to taxidermy or fixed with 10% formaldehyde solution and preserved in 70% alcohol (SISBIO 50658-3 collection permit). These vouchers will be deposited in the mammal collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. All procedures of capture and collection were made following the ASM guidelines for the use of wild mammals in research (Sikes et al., 2016) and were approved by the Animal Ethical Committee (#CEUA-IB-USP 241/2016).

Habitat and Microhabitat Use

In order to assess the habitat use by the SBES small mammals, we used the number of individuals captured in the 2017–2018 survey along the four habitat types sampled. These habitats were chosen in the field and represent a gradient of natural increasing woody cover, typical of Cerrado mosaics. The "*campo sujo*" and "*campo cerrado*" are both open formations with a predominance of herbaceous layer, but "*campo sujo*" is a grassland characterized by scattered shrubs and small trees, and "*campo cerrado*" by sparse trees and higher shrub cover, but still with a large proportion of herbs; "*cerrado sensu stricto*" is also known as "typical cerrado," and is a savanna formation dominated by shrubs and trees up to 3–8 m tall often covering 30% of the crown canopy, but still with a high herb cover; and "*cerradão*" is a forest formation, a woodland savanna with often 50–90% of canopy coverage composed of higher trees 8–12 m tall (see Oliveira-Filho and Ratter, 2002). The field classification was later confirmed by the enhanced vegetation index (EVI) obtained at each habitat surveyed.

To evaluate the potential role of microhabitat features in structuring small mammal communities, we measured seven variables at each live trap station during the 2017–2018 survey: (1) percentage of canopy cover; (2) number of trees with diameter at breast height (DBH) > 10 cm; (3) percentage of herbaceous soil cover; (4) percentage of soil covered by the invasive grass, *Brachiaria* sp.; (5) number of stems of shrubs that branch up to 1 m in height; and understory density, through (6) the number of touches up to 0.5 m height, and (7) between 0.5 and 1 m in height on a stick held vertically in different directions (S, N, L, and O). Variables 1–3 were visually estimated within a radius of 5 m from each live trap, and variables 4–7 were measured within a radius of 2 m from the live traps. These variables were selected based on their use in previous microhabitat small mammal studies (e. g., Freitas et al., 2002; Vieira et al., 2005; Rocha et al., 2011), and due to their close relationship with vegetation cover (herb, shrub, and trees) and canopy openness, differentiating well the distinct Cerrado habitats analyzed. We did not measure the microhabitat variables for pitfall stations since the area near each trap was cleared for the installation of pitfall traps. Therefore, the capture data used for microhabitat analysis were restricted to live trap stations. To increase independence of records, we did not consider recaptures of the same individual in the same live trap and month. Recaptures in different field trips and live trap lines were kept, as they could indicate the suitability of microhabitats for that species.

Woody Encroachment

We used the enhanced vegetation index (EVI) to quantify the vegetation change over the 15 years between both surveys (2003 and 2017–2018) across the sampled habitats. We calculated the mean EVI values for each sampling point based on surface reflectance images from Landsat 7 for 2003, and from Landsat 8 for 2018, obtained from the United States Geological Survey satellite products (USGS[1]). Furthermore, we used the available images from the survey periods, or as near as possible to the date, that presented conditions with minimum cloud cover. The satellite image manipulation and EVI values calculation were performed in the software QGis version 3.4.14 (QGIS, 2021). Abreu et al. (2017) showed that the EVI index is highly correlated with tree basal area, and Chaves et al. (2013) also argue that the EVI index is more sensitive to canopy changes, mainly in places with a higher concentration of biomass when compared with the NDVI index. Thereby, we consider the EVI index a suitable proxy to quantify woody encroachment in our study site.

Data Analysis

We used different datasets for each analysis performed here, according to its scale and goals. The datasets are derived from the total data we collected in both surveys (2003 and 2017–2018) and are described in **Table 1** and at each analysis item below.

Statistical analyzes were performed in R (version 4.1.0; R Core Team, 2021). The model selection for all linear models described below was made through hypothesis testing approach ($\alpha = 0.05$), comparing nested models through ANOVA function using the variance partition from the F-statistic for linear models and the residual deviance and chi-square tests for generalized linear models (Zuur et al., 2009). The diagnoses of the fitted models were made with the "DHARMa" package, we tested the model fitness for over and underdispersion, uniformity, outliers (along with Cook's distance plot), and zero-inflation (Harting, 2021, **Supplementary Table 1**). The prediction graphics of the models were made with the package "ggiraphExtra," function *ggPredict* (Lüdecke, 2018).

Small Mammal Community Structure

To characterize the community structure and compare patterns of small mammals between the two distinct surveys, we considered all data (Dataset 1, **Table 1**) from pitfalls and live traps (except for recaptures, which were removed) from both the 2003 and 2017–2018 surveys. Community structure was characterized by its alpha taxonomic diversity with the CHAO1 estimator, which allows estimating the absolute number of species in a community based on the number of rare species in the sample (Whittaker, 1972; Dias, 2004). We also estimated species richness through rarefaction/extrapolation species curves (Colwell et al., 2012; Chao et al., 2014). To evaluate the adequacy of sampling effort, the abundance data were used to calculate the coverage estimator which 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. These analyses were made using the "iNEXT" R package (Hsieh et al., 2016). Confidence intervals (95%) were used as thresholds in comparisons (Chao and Chiu, 2016). Abundance was defined as the total number of individuals captured per species, and to determine the dominance and

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[1] https://espa.cr.usgs.gov/

identify rare species in the communities, we used the Abundance-based Coverage Estimator (ACE) with the *ChaoSpecies* function from the "SpadeR" package (Moreno, 2001; Chao and Chiu, 2016).

Habitat and Microhabitat Use

In order to investigate the habitat use by the SBES small mammals, we performed a Non-Metric Multidimensional Scaling (NMDS) ordination with the "vegan" R package (Oksanen et al., 2020), function *metaMDS*, based on the number of individuals captured in the four habitats surveyed ("*campo sujo*," "*campo cerrado*," "*cerrado sensu stricto,*" and "*cerradão*"). For the NMDS, we used Dataset 2 (**Table 1**), which consisted of the total number of individuals captured in pitfalls and live traps (except for recaptures, which were removed) in the 2017–2018 survey. In order not to obscure the patterns found, we considered only species with n > 5 individuals. We also performed the Shepard plot (or stress plot), in order to observe the goodness of fit of the data into the NMDS analysis, using the *stressplot* R function.

The microhabitat analyzes were performed only for the 2017–2018 survey, considering only the live trap data (Dataset 3, **Table 1**), as explained above. First, we reduced the dimensionality of the seven microhabitat variables through a principal components analysis (PCA) with a correlation matrix using the "stats" package and retained the principal components with eigenvalues > 1. Then we fitted generalized linear mixed models (GLMM) with the package "lme4" (*glmer* function, family = poisson, link = log; Bates et al., 2021) for the abundance (number of captures per species) and richness of the small mammals as a function of the two principal components extracted from the PCA. The random effect considered for these GLMM was the 12 sampling points (three for each habitat), since for the microhabitat analyzes we treated each trap station as our sampling unit and considered it as non-independent within the 12 sampling points analyzed. For species with *n* > 10 individuals, we also built GLMM for the number of captures of each species in relation to the principal components selected.

Woody Encroachment

In order to investigate the effect of woody encroachment across time on small mammals, we used the Dataset 4 (**Table 1**), which included the total number of individuals captured in both pitfall and live traps (except the recaptures), of the 2003 survey (3,045 trap-nights). For the 2017–2018 survey, we restricted our data to those obtained in January-February (3,840 trap-nights), in order to standardize the capture effort between the two surveys analyzed. The same approach was employed for the analysis of satellite images, as explained in the data sampling item above.

To quantify the increase in tree cover between the two surveys, we fitted linear models ("stats" R package, *lm* function) using the mean EVI values for each sampling point as a function of the sampling period (2003 × 2018) and habitat ("*campo limpo*," "*campo sujo*," "*campo cerrado*," "*cerrado sensu stricto,*" and "*cerradão*"). To test the woody encroachment impact on the small mammal community, we fitted generalized linear models (GLM) for total richness and abundance of small mammals, and per order (rodents and marsupials), as a function of the EVI mean values for each sampling unit for the 2003 and 2018 surveys. A dissimilarity analysis based on the number of individuals captured between the two surveys was made by estimating beta diversity using the function *beta* from the "BAT" package (Carvalho et al., 2012; Cardoso et al., 2015) in order to detect changes in species composition across time between the two assemblages analyzed.

TABLE 1 | Description of each dataset used in this study.

Dataset	Definition	Topic addressed
1	Total number of individuals captured from both surveys (2003 and 2017/2018) in live and pitfall trap lines, excluding all recaptures.	Small mammal community structure
2	Total number of individuals captured in the 2017/2018 survey, in both live and pitfall trap lines, excluding all recaptures.	Habitat selection
3	Number of individuals captured in the 2017/2018 survey, only in the live traps, excluding recaptures of the same individual in the same live trap and month. Recaptures in different field trips and trap lines were kept.	Microhabitat selection
4	Number of individuals captured in Jan/Feb 2003 and Jan/Feb 2018, in live and pitfall trap lines, excluding all recaptures.	Woody encroachment

RESULTS

Small Mammal Community Structure

We captured 1,112 individuals of 17 native species of marsupials and rodents, in the gradient from grasslands to woodland savanna, considering both surveys (2003 and 2017–2018). Rodents and marsupials represented 67 and 33% of the total richness, respectively, (**Table 2**).

The 2003 survey recorded 10 species of small mammals (60% of total SBES richness), of which 70% were rodents and 30% marsupials, with a total of 124 individuals captured. In the 2017–2018 survey, 988 individuals were captured belonging to 17 species (100% of SBES total richness), of which 65% were rodents and 35% marsupials. Comparing both surveys, for 2003 we did not record the rodents *Hylaeamys megacephalus*, *Nectomys* cf. *squamipes, Oxymycterus delator,* and *Rhipidomys* cf. *macrurus*, and the marsupials *Didelphis albiventris*, *Gracilinanus agilis,* and *Gracilinanus microtarsus* in the habitats analyzed.

The species richness observed for the complete 2003 survey and for "*campo sujo*" and "*cerradão*" habitats were relatively close to the richness estimated by the Chao1 estimator (**Table 3**), indicating that the sampling effort was appropriate to survey this community, as was shown also by the coverage estimate (98, 97, and 83%, respectively). On the other hand, for the "*campo limpo*" and "*cerrado sensu stricto*," the observed richness was only half of the estimated richness, which is clear through the low coverage value for "*cerrado sensu stricto*" (55%), but not for "*campo limpo*" (92%), indicating that a more extensive sampling in the "*cerrado sensu stricto*" would be necessary (**Table 3**). Despite the

TABLE 2 | Relative abundance (%) of small mammals in the Santa Bárbara Ecological Station, São Paulo, Brazil, in the 2003 and 2017–2018 surveys.

Species	Habitat use	2003					2017–2018				
		CL	CS	CE	CD		CS	CC	CE	CD	
Didelphimorphia Didelphidae											
Cryptonanus chacoensis	G	0.8	3.2	0.8	–		1.2	1.4	0.6	–	
Cryptonanus aff. *chacoensis**	G	1.6	1.6	0.8	–		0.6	–	–	–	
Didelphis albiventris	F	–	–	–	–		0.2	0.3	1.2	4.1	
Gracilinanus agilis	F	–	–	–	–		–	0.4	1.6	2.3	
Gracilinanus microtarsus	F	–	–	-	–		0.3	–	0.4	3.4	
Monodelphis kunsi	G/S/F	–	–	–	1.6		–	0.2	0.2	0.4	
Rodentia Cricetidae											
Akodon cf. *montensis*	S/F	0.8	–	–	–		0.2	0.2	0.7	1.6	
Calomys tener	G	–	0.8	–	–		8.8	2.6	2.6	0.8	
Cerradomys scotti	G	0.8	4.8	0.8	–		3.0	6.4	2.1	0.2	
Hylaeamys megacephalus	F	–	–	–	–		0.2	–	0.1	2.4	
Necromys lasiurus	G/S	30.6	39.5	0.8	–		0.6	0.3	0.4	0.4	
Nectomys cf. *squamipes*	–	–	–	–	–		0.1	–	0.1	–	
Oligoryzomys mattogrossae	G	–	0.8	4.0	–		5.5	8.4	3.7	1.0	
Oligoryzomys nigripes	S/F	0.8	1.6	–	0.8		0.8	1.3	7.6	15.7	
Oxymycterus delator	–	–	–	–	–		0.1	–	–	–	
Rhipidomys cf. *macrurus*	F	–	–	–	–		–	–	0.2	0.8	
Echimyidae											
Clyomys laticeps	G	2.4	–	–	–		1.8	–	–	–	
TOTAL		37.9	52.4	7.3	2.4	**100**	23.5	21.6	21.7	33.3	**100**
N species		7	7	5	2	**10**	14	10	14	12	**17**
Survey effort (trap-nights)		790	790	715	750	**3,045**	5,760	5,760	5,760	5,760	**23,040**

*Habitats are ordered by increasing woody cover: CL = "campo limpo," CS = "campo sujo," CC = "campo cerrado," CE = "cerrado sensu stricto," CD = "cerradão." The habitat use is expressed by G for grasslands (here including CS = "campo sujo" and CC = "campo cerrado"), S for savannas (CE = "cerrado sensu stricto") and F for forest habitats (CD = "cerradão") according to the NMDS analysis performed for the 2017–2018 data (see **Figure 3**).*This taxon refers to Cryptonanus chacoensis lineage B of Fegies et al. (2021). The name C. chacoensis (Tate, 1932) was applied for C. chacoensis lineage A. Bold values express the total values for abundance, richness, and survey effort per year of survey.*

extremely low species richness value obtained for "*cerradão*," the rarefaction-extrapolation curves for the 2003 assemblage indicate no differences in the species richness among the habitats sampled, with values estimated for extrapolated data, corroborating the results of the Chao1 richness estimator (**Figure 1A**).

For the 2017–2018 survey, all the observed and estimated species richness were also similar, with high coverage values (99% for total data and habitats), evidencing that the sampling effort was sufficient to estimate the community richness (**Table 3**). This result corroborates those obtained by the rarefaction/extrapolation curves, which also indicates that only the "*campo cerrado*" differed in relation to the other habitats surveyed, showing comparatively lower richness (**Figure 1B**).

The species with the highest abundance for the 2003 survey was *Necromys lasiurus*, representing 71% of the assemblage (**Figure 2A**), followed by other rodents such as *Cerradomys scotti* (6.5%) and *Oligoryzomys mattogrossae* (4.8%). Furthermore, the less abundant species were the rodents *Akodon* cf. *montensis* and *Calomys tener*, with only one individual captured each, representing, together, 1.6% of total abundance (**Figure 2A**). This pattern became clear in the Abundance-based Coverage Estimator (ACE) analysis, which considered only *N. lasiurus* as an abundant species, and the nine remaining species as rare ($k < 10$). For the 2017–2018 survey, the species of *Oligoryzomys* were the most abundant, with *O. nigripes* comprising 25.4% of the assemblage and *O. mattogrossae* 18.6%. Other abundant species

TABLE 3 | Observed and estimated species richness, with standard errors and sample coverage, of small mammals for the 2003 and 2017–2018 surveys in distinct habitats surveyed at SBES.

Assemblages	Richness observed	Richness estimated Chao1	Standard error	Sample coverage
2003	10	12.0	3.7	98%
CL	7	14.8	11.4	92%
CS	7	8.0	1.8	97%
CE	5	10.3	6.3	55%
CD	2	2.3	0.9	83%
2017–2018	17	17.5	1.3	99%
CS	14	14.7	1.3	99%
CC	10	10.0	0.6	100%
CE	14	15.0	1.9	99%
CD	12	12.0	0.4	100%

The habitats are: CL: "campo limpo"; CS: "campo sujo"; CC: "campo cerrado"; CE: "cerrado sensu stricto"; and CD: "cerradão."

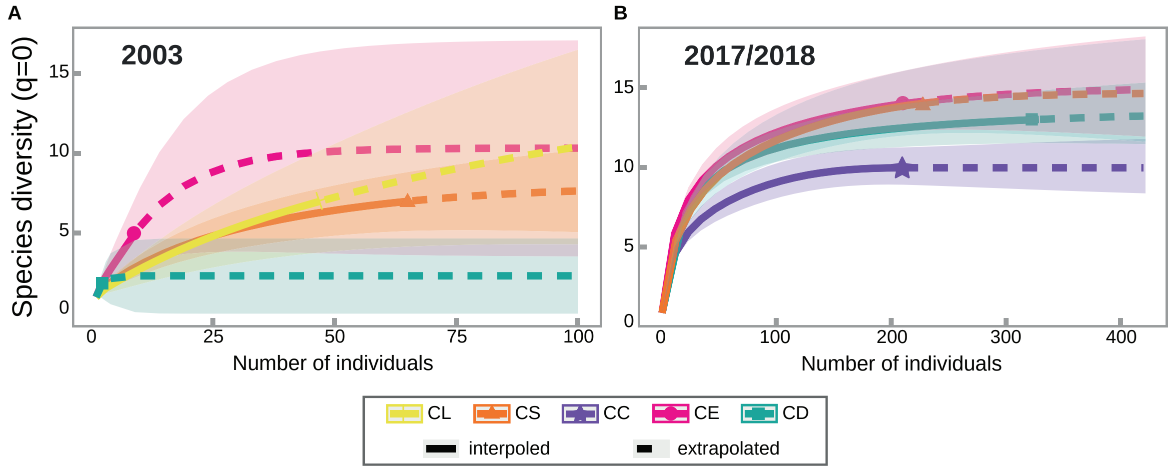

FIGURE 1 | Rarefaction/Extrapolation curves for **(A)** the 2003 survey generated with 1,000 bootstraps and 100 individuals as endpoint and for **(B)** the 2017–2018 survey generated with 1,000 bootstraps and 420 individuals as endpoint. The shadow surface represents the 95% confidence interval for each curve. The habitats are: CL: "*campo limpo*"; CS: "*campo sujo*"; CC: "*campo cerrado*"; CE: "*cerrado sensu stricto*"; and CD: "*cerradão*."

in this assemblage were the rodents *Calomys tener* (14.8%) and *Cerradomys scotti* (11.2%). The rarest species were the rodents *Nectomys* cf. *squamipes* (one individual) and *Oxymycterus delator* (two individuals), representing, together, less than 0.4% of total abundance (**Figure 2B**). For 2017–2018, the ACE analysis indicates 12 abundant species (k > 10), and five rare species.

Habitat and Microhabitat Use

For patterns of habitat use, the non-metric multidimensional scaling for the 2017–2018 survey (**Figure 3**; stress = 0.09, **Supplementary Figure 1**) showed distinct species groups, one composed by *Calomys tener*, *Cerradomys scotti*, *Oligoryzomys mattogrossae,* and *Cryptonanus chacoensis* that seemed more related to "*campo cerrado*," a grassland formation; and another formed by *D. albiventris*, *Gracilinanus agilis,* and *Hylaeamys megacephalus* that were located closer to "*cerradão*," a forested habitat. Also related with "*cerradão*" are *Gracilinanus microtarsus* and *Rhipidomys* cf. *macrurus*, but more dispersed than the previous species. *Akodon* cf. *montensis* and *Oligoryzomys nigripes* were located in between "*cerrado sensu stricto*" (savanna) and "*cerradão*" (forest). The species *Cryptonanus* aff. *chacoensis* and *Clyomys laticeps* were a bit more dispersed, but relatively close to the "*campo sujo*," the most open habitat at SBES. *Monodelphis kunsi* was located in a transition between "*cerradão*," "*cerrado sensu stricto*," and "*campo sujo*," and *Necromys lasiurus* between "*cerrado sensu stricto*," "*campo cerrado*," and "*campo sujo*."

The seven microhabitat variables were reduced to two principal components with eigenvalues > 1 (3.12 and 1.58, respectively, **Supplementary Table 2**) that represented about two-thirds of the total variance in our dataset (67.2%, **Supplementary Table 2** and **Supplementary Figure 2**). The first principal component (hereafter PC1 variable) represented 44.6% of the total variance and is an indicator of high herb cover and low tree cover. The second principal component retained (hereafter PC2 variable) is an indicator of high shrub cover and low herb cover and represented 22.6% of the total variance (**Supplementary Table 3**). The gradient in relation to vegetation cover and canopy openness is visible in the PCA graph and is evidently related to the PC1 and PC2 variables (**Supplementary Figure 2**). There was no difference in richness considering the PC1 and PC2 variables (null model: $p = 0.50$), i.e., richness did not differ across the habitat gradient. Despite that, total abundance was positively affected by shrub cover and negatively by herb cover (PC2), with an average increase of 18% in abundance per unit of PC2 ($p < 0.001$).

For the relative abundance (for species with $n > 10$ captures), the rodents *Calomys tener* ($p < 0.001$) and *Clyomys laticeps* ($p = 0.01$) were positively associated with herb cover. The estimated average increase in the relative abundance of *Calomys tener* in areas with high herb cover was 80.7% per PC1 unit ($p < 0.001$). On the other hand, *Clyomys laticeps* showed an average decrease of 74% per unit of PC2 ($p = 0.004$), which indicates a high positive relation with herb cover and a negative relation with shrub cover. *Cerradomys scotti* ($p = 0.015$) and *Oligoryzomys nigripes* ($p = 0.02$) were the species positively associated with shrub cover, with an average increase of 45 and 51.8% ($p = 0.02$) in their relative abundance per unit of PC2, respectively. *Oligoryzomys mattogrossae* was associated with both herb and shrub habitats ($p < 0.001$), with an estimated average increase of 53% ($p = 0.04$) in herbaceous areas and 58% in shrub units ($p < 0.001$). The marsupial *D. albiventris* was positively related to tree and shrub cover ($p < 0.001$), with an average increase of 67.3% in its abundance in forest areas and 18% for shrublands. The marsupial *Gracilinanus agilis* and the rodent *Hylaeamys megacephalus* were not influenced by PC1 and PC2 in their relative abundances ($p = 0.14$ and 0.58, respectively).

Woody Encroachment

Our linear model showed an increase of 0.1 on the EVI mean between the 2003 and 2018 survey (R^2 adj. = 0.26, $F_{1,14}$ = 6.38,

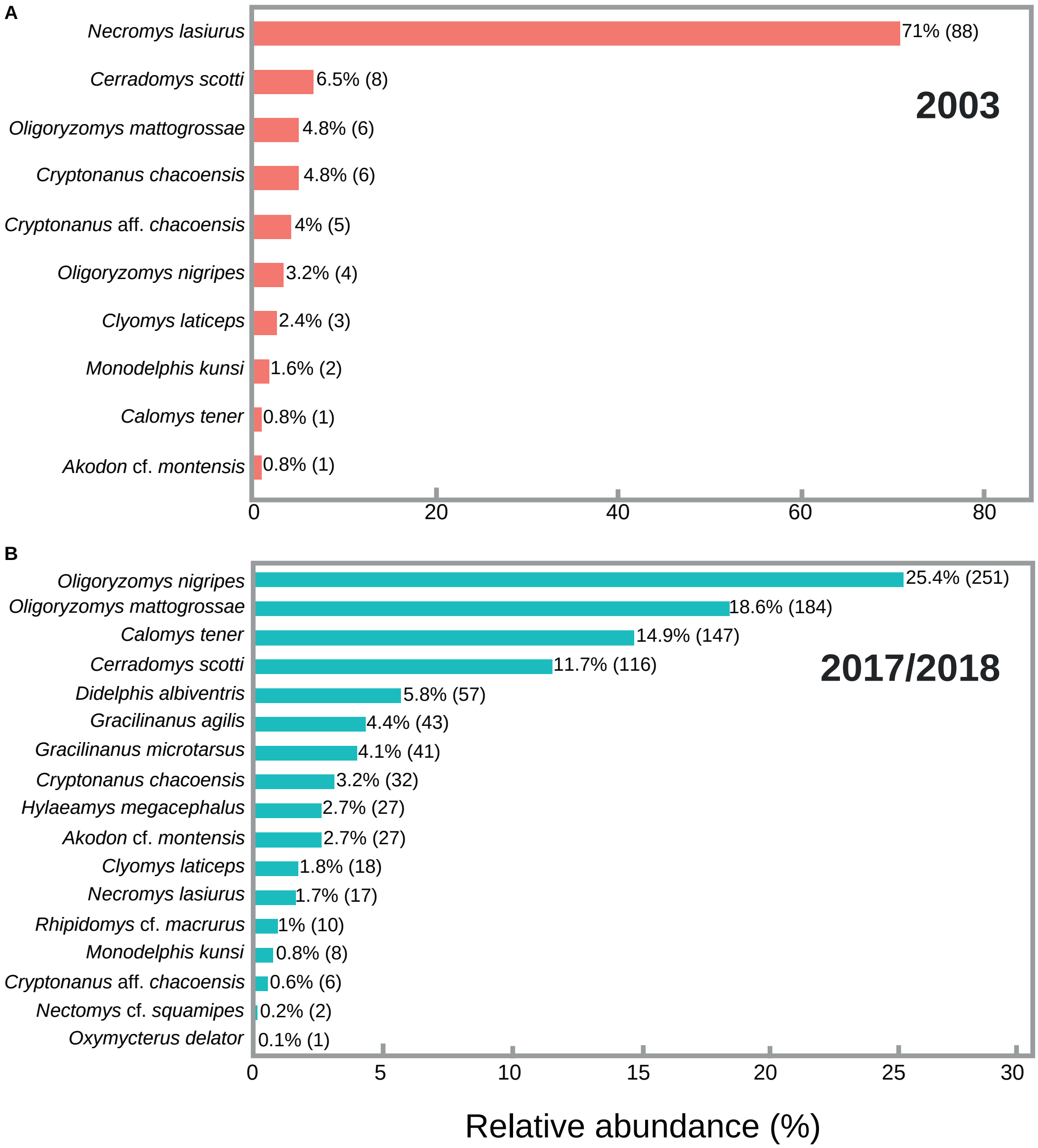

FIGURE 2 | Relative abundances and number of individuals (in parentheses) of small mammals from SBES captured in **(A)** 2003 survey (3,045 trap-nights) and **(B)** 2017–2018 survey (23,040 trap-nights).

p = 0.02). This result indicates an increase in vegetation density of 27.4% in 15 years, affecting primarily the open areas (**Figures 4**, **5A**). The linear model for EVI regarding the habitat types demonstrated a clear difference in its EVI mean values (R^2 adj. = 0.62, $F_{4,11}$ = 7.1, p = 0.004, **Figure 5B**), with the open habitats ("*campo limpo*," "*campo sujo*," and "*campo cerrado*") not different considering their EVI mean values, despite following a gradual increase on averages (0.30, 0.36, and 0.41, respectively). However, for the intermediate habitat, "*cerrado sensu stricto*," we estimate an increase of 46.6% on the EVI mean value compared to the more open habitat ("*campo limpo*"), with an EVI mean value of 0.44. For the forest formation, "*cerradão*," the model estimated a difference in the EVI mean value of 70% higher in relation to the "*campo limpo*" area, reaching the highest EVI mean value, 0.51 (**Figure 5B**).

The richness of small mammals was not affected by the increase in wood density (p = 0.39). We also tested the richness per mammal order, and obtained the same results, with no difference in richness as a function of EVI mean (Rodents: p = 0.27; Marsupials: p = 0.90). The total abundance of small mammals, on the other hand, was negatively affected by an increase in wood density (p = 0.02, **Figure 6A**), and for the rodents alone, a similar result was obtained (p = 0.01, **Figure 6B**). However, the total abundance of marsupials was not affected by

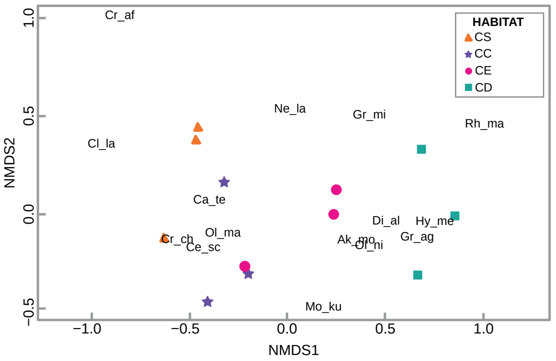

FIGURE 3 | Non-metric multidimensional scaling (NMDS) for small mammal abundances during the 2017–2018 survey. Small mammal species are: Ak_mo: *Akodon* cf. *montensis*; Ca_te: *Calomys tener*; Ce_sc: *Cerradomys scotti*; Cl_la: *Clyomys laticeps*, Cr_ch: *Cryptonanus chacoensis*; Cr_af: *Cryptonanus* aff. *chacoensis*; Di_al: *Didelphis albiventris*; Gr_ag: *Gracilinanus agilis*; Gr_mi: *Gracilinanus microtarsus*; Hy_me: *Hylaeamys megacephalus*; Mo_ku: *Monodelphis kunsi*; Ne_la: *Necromys lasiurus*; Ol_ma: *Oligoryzomys mattogrossae*; Ol_ni: *Oligoryzomys nigripes*; Rh_ma: *Rhipidomys* cf. *macrurus*. The habitats are: CS: "*campo sujo*"; CC: "*campo cerrado*"; CE: "*cerrado sensu stricto*"; and CD: "*cerradão*."

changes in mean EVI ($p = 0.61$). We also fitted models excluding captures of *Necromys lasiurus* (due to its dominance in the 2003 survey), and the null models were selected for total and rodent abundances (Total community: $p = 0.17$; Rodents: $p = 0.06$).

Among the species with at least 10 individuals captured, the rodents *Calomys tener* and *Oligoryzomys mattogrossae* seemed to be unaffected by the increase in EVI mean values ($p = 0.44$ and 0.20, respectively). The marsupial *Cryptonanus chacoensis* and the rodents *Cerradomys scotti* and *Necromys lasiurus* were negatively affected by the local woody encroachment, with a decrease in their abundances related to higher mean EVI ($p = 0.001$, <0.001, and 0.01, respectively, **Figures 6C,E,G**). The marsupial *D. albiventris* and the rodent *Oligoryzomys nigripes* were positively affected by increases in EVI mean ($p = 0.001$ and $p < 0.001$, respectively, **Figures 6D,F**).

The Beta diversity analysis showed high dissimilarity between the 2003 and 2018 surveys ($\beta_{total} = 0.84$), which is explained by the replacement of species ($\beta_{repl} = 0.84$ and $\beta_{rich} = 0$). The composition in the 2018 survey presented an increase of four species compared to the 2003 survey, *D. albiventris*, *Gracilinanus agilis*, *Hylaeamys megacephalus,* and *Rhipidomys* cf. *macrurus*, most of them associated with the "*cerradão*," a forest formation (**Figure 3**).

DISCUSSION

We found that SBES small mammal community is structured by the main microhabitat characteristics associated with the different habitats, including herb and canopy cover, and shrub and tree density. This community is responding to the advancing woody encroachment in the area through time. Our models indicated that such changes are predictable, with species typical of open-vegetation habitats (such as *Cryptonanus chacoensis* and *Cerradomys scotti*) showing declines while forest-dwellers (such as *D. albiventris* and *Oligoryzomys nigripes*) are increasing in abundance. Therefore, woody encroachment is changing this community structure in predictive ways and creating "winners and losers," which turn on an alert about the future of open-area specialists in face of the Cerrado encroachment.

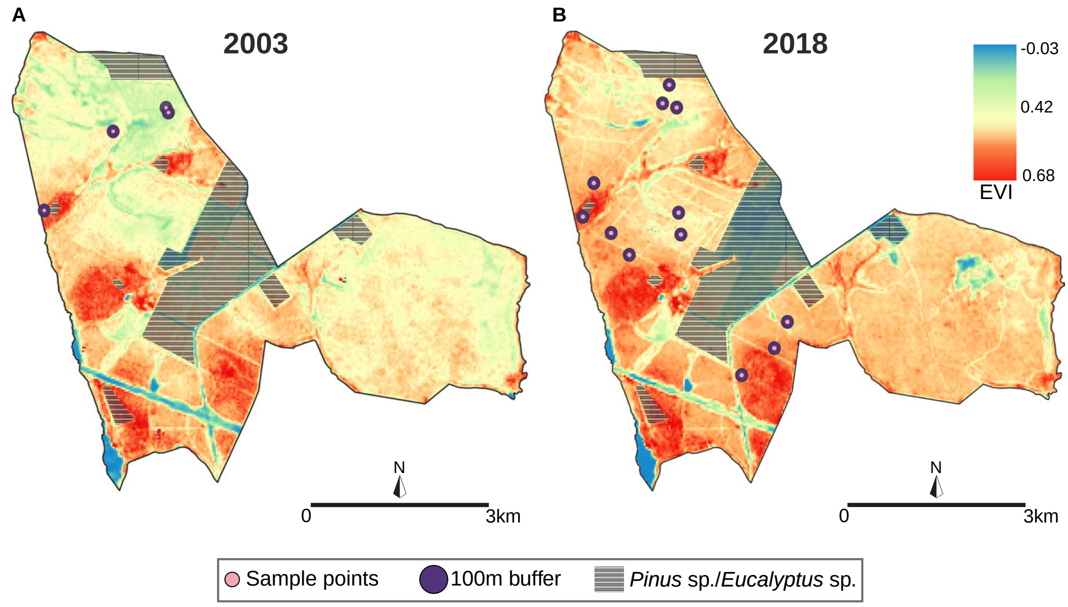

FIGURE 4 | Variation in the enhanced vegetation index (EVI) between the sampling periods of **(A)** 2003 and **(B)** 2018 for the study area, Santa Barbara Ecological Station (SBES), São Paulo, Brazil. Dots indicate the location of sampling units.

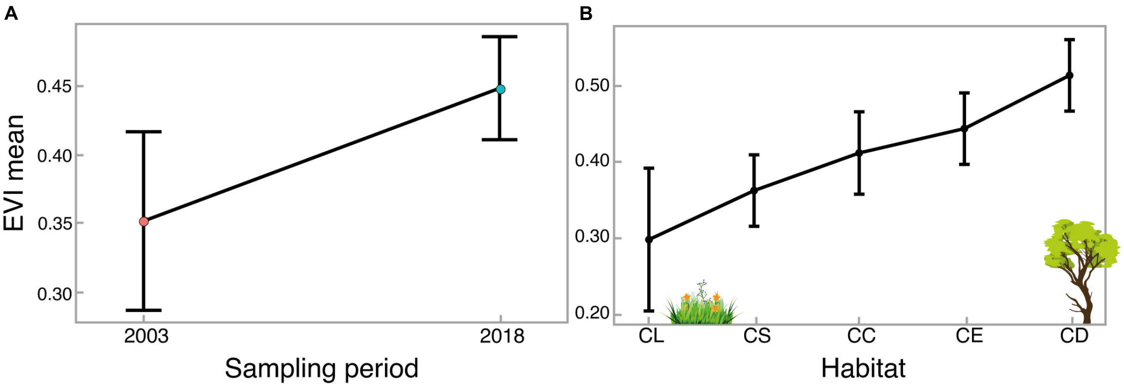

FIGURE 5 | Means of enhanced vegetation index (EVI) and standard deviation estimated by linear models for **(A)** sampling periods and **(B)** Cerrado habitats. The habitats are: CL: "*campo limpo*"; CS: "*campo sujo*"; CC: "*campo cerrado*"; CE: "*cerrado sensu stricto*"; and CD: "*cerradão*."

Small Mammal Community Structure

A high diversity of small mammals was found in our study area. We recorded at SBES 15% of the 113 native small mammal species from Cerrado (Mendonça et al., 2018; Fegies et al., 2021). The total richness observed (17 species) is high, given that only about 8% of the Cerrado small mammal communities are composed of more than 10 species (Mendonça et al., 2018), evidencing the completeness of the surveys in SBES. Rodents were the richest order, a recurrent pattern (Quintela et al., 2020; Abreu et al., 2021), with five sigmodontine rodents representing 74% of the total abundance in the SBES assemblage (*Oligoryzomys nigripes*, *O. mattogrossae*, *Calomys tener*, *Cerradomys scotti,* and *Necromys lasiurus*). The general abundance pattern recorded for SBES is also in accordance with previous Cerrado studies (see Mendonça et al., 2018 review), with *Necromys lasiurus* being the dominant species in the 2003 survey, and *O. nigripes* in the 2017–2018 survey.

Although based on different sampling designs and efforts, the two temporally spaced surveys showed high values of sampling coverage, both for the total assemblages, and for each similar habitat surveyed, allowing general comparisons between the community structure patterns found. While the 2003 survey was characterized by lower species richness, the habitats with higher observed and estimated richness were the grasslands ("*campo limpo*" and "*campo sujo*") and the savanna ("*cerrado sensu stricto*"), with the forest "*cerradão*" being the poorest habitat. On the other hand, the higher species richness found in the 2017–2018 survey was evenly distributed among grasslands ("*campo sujo*"), savannas ("*cerrado sensu stricto*") and "*cerradão*," but with "*campo cerrado*," a grassland habitat, showing lower species richness. Moreover, the seven additional species recorded in the 2017–2018 survey are mostly associated with denser covered habitats, such as savannas and forests, as is the case of *D. albiventris*, *Gracilinanus agilis*, *Hylaeamys megacephalus*, and *Rhipidomys* cf. *macrurus* (e.g., Santos-Filho et al., 2012; Carmignotto et al., 2014; Carmignotto, 2019; this study). Indeed, two species typical of the Atlantic Forest (*G. microtarsus* and *Nectomys* cf. *squamipes*), which also occur in southern and eastern Cerrado, especially using gallery forests, seasonal forests, and "cerradão" patches (Costa, 2003; Carmignotto et al., 2012), were only represented in the 2017–2018 survey.

Regarding species abundances, we observed that in the 2003 survey, the most abundant species were also represented by grassland and savanna species. Although *Necromys lasiurus* is considered a habitat generalist (Vieira et al., 2005; Ribeiro et al., 2019), in Cerrado, it prefers open habitats, represented by grasslands and savannas (Becker et al., 2007; Carmignotto, 2019). A similar pattern was found for *C. scotti* and *O. mattogrossae* (Henriques et al., 1997; Vieira et al., 2005; Weksler and Bonvicino, 2015). In the 2017–2018 survey, in turn, the most abundant species, the rodent *O. nigripes*, is more associated with savanna and forests (Weksler and Bonvicino, 2005, 2015). Moreover, some species that were more abundant in the 2003 survey, became rare in 2017–2018, such as the grassland specialist *Cryptonanus* aff. *chacoensis* (Fegies et al., 2021). Vegetation shifts may trigger shifts in small mammal abundance (Loggins et al., 2019), but other factors, such as resource availability, reproductive activity, and presence of competitors (Verberk, 2011), may also play a role. Since several of our comparisons were made between 2003 and 2017–2018 surveys controlling for the period of sampling (January–February), we believe we were able to reduce the influence of some of these confounding factors in our results.

Habitat and Microhabitat Use

Cerrado small mammals present high habitat association, contributing with the well-known pattern of open (grasslands and savannas) versus forest specialists found across this ecoregion (e.g., Alho, 2005; Carmignotto et al., 2012). The SBES assemblage also fits into this pattern, showing open and forest specialists as well as generalists (occupying both open and forest habitats). Considering habitat use, the 2003 survey was mostly represented by open-habitat species, with few generalists. In the 2017–2018 survey, we observed an increase in generalists and forest specialists. Despite the maintenance of grassland specialists between surveys, two species (*Cryptonanus* aff. *chacoensis* and *Clyomys laticeps*) were restricted to the most open habitat currently present at SBES ("*campo sujo*"), indicating a strong association with open grasslands (Carmignotto et al., 2014;

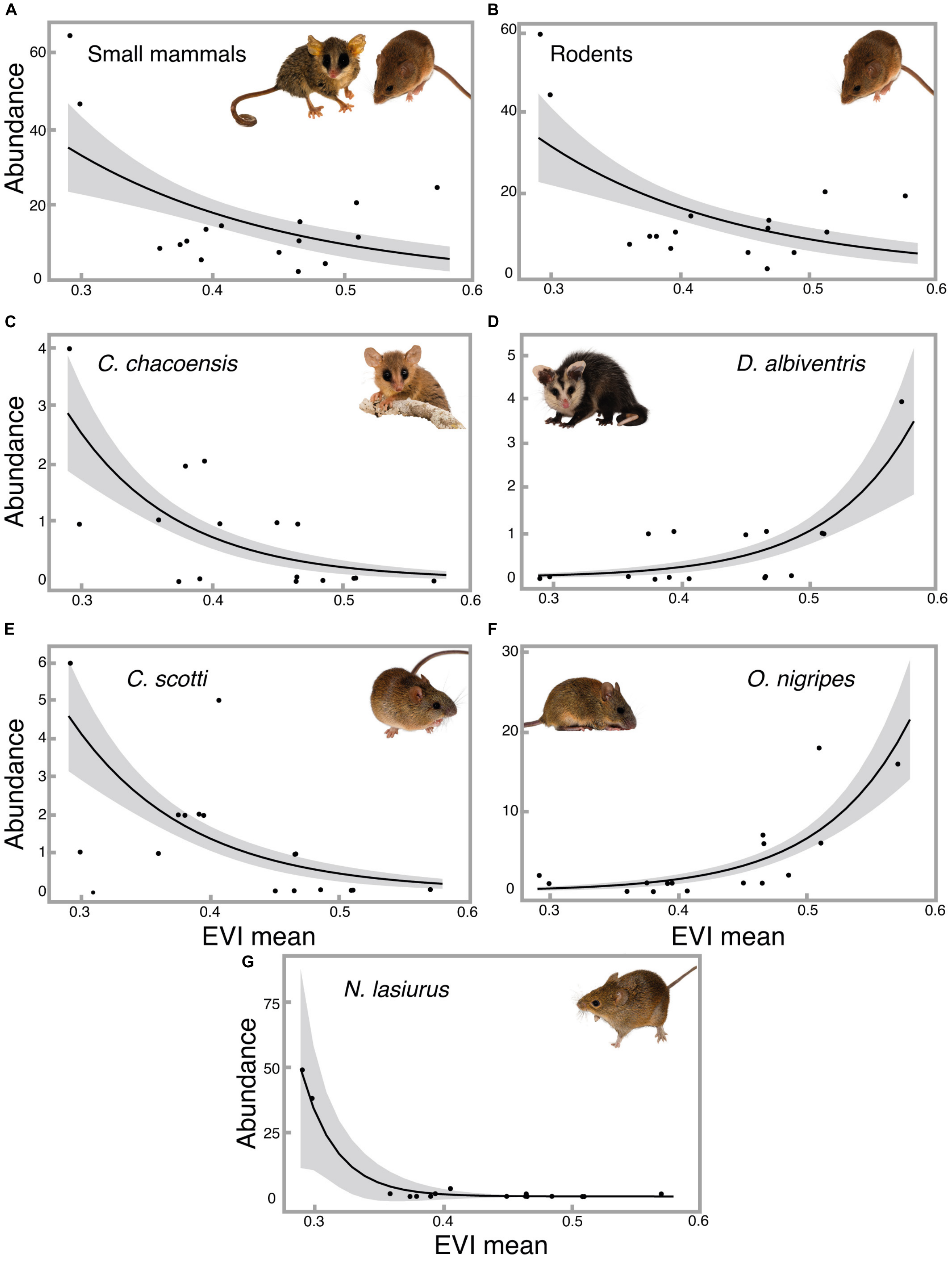

FIGURE 6 | Predicted effect of mean EVI on the **(A)** total abundance of small mammals, **(B)** abundance of rodents, and abundance of different species: **(C)** *Cryptonanus chacoensis*, **(D)** *Didelphis albiventris*, **(E)** *Cerradomys scotti*, **(F)** *Oligoryzomys nigripes*, and **(G)** *Necromys lasiurus* estimated by generalized linear models for the sampling units in SBES. The shadows represent the 95% confidence intervals. All photos by Bruno Ferreto Fiorillo.

Bezerra and Bonvicino, 2015; Bezerra et al., 2016; Fegies et al., 2021).

The microhabitat preference of species corroborates the results found at a larger, habitat scale in our study. For instance, *Calomys tener* and *Clyomys laticeps* show a higher association with high herbaceous cover (Carmignotto and Aires, 2011; Rocha et al., 2011; Bezerra et al., 2016). For *Clyomys laticeps*, however, our models indicate a negative relationship with high shrub cover, highlighting the dependence of this species on open grasslands (Vieira, 2003; Bezerra and Bonvicino, 2015). Other rodents (*Cerradomys scotti*, *Oligoryzomys nigripes,* and *O. mattogrossae*) were positively affected by shrub density. *Cerradomys scotti* and *O. mattogrossae* are open-habitat species, exhibiting a preference for grassland areas with higher shrub cover (Vieira et al., 2005). *Oligoryzomys nigripes*, however, is known to be associated with forest habitats, such as gallery forest in the Cerrado (Weksler and Bonvicino, 2005). Our findings are in accordance with these results since most captures were recorded in the "*cerradão.*" Püttker et al. (2008) also reported a higher association of this species with areas with low canopy and dense understory in the Atlantic Forest. *D. albiventris*, on the other hand, seems to benefit from increasing canopy cover and tree density, agreeing with previous studies where its presence was related to fallen logs and shrub (*Piper* sp.) density (Melo et al., 2013). *Gracilinanus agilis* and *Hylaeamys megacephalus* showed no clear response to the microhabitat variables tested, and their presence should be due to other factors not considered in our study, such as resource abundance or disturbances (Verberk, 2011; Loggins et al., 2019). These results highlight the importance of evaluating habitat use at different scales to better understand the potential reasons behind differential occurrence of small mammal species across the Cerrado, and to reinforce why some species would be favored or disfavored in a woody encroachment scenario.

Woody Encroachment

We observed an increase in vegetation density in SBES throughout the 15 years between the two surveys analyzed (from 2003 to 2018), corroborating that woody encroachment may be a common phenomenon in the Cerrado (e.g., Moreira, 2000; Roitman et al., 2008; Pinheiro and Durigan, 2009; Abreu et al., 2017, 2021). The 27% increase in the mean EVI affected primarily the grasslands. Indeed, the "*campo sujo*" surveyed in 2018 were located at the same areas previously classified as "*campo limpo*" in the 2003 survey, clearly showing a shift in vegetation with the increase in density of shrubs and small trees (see also Melo and Durigan, 2011). Overall, the small mammal species richness was not affected by the woody encroachment observed in the study area, but the total abundance was negatively related to the increase in mean EVI, as observed for other plant and invertebrate groups studied at SBES (Abreu et al., 2017). Indeed, our results show a clear negative effect of woody encroachment on the density of rodents, but not for marsupials. This is expected since most marsupials are associated with savannas or forest habitats due to their scansorial and arboreal habits (Astúa, 2015). Rodents have shown a two-way relationship with vegetation thickening in other open regions. On one hand, they can contribute to seed removal and consequently decrease woody density at habitats in the initial phase of encroachment, as recorded for open habitats of Africa, Argentina, and Australia (Busch et al., 2012; Bergstrom, 2013; Teman et al., 2021). On the other hand, they can be negatively affected by the encroachment, which impacts their ecological features, such as reducing predator detection, habitat use, and local persistence (Loggins et al., 2019), similar to what our results have indicated here. Our results for total and rodent abundance may have been influenced by the high number of *Necromys lasiurus* individuals in the 2003 survey. When we excluded this species from the analyses, no influence of woody encroachment for small mammals and rodent abundance was detected. Thus, these results should be carefully interpreted due to this outlier influence and low sample size, and additional sampling should be made to confirm our interpretations.

Regarding the seven most abundant species, two open-habitat specialists (*C. tener* and *O. mattogrossae*) were not affected by woody encroachment. These species can occupy a wide range of open habitats, from grasslands to savannas in the Cerrado (Carmignotto et al., 2014; Salazar-Bravo, 2015; Weksler et al., 2017; Bezerra et al., 2020). This pattern indicates plasticity in their habitat use. On the other hand, the open-habitat specialists *Cryptonanus chacoensis, Cerradomys scotti,* and *Necromys lasiurus* were negatively affected by woody encroachment, indicating a dependence on grasslands formations at SBES. The negative impacts of woody encroachment on species of the genus *Cryptonanus* are expected, since its diversification is highly associated with the open habitats of the Cerrado (Fegies et al., 2021). In fact, SBES shelters a sympatric species, *Cryptonanus* aff. *chacoensis*, considered rare and endemic of Brazilian Cerrado, which may face even more severe impacts by the woody encroachment (Fegies et al., 2021). *Cerradomys scotti* showed a slight preference for shrubby habitats in our microhabitat analyzes, which is in accordance with the negative response to the tree encroachment found here, a pattern previously observed by Vieira et al. (2005), where this species was related to grass height but not to arboreal cover. In fact, there seems to be a tenuous line for species that may benefit from shrub cover due to protection against predation, and also may be negatively affected by a decrease in food resources, since several species use herbaceous sources for feeding (Vieira et al., 2005; Ribeiro et al., 2019), which, in turn, decrease with shrub encroachment, as shown for small mammals in African shrub-invaded grasslands (Loggins et al., 2019).

The rodent *Necromys lasiurus* also showed a decrease in abundance between 2003 and 2017–2018 potentially due to woody encroachment, since it is associated with open and grassy areas (Vieira et al., 2005; Becker et al., 2007; Rocha et al., 2011). This species was the most abundant in open areas in 2003 but among the rarest ones in 2018, extending its distribution to savanna habitats, its preferred habitat in other studies (Henriques and Alho, 1991), indicating its habitat plasticity within open formations. Our results show that *Cryptonanus chacoensis* and *Cerradomys scotti* may not persist in areas with woody encroachment if grasslands disappear. Meanwhile, forest-specialists and opportunistic species seem to benefit from woody encroachment at the SBES. *D. albiventris*, although considered a habitat generalist (Cáceres et al., 2012), was not captured in the 2003 survey, but in 2018 became the most abundant marsupial in the assemblage. This didelphid was also the only species that was positively associated with microhabitats with higher tree density, which corroborates its fostering by woody encroachment. The rodent *Oligoryzomys nigripes* was also favored by the encroachment, and its higher association with forest habitats may allow its spread in habitats with higher woody density (Weksler and Bonvicino, 2015). Mammals across savannas worldwide are differently influenced by vegetation encroachment (Stevens et al., 2016a), but they seem to be more sensitive than other vertebrates, such as birds, due to their specialized habitat preferences and foraging strategies. Turnover in species composition following woody encroachment is also recorded in African savannas, with browser mammals replacing grazers (Smit and Prins, 2015), pointing to woody encroachment as a general concern across savannas.

Our models indicate shifts in species abundance across time, with such changes being predictable to some extent. Species typical of grasslands show declines, while forest-dwellers are increasing in abundance. In the case of forest-savanna ecotone regions, climate, and land-use change, especially fire and deforestation, are leading to an invasion of savanna species into disturbed forests, shifting the forest fauna assemblages toward a "savannization" (Sales et al., 2020). Similarly, the woody encroachment is changing southern Cerrado assemblages toward a "forestization," with the invasion of species from adjacent forest biomes and the loss of savanna specialists (Abreu et al., 2017, 2021). Our findings highlight the importance of the maintenance of the mosaic of open formations in Cerrado remnants in order to shelter a high diversity of small mammal grassland specialists. Species that showed a clear decline and high association with open vegetation structure in fact can become locally extinct, consequently altering species range, since these areas are mainly located at Cerrado boundaries. This may be particularly true for Cerrado endemics and regionally vulnerable species such as *Clyomys laticeps* and *Cerradomys scotti* (Percequillo et al., 2008; São Paulo, 2018), besides a rare and still undescribed species (*Cryptonanus* aff. *chacoensis*; Fegies et al., 2021). In fact, the SBES was created with the goal to protect the open formations of the southern Cerrado, but 30 years of fire suppression are probably the main cause of the local woody encroachment and the resulting changes in biodiversity (Abreu et al., 2017, 2021). Fire management is considered a key tool to maintain open savannas and its associated diversity, and the current fire experiments at SBES so far demonstrate no loss in small mammal diversity with prescribed fire (Durigan and Ratter, 2016; Durigan et al., 2020). Without active management of the landscape to keep open habitats, the long-term maintenance of the open-habitat specialists (with special attention to the rarest ones) will give place to an increasing replacement by forest specialists and habitat generalists in the SBES small mammal community and in other remnants in the southern portion of the Cerrado. Woody encroachment needs to be treated as a global scale problem to natural open ecosystems (Stevens et al., 2016a), and its impacts on biodiversity at local scales should continue to be investigated in order to guarantee the conservation of savanna and grassland biodiversity.

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/s.

ETHICS STATEMENT

The animal study was reviewed and approved by Comissão de Ética no Uso de Animais (CEUA), Instituto de Biociências da Universidade de São Paulo (#CEUA-IB-USP 241/2016).

AUTHOR CONTRIBUTIONS

APC, AVC, and MM conceived this study and designed the methodology. APC, PL, GF, and LF collected the data. LF performed the statistical analysis and led the manuscript writing. APC, AVC, LF, and MM interpreted results and contributed to the writing and reviews. All authors 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.2021.774744/full#supplementary-material

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Fire Occurrence Mediates Small-Mammal Seed Removal of Native Tree Species in a Neotropical Savanna

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Seed dispersal and predation are critical processes for plant recruitment which can be affected by fire events. We investigated community composition of small mammals in gallery forests with distinct burning histories (burned or not burned ∼3 years before) in the Cerrado (neotropical savanna). We evaluated the role of these animals as seed removers of six native tree species, potentially mediated by the occurrence of fire. We sampled four previously burned sites and four unburned ones. Seed removal was assessed using two exclusion treatments: exclusive access of small rodents and access of all seed-removing vertebrates. The previous burning changed the structural characteristics of the forests, increasing the density of the understory vegetation and herbaceous cover, which determined differences in species composition, richness, and abundance of small rodents (abundance in the burned forests was 1/6 of the abundance in the unburnt ones). Seed removal rates across the six species were reduced in burnt forests in both treatments and were higher for the "all vertebrates" treatment. Other vertebrates, larger than small rodents, played a significant role as seed removers for five of the six species. The effects of fire were consistent across species, but for the two species with the largest seeds (*Hymenaea courbaril* and *Mauritia flexuosa*) removal rates for both treatments were extremely low in the burned forests (≦5%). The observed decline in small rodent seed predation in the burned forests may have medium to long-term consequences on plant communities in gallery forests, potentially affecting community composition and species coexistence in these forests. Moreover, fire caused a sharp decline in seed removal by large mammals, indicating that the maintenance of dispersal services provided by these mammals (mainly the agouti *Dasyprota azarae*) for the large-seeded species may be jeopardized by the burning of gallery forests. This burning would also affect several small mammal species that occur in the surrounding typical savanna habitats but also use these forests. Fire events have been increasing in frequency and intensity because of human activities and climate changing. This current scenario poses a serious threat considering that these forests are fire-sensitive ecosystems within the Cerrado.

Keywords: Cerrado (Brazilian savanna), gallery forest, rodents, seed predation, seed dispersal, fire

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INTRODUCTION

Seed dispersal and predation are among the major factors limiting the recruitment of new individuals into plant communities (Schupp, 1988; Wang and Smith, 2002). After leaving the parent tree, seeds are often vulnerable to predation (Mittelbach and Gross, 1984; Hulme, 1993, 1998; Cummings and Alexander, 2002) and high rates of predation can suppress the recruitment, establishment and even population growth of some species (Maron and Kauffman, 2006; Bricker et al., 2010; Zwolak et al., 2010; Pearson et al., 2011) with potential to change the composition of the plant community (Brown and Heske, 1990; Curtin et al., 2000; Harms et al., 2000; Howe and Brown, 2000; Salazar et al., 2012). These changes are affected by the identity of the seed predator, which in some cases may also act as seed disperser (Li and Zhang, 2007; Mittelman et al., 2021). Both dispersal and predation of seeds may also be affected by disturbance events, such as wildfires. Fire events may affect not only the number of available seeds for recruitment but also the abundance of specific faunistic groups that may provide distinct services as seed predators or seed dispersers (Auld and Denham, 2001; Reed et al., 2004; Rusch et al., 2014). Fire-induced changes in the relative services (i.e., seed predation or dispersal) provided by distinct groups of seed-eating animals may alter the probability of establishment of new plant individuals in natural areas. The evaluation of such changes is highly relevant, mainly in fire-prone ecosystems, such as tropical savannas. The understanding of these and other aspects of the ecology of fire is essential for comprehending past or future changes in these ecosystems (Bond and Keeley, 2005).

Patterns of seed dispersal and seed predation produced by mammals can be affected by large-scale disturbances such as wildfires (Reed et al., 2004; Tasker et al., 2011). Fire events rapidly destroy the plant biomass of a region, including the propagules, but also markedly affect the fauna capable of interacting with them (Mutch, 1970; Bendell, 1974; Crowner and Barret, 1979; Catling et al., 1982; Happold, 1983; Simons, 1991). Fires of high severity and extension in forests results in drastic changes such as reduction of vegetation cover and biomass, formation of gaps consequent increasing in edge area, and reduced availability of shelter and food for the animals (Hoffmann and Moreira, 2002; Barlow and Peres, 2006; Legge et al., 2008; Vasconcelos et al., 2009; Diniz et al., 2011). In addition, forest fires also lead to habitat fragmentation by altering the size of the remaining areas and the spacing between them, which may increase rates of local extinction of animal species by reducing fecundity, population size and colonization of species from similar environments (Banks et al., 2011; Lindenmayer et al., 2013). An increasing number of studies point to the susceptibility of mammals from forest environments to the effects of fire (e.g., Converse et al., 2006; Banks et al., 2011; Mendonça et al., 2015; Chia et al., 2016), and this sensitivity is apparently related to the severity of the fire (Legge et al., 2008; Fontaine and Kennedy, 2012; Lindenmayer et al., 2013).

Besides the direct fire influence on involved organisms, there are also indirect effects, in the medium or long term, that burning events can cause on animal-plant interactions. These effects, which may be subtle and often neglected (Dafni et al., 2012), are related to medium- and long-term post-fire changes in the abundance and composition of the faunal assemblage, in the quantity and quality of resources available to the animals, and also in the structural characteristics of the vegetation (Barlow and Peres, 2006; Andersen, 2021; González et al., 2021). Post-fire vegetative cover and the availability of unburnt patches are affected by fire attributes, such as severity and extent of the burned area (Leonard et al., 2014; Tran et al., 2020). These factors, in their turn, alter the abundance and behavior of rodents, ants, and birds, which are the main predators of post-dispersed seeds (e.g., Manson and Stiles, 1998; Monamy and Fox, 2000; Fox et al., 2003; Lassau et al., 2004; Camargo et al., 2018). Some studies have already shown changes in seed predation rates due to the occurrence of fire events (e.g., Reed et al., 2005; Broncano et al., 2008; Tasker et al., 2011; Stuhler and Orrock, 2016).

Fire events might not only change predation rates but also alter the relative role of distinct groups within a guild of seed eaters. In Neotropical environments, small rodents, play a major role in the removal of post-dispersed seeds (Ostfeld et al., 1997; Díaz et al., 1999; Forget et al., 1999; Kelt et al., 2004; Iob and Vieira, 2008; Terborgh, 2012), being generally recognized as primarily seed predators (Vieira et al., 2003, 2006; Galetti et al., 2015b). In contrast, large rodents, such as agoutis, also predate seeds but provide plant dispersal services on a regular basis (Hallwachs, 1986). These distinct roles might be affected by disturbance events. Small seed predators, for instance, might replace larger animals as main seed removers after fire (a similar process is suggested to occur in Atlantic Forest sites defaunated by human disturbance; Galetti et al., 2015a). In case the large animals were the main group to provide real dispersal services, dispersal rates for some plant species could be lower in comparison to pre-fire patterns. Considering that seed establishment and recruitment are critical phases for the plant growth cycle (Hadas, 2005), the indirect effects of wildfires as mediators of the relative role of distinct seed-consumer groups are potentially highly relevant for tree species in fire-prone tropical systems.

Fire episodes occur frequently in areas of Cerrado (Miranda et al., 2002), the largest and biologically richest savanna in the world, with an original extension of about 2,000,000 km^2 mainly in central Brazil (Oliveira-Filho and Ratter, 2002). In the Cerrado, fires are historically common, being a relevant ecological and evolutionary factor since at least 4 million years ago (Simon et al., 2009). Recent human action, however, has amplified the frequency of fire and its negative effects on flora, fauna, and water resources (Miranda et al., 2009). Fire events usually extinguishes at the edge of gallery forests (corridors of evergreen forests that typically occur along permanent water courses within the Cerrado; Felfili, 1995; Hoffmann et al., 2012). In extreme drought situations, however, very intense fires can overcome the edges of these forests, reaching their interior (Felfili, 1997; Hoffmann et al., 2009). In these situations, the passage of fire is usually devastating, since forest plant species generally do not possess characteristics that confer greater resistance to fire as those plants present in savanna and grassland phytophysiognomies (Walter and Ribeiro, 2010). This lack of protection causes structural and functional changes in this forest type (Hoffmann et al., 2009; González et al., 2021) and also on its associated fauna (González et al., 2021).

Fire effects on vertebrate fauna are related to animal body size. Medium and large animals generally have a significant post-fire reduction in abundance, which can be attributed to fire-induced changes in vegetation structure (Barlow and Peres, 2006). For small mammals, in areas where fire occurrence is not common, there may also be a reduction in species richness (Ojeda, 1989) or in abundance of some species (Lunney et al., 1987; Simons, 1991; Camargo et al., 2018; González et al., 2021). The small mammals, however, generally are less affected by fire than larger animals, because of their high densities and small body sizes (which allow them to find shelter from fire in small burrows and termite mounds; Vieira, 1999). The effects of fire on small mammals have been studied in the dominant savanna environments (Vieira and Marinho-Filho, 1998; Vieira, 1999; Vieira and Briani, 2013) and in woodland forests in the Cerrado (Mendonça et al., 2015; Camargo et al., 2018). In gallery forests, however, there are very few studies evaluating the effects of burning on small mammals (but see González et al., 2021). Moreover, to the best of our knowledge, the indirect effects of fire on keystone ecological processes occurring in gallery forests, such as seed predation by small mammals, have not been investigated at all.

We investigated small-mammal seed removal of native plant species in gallery forest areas with distinct burning histories (burned or not burned ∼3 years before). We aimed to evaluate the role of these animals as seed removers of six tree species, potentially mediated by the occurrence of fire. We hypothesized that because of the profound effects of fire burned forests have lower overall abundance and distinct species composition of small mammals compared to non-burned forests even after almost 3 years after the last fire event. In relation to seed removal, we expected overall seed removal to be lower in burned forests due to the reduction in abundance of seed-removing mammals. In relative terms, however, we expected that small rodents (<400 g) play a more relevant role as seed removers than large species (e.g., large rodents—agoutis and pacas) in burned forests in comparison to unburned ones, since those larger species would be more adversely affected by fire (Barlow and Peres, 2006).

MATERIALS AND METHODS

Study Area

We conducted our study in the core area of the Cerrado, which is characterized by two well-marked seasons, a cool-dry season and a warm-wet season, which occurs between October and April, when 90% of the annual precipitation of 1,100–1,600 mm occurs (Miranda et al., 1993). Fieldwork was conducted in the Ecological Reserve of the Instituto Brasileiro de Geografia e Estatística (RECOR/IBGE, hereafter IBGE) and in the Fazenda Agua Limpa (FAL), the research station of the Universidade de Brasilia. These two locations and the Ecological Station of the Botanic Garden of Brasília (EEJBB, in Portuguese) are part of the Area of Environmental Protection (APA) Gama e Cabeça-de-Veado, which covers about 15,000 ha of continuous native Cerrado vegetation. Its vegetation includes mainly typical savanna habitats (open woodlands) and grasslands, with gallery forests tracing the courses of streams that cross the landscape. This study was part of the Brazilian Long-term Ecological Research Program of the Brazilian National Research Council (Programa de Pesquisas Ecológicas de Longa Duracão—PELD/CNPq, in Portuguese)—Cerrados from the Central Plateau—Structure, dynamics and ecological processes—Phase 2.

In September 2011, an extensive wildfire occurred in the area, burning about 6,240 ha of native Cerrado vegetation (Mendonça et al., 2015), including 100% of IBGE, about 50% of FAL and 60% of EEJBB (**Figure 1**). The fire lasted 3 days and severely damaged most of the gallery forests that occurred within the burned area. For evaluating the effects of burning on seed removal patterns in these forests we selected for sampling eight gallery forest sites in the two adjacent conservation areas. Four of which were in gallery forests that burned in the fire in 2011 and four gallery forest areas that did not burn that year (three forests burned in RECOR and one in FAL and four non-burned forests in FAL). The selection of forest sites in relation to fire occurrence was based on observation of satellite images and information of FAL and RECOR employees. The maintenance of an apparent forest structure, even for the forests that had burned, was also a criterion for selecting the sites to be sampled. We sampled all the sites in 2014, 2.8 years after burning. We maintained a straight-line distance between the sites of at least 500 m for assuming independence among them (**Figure 1**).

Tree Species Studied

We experimentally tested removal rates of seeds from six native tree species that occur associated to Cerrado gallery forests of Central Brazil (Felfili et al., 2001). The species names are

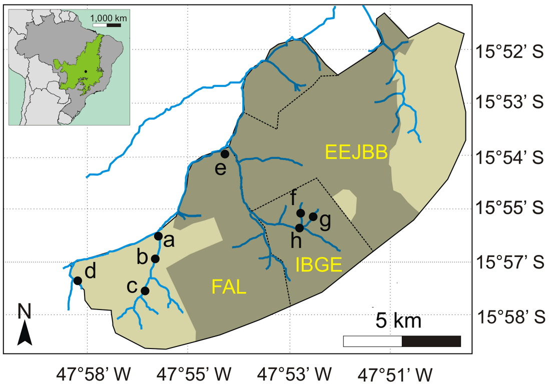

FIGURE 1 | Location of the eight sampled sites in gallery forests of the Cerrado (neotropical savanna) in Brazil and extent of the area burned in 2011 (shaded area on the largest map). The green area on the inset map (top left) indicates the area covered by Cerrado in Brazil. Letters 'a' to 'd' indicate the sites located in the unburned forests (a = Entrada, b = Ponte, c = Capetinga, and d = Represa) and letters 'e' to 'h' indicate the sites in the previously burned forests (e = Taquara, f = Monjolo, g = Pitoco, and h = Coruja). EEJBB refers to the Ecological Station of the Botanical Garden of Brasília, FAL refers to the Experimental Farm of the University of Brasília, and IBGE refers to the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE, in Portuguese). Adapted from Mendonça et al. (2015).

as follows [average length of the major axis ± SD (n = 30 for each species) and individual seed mass, obtained in this study, are also indicated]: *Cariniana estrellensis* (Raddi) Kuntze (Lecythidaceae; 1.25 ± 0.15 cm, 0.08 g), *Copaifera langsdorffii* Desf. (Fabaceae; 1.3 cm ± 0.16, 0.8 g), *Dipteryx alata* Vogel (Fabaceae; 2.4 ± 0.23 cm, 1.2 g), *Platypodium elegans* Vogel. (Fabaceae; 2.3 ± 0.18 cm, 1.3 g), *Hymenaea courbaril* L. var. stilbocarpa (Hayne) Lee and Lang. (Fabaceae; 2.53 ± 0.31 cm, 4.5 g), and *Mauritia flexuosa* L. f. (Arecaceae; 2.2 ± 0.11 cm, 7.4 g). We selected these species according to their range in size, possible occurrence in gallery forests of the studied region (Felfili et al., 2001; Marimon et al., 2010) and local availability for acquisition.

Field Methods

Fieldwork consisted of the structural characterization of the studied forests (from November to December 2014), capture of small mammals (from August to October 2014), and seed removal experiments (from July to August 2014). Additionally, we evaluated the consumption of seeds by the most abundant rodent species captured in the study sites. This evaluation was based on cafeteria experiments, in which we offered seeds of the six studied plant species to captive individuals.

We established linear transects in each forest site in order to carry out the structural characterization of the studied forests, small mammal trapping, and seed removal experiments. Each of these sampling transects was placed parallel to the forest stream, with 34 experimental stations in each forest site. The stations within the same transect were 15 m apart and the total length of each transect depended on the length of the forest. Whenever necessary, we placed a second transect parallel to the first one and separated at least 20 m from it, maintaining the 15-m distance between stations. The established transects had a minimum distance of ten meters from the border into the forest interior.

Structural Characterization of the Study Sites

For the structural characterization of the studied forests, in each forest site we established a plot of 400 m^2 (100 m × 4 m) along the sampling transect. Within this plot, we recorded the diameter at the breast height (DBH = 1.3 m) of all live trees with minimum height of 1.5 m, the number of trees with fire marks and the total number of trees. We also estimated the canopy cover of the forests through photographs taken with a hemispherical 180° (fisheye) lens (FC-E8, Nikon, Japan) coupled in a digital camera (Coolpix 950, Nikon, Japan) placed 1.3 m above ground supported by a tripod. We took one photograph every 15 m (seven photos per site) along the center of the major axis of each transect. We also evaluated understory plant density at each of the seven sampling points by taking four digital photographs (using a Sony® model DSC-HX1 digital camera) 1.2 m above the soil aiming to a white sheet (1.5 by 1.5 m) at a 3-m distance as a background. Each photograph was taken from the sampling point aiming at one of the four cardinal points. We also evaluated ground cover of the herbaceous vegetation using the same camera (mounted on a tripod at a height of 1.3 m) and taking, at each sampling point, four perpendicular photographs aiming to the soil. Each photograph was taken 2 m from the sampling point, in the four cardinal directions. We analyzed the photographs using the ImageJ program (Abramoff et al., 2004) calculating the average percentage of canopy cover and the average percentage of the green area of the photographs (from both understory and forest ground) of each transect.

Small Mammal Sampling

We evaluated the abundance and composition of local small mammal assemblages by live trapping animals in each of the eight forest sites. In each sampling transect, we placed Sherman® traps (H. B. Sherman Co., Tallahassee, FL, United States) of two sizes alternately on 30 experimental stations [15 "large" (12 cm × 10 cm × 38 cm) and 15 "small" (9 cm × 8 cm × 24 cm) traps] and one wire mesh cage trap (45 cm × 16 cm × 16 cm) in the remaining four stations. We also placed 20 additional wire mesh cage traps at 20 randomly selected intermediate points (at mid-distance between transect stations) along the transect, for a total of 54 traps per site. We set up the traps only on the ground because we intended to capture individuals who used this stratum to search for food. In each site trapping campaign lasted nine consecutive nights.

We baited traps with a mixture of peanut butter, vanilla essence, corn flour, cod liver oil, and mashed banana. Every early morning, we inspected the traps and rebaited them. We identified captured animals by species and then weighed, sexed, ear-tagged (National Band and Tag; model 1005-1), and released them at the point of capture. Some individuals of the most common species were taken to the laboratory for the cafeteria experiments in captivity and released in the same point of capture after that. All field methods were consistent with the animal care guidelines of the American Society of Mammalogists (Sikes et al., 2011).

Seed Removal Trials

All seed removal experiments were conducted between July and August of 2014. We evaluated rates of seed removal by distinct fauna groups (small rodents and vertebrate fauna in general) in burned and unburned gallery forests. For that evaluation, we placed seeds on the ground at the experimental stations of the sampled forest sites. Seed trial in each experimental station was submitted to one of the two following treatments. (1) Access of small rodents (<400 g): seeds were surrounded with a semi-permeable exclosure using a wire-mesh cage staked to the ground with one opening at each side along the bottom edge, thus permitting access to small rodents only [SMRO = small rodent access; as in Iob and Vieira (2008); see **Supplementary Figure 1** and **Supplementary Video 1** for details]. (2) No exclusion: an open control where seeds were placed on the ground without any protection (ALAG = access to all animal groups). For the SMRO treatment we used cages with two different sizes (size #1: 24 cm × 24 cm wide and 10 cm high, mesh = 1.5 cm, side opening with 12 cm wide and 5 cm high; size #2: 40 cm × 40 cm wide and 13 cm high, mesh = 2.5 cm, side opening 12 cm wide and 8 cm high) available at the Laboratory of Vertebrate Ecology of the University of Brasília. The largest size still would not permit access of mammals with more than 700 g (hereafter large mammals), but we maintained the same proportion of both cage sizes for all sampled sites (10 size #1 and 7 size #2 in each site).

Each experimental station received one of the two treatments (SMRO or ALAG) randomly chosen. Thus, of the total of 34 experimental stations per area, 17 stations contained seeds under the treatment SMRO (exclusion cages) and the other 17 contained seeds without cover (ALAG). In all treatments, we placed the seeds in plastic Petri dishes (diameter = 90 mm and height = 15 mm) on the soil. We covered the outer border of the petri dishes with insect-trapping barrier (Tanglefoot®) to limit the access of non-flying insects to the seeds. We checked for the efficiency of the cages by always inspecting the petri dishes for any sign of invertebrates that might be removing the seeds. Only a very few times we found very small ants inside the petri dishes, which were not able to carry the seeds out. At all experimental stations, we removed the litter within a circular area (radius = 0.5 m) around the petri dishes, leaving the soil exposed to facilitate the visualization of fallen seeds outside the dishes.

The available space within the petri dishes did not allow the placement of seeds of the six studied species simultaneously in each experimental station. Because of that, we placed seeds into randomized groups of four species per experimental station. With this procedure, in each site there was a total of 22–24 stations with seeds of each plant species, keeping the same number of stations for each treatment (SMRO or ALAG) per site for each of the six studied plant species. The number of seeds of each species deposited in each experimental station was (from the lowest to the largest seed mass): *C. estrellensis*—10 seeds, *Co. langsdorffii*—6 seeds, *P. elegans*—6 seeds, *D. alata*—6 seeds, *H. courbaril*—5 seeds, and *M. flexuosa*—3 seeds.

We conducted the seed removal experiments by sampling alternately forest sites of the two fire treatments (burned in 2011 or unburned). In each site the experiment was conducted for 10 consecutive days and on the fifth and tenth days we verified the quantity of seeds of each species that had been removed or showed signs of damage. On the 5th day we replaced any removed or damaged seeds with new intact seeds. We considered seeds that were partially or totally eaten by vertebrates and seeds not found in the vicinity of the plates (up to 0.5 m) as "removed." Thus, we included in our estimates of removal rates also seeds that might have been removed but not predated by the removal agent.

Seed Offering in Captivity

We evaluated how the studied seeds were handled by rodents by conducting experiments on seed offering in captivity (i.e., "cafeteria" type). We performed these experiments between August and October 2014 and used 19 rodent individuals (captured during fieldwork) of the following species (mean body mass ± standard deviation, number of individuals): *Oligoryzomys nigripes* (22.9 ± 8.3 g, $N = 4$), *Rhipidomys macrurus* (42.7 ± 15.5, $N = 3$), *Hylaemys megacephalus* (57.0 ± 9.0 g, $N = 3$), *Nectomys squamipes* (312.5 ± 47.7 g, $N = 6$), and *Proechimys roberti* (307.8 ± 172.7 g, $N = 3$). We selected these species because they were the most commonly rodents captured in this study and they are all reported as seed or fruit eaters (Paglia et al., 2012; Ribeiro et al., 2019). We avoided using seeds of unripe, old, or infested fruits.

During the period of experimental seed offering in captivity we kept live animals in small individual cages (25 cm × 15 cm × 15 cm or 45 cm × 16 cm × 16 cm). After the seed-offering period (3 days), we released the animals in the same place of capture. During this experiment period, all cages contained water *ad libitum* and small amounts of alternative food sources (dog chow and banana, in addition to the seeds offered). In this way, we avoided rodent starvation and hypothermia and the animals would not have to obligatorily feed on the offered fruits. The seeds were offered to the animals 24 h after they were placed in the cages and remained for 48 h, so that the animals had time to get used to the captivity and felt enough hunger to search for food.

We provided for the rodents, simultaneously, all seed species used in the field experiments, arranged in plastic petri dishes (90 mm × 15 mm) placed inside the cages, in the following amounts: *C. estrellensis*—6 seeds; *Co. langsdorffii*—3 seeds; *P. elegans*—3 seeds; *D. alata*—3 seeds; *H. courbaril*—2 seeds and *M. flexuosa*—1 seed. At the end of the experiment, we inspected the cages and recorded the quantity and state of the remaining seeds (for signs of predation). We considered as consumed the seeds that were totally or partially (at least 30%) eaten.

Data Analysis

We tested the hypothesis that species richness and abundance differ between burning treatments using Mood's median test (Mood, 1954) mainly because of the limited sample size. This conservative this test has low power compared with alternatives such as ANOVA or Kruskal–Wallis test, but it is robust to heteroscedasticity, non-normality and outliers (Siegel and Castellan, 1988). For this test, we used the number of captured individuals as a proxy for rodent abundance per forest site. The limited number of recaptures per site precluded the use of capture-recapture models for assessing population sizes.

We evaluated potential differences in small-mammal community composition according to previous fire occurrence by performing non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarities on the site-by-species matrix. We included the habitat-structure variables as passive variables in the ordination. This approach enabled comparison of previously burned and unburned sites (with similar small-mammal communities appearing close to each other) and the evaluation of their association with the structural habitat variables. We tested for differences in species composition between the two forest groups (unburned and burned) using a Permutational Multivariate Analysis of Variance (PERMANOVA) with 10,000 iterations (Anderson, 2001). These analyses were performed with the Past software (Hammer et al., 2001).

We assessed the occurrence of spatial autocorrelation within our data sets using spatial correlograms of the Moran's I coefficient with their relative p-values, calculated using Spatial Analysis in Macroecology (SAM; Rangel et al., 2010) and found no significant correlation for any of the six plant species studied ($p > 0.28$ for all species). We used a generalized linear mixed model (GLMM) with binomial errors to analyze variation in the proportion of seeds removed in response to previous occurrence of fire and exclosure treatment. Although size #2 cages could potentially allow access to rodents of a size slightly larger than size #1, preliminary tests indicated that there was no significant difference in removal rates between cage types (t-test, $p \geq 0.12$ for all seed species in comparisons made within each forest site). Thus, for the analysis we pooled the data obtained in these two exclosure sizes, considering them as a single treatment. We considered as predictor variables fire history (fixed effect with two levels, previously burned vs. unburned) and exclosure treatment (fixed effects with two levels, small rodent access—SMRO vs. access to all animal groups—ALAG). Forest sites (nested within fire history) and experimental stations (nested within sites) were considered random effects. We also included species as a random effect (six levels, one for each species included in the analysis), with random intercepts and random slopes. In doing that, we were able to assess whether the effects of treatment were consistent across species. To evaluate species-specific responses to treatments, we also ran separate models for each of the six species (as in Williams et al., 2021). For these analyses, we used the lme4 package (Bates et al., 2014). We tested for overdispersion using the function dispersion_glmer from library blmeco (Korner-Nievergelt et al., 2015). Residuals of all GLMMs were inspected with the "DHARMa" package (Hartig, 2017). No deviations from the specified error distributions were detected for any species. All these analyzes were performed using the software RStudio (RStudio Team, 2020; RStudio: Integrated Development for R. RStudio, PBC, Boston, MA, United States, URL[1]).

RESULTS

Small Mammal Abundance, Community Composition and Site Characteristics

We obtained 153 captures of 104 small mammal individuals distributed in eight species, seven rodents and one marsupial, with a total trapping effort of 3,780 trap nights (not considering malfunctioning traps). The marsupial *Gracilinanus agilis* was the most abundant species in this study (33.3% of the total number of individuals), followed by the rodent *Oecomys* sp. (21.6%). Five rodent species were captured only in the unburned forest patches, and none was captured exclusively in the burned patches (**Supplementary Table 1**). The overall trapping success was 4.05%, with trapping success being 84% lower for the burned forests (1.20%; 23 captures of 15 individuals from three species) in comparison to unburned forests (7.75%; 130 captures of 89 individuals from eight species). The overall abundance of small mammals also was significantly lower in the burned forests than in the unburned ones (Mood's test for equal medians; $\chi^2 = 4.8$, $p = 0.028$), with the median value for burned sites being 79% lower than the median value for the unburned sites. A similar and significant pattern was observed for species richness (Mood's test for equal medians; $\chi^2 = 8.0$, $p = 0.005$), with the median values in the burned sites being about 55% lower than in the unburned ones (**Figure 2**).

Our evaluation of the species composition of small mammals in the study sites indicated a clear separation according to the fire history, as shown by the NMDS ordination (**Figure 3**). This separation was corroborated by the PERMANOVA test, which indicated that species composition differed significantly between burned and unburned forests (total SS = 2.096, within-group SS = 1.389, $F = 3.057$, $p = 0.029$). The evaluation of the relative position of environmental variables (passive variables in the analysis) indicated that both groups of forest sites differed in structural characteristics related to the previous occurrence of fire (i.e., understory density, herbaceous cover and number of trees with fire scars; **Figure 3**).

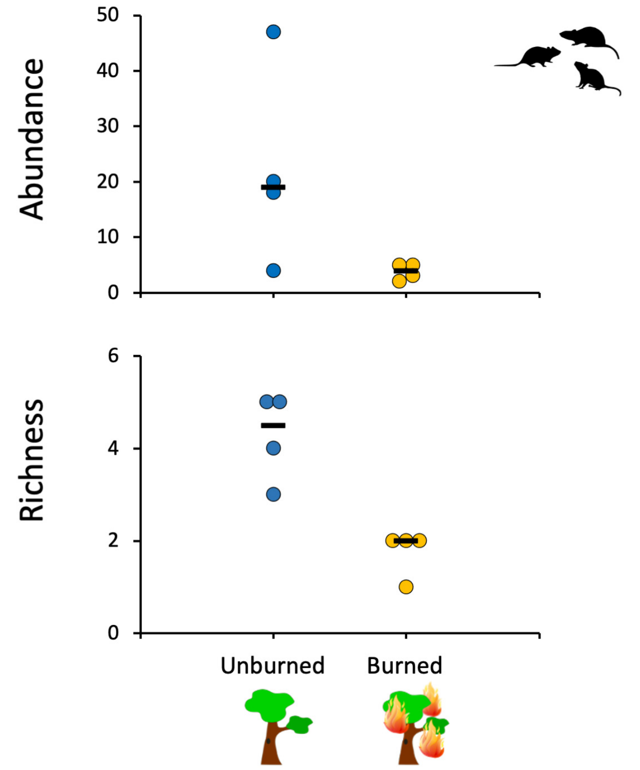

FIGURE 2 | Mean small mammal abundance and richness in the sampled gallery forest sites in relation to previous fire history (burned or unburned ~3 years before).

Seed Removal by Rodents

The evaluation of the effects of fire and exclosure treatment on seed removal across all tree species indicated that the previous occurrence of fire caused a decline in seed removal (23.9% of seeds removed) in comparison with unburned sites (52.2% removed). Moreover, vertebrate seed removal significantly declined inside cages with access only to rodents (29.7% of seeds removed) as compared to uncaged seeds (46.5% removed), indicating that other vertebrates than small rodents were significant seed removers (**Figure 4** and see **Table 1** for statistical results).

In models with each species analyzed separately, for all species seeds were less removed in previously burned gallery forests than in the unburned forests and in uncaged stations than

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[1] http://www.rstudio.com

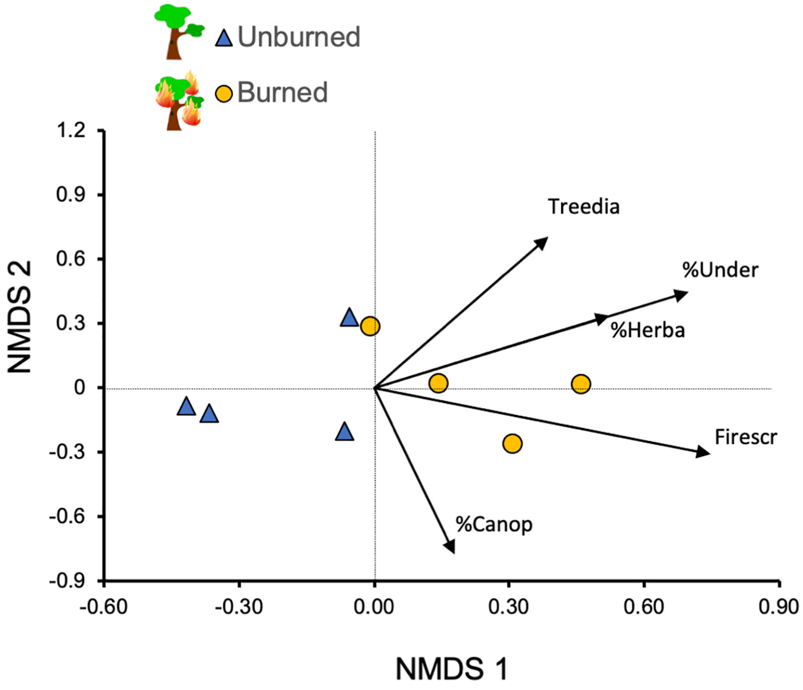

FIGURE 3 | Non-metric multidimensional scaling (NMDS; Bray-Curtis dissimilarity) for small mammal abundance in the eight sampled sites in the Brazilian Cerrado (stress = 0.16). We included habitat-structure variables as passive variables in the ordination. Habitat variables codes: Firescr—mean number of trees with fire scars; Treedia, tree diameter at breast height; %Under, understory density (%); %Herba, herbaceous cover (%); %Canop, canopy cover (%). Sites that burned ~3 years before (circles) differed from those that did not burn (triangles; PERMANOVA test, see text for details).

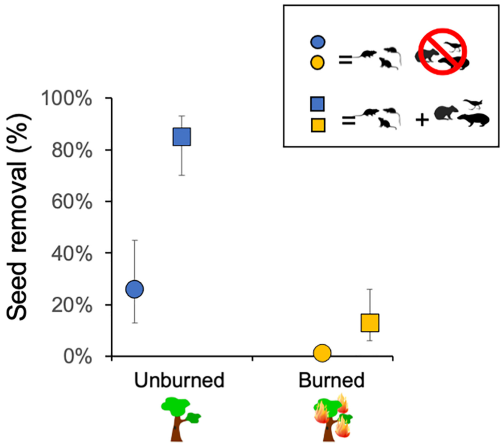

FIGURE 4 | Estimates of percentage of seeds removed differed in relation to fire history (burned *vs.* not burned ~3 years before; mixed-effects logistic regression: *P* = 0.045) and to access of medium and small vertebrates (squares) *vs*. small rodents only (circles; *P* < 0.001) across the six studied plant species. Error bars show confidence intervals of the estimates (see **Table 1** for complete statistical results).

in caged ones (**Figure 5**). The decline in previously burned sites, however, was significant only for *C. estrellensis* (**Table 2**). But the interaction between fire and exclosure treatment was significant for two of the six species (*P. elegans* and *D. alata*), indicating that for these species the previous occurrence of fire was more detrimental to seed removal by all vertebrate groups in comparison to seed removal by rodents only. For other two species (*C. langsdorffii* and *H. courbaril*), seed removal was significantly lower in caged than in uncaged seeds, suggesting that other vertebrates than small rodents were significant seed removers of these species (**Figure 5**).

Seed Offering in Captivity

All species of seeds offered were consumed by at least three of the five rodent species in captivity. Mean seed consumption rates of seed species ranged from 30 to 100% (**Supplementary Figure 2**). The preferred plant species were *D. alata* and *C. estrellensis*, with > 90% of mean seed consumption rates considering the five rodent species. On the other hand, *P. elegans*, *H. courbaril*, and *M. flexuosa* had average consumption rates between 30 and 40% and were not consumed by at least one of the rodent species tested (**Supplementary Figure 2**).

DISCUSSION

We investigated the effects of fire on seed removal by distinct vertebrate groups and observed that the burning regime in gallery forests strongly influenced seed removal patterns by vertebrates about 3 years after the fire occurrence. This previous burning changed the structural characteristics of the forests, mainly increasing the density of the understory vegetation

TABLE 1 | Results of a generalized linear mixed model testing the effects of previous fire occurrence (burned or not burned ~3 years before) and exclosure treatment (caged = access only to small rodents vs. uncaged = access to all vertebrate groups) on seed-removal proportion of six plant species in gallery forests in the Cerrado (neotropical savanna).

Predictors	β	CI	Odds ratio	CI	*p*
(Intercept)	1.59	−1.14 to −4.32	4.90	0.32–74.99	0.254
Fire (burned)	−3.73	−7.39 to −0.08	0.02	0.00–0.93	**0.045**
Exclosure (caged)	−3.11	−4.34 to −1.86	0.04	0.01–0.15	**<0.001**
Fi × Ex	0.49	−1.09 to 2.08	1.64	0.34–8.01	0.541

Seed-depot stations were nested within sites (4 sites for each fire treatment) which were nested within fire treatment (burned or not burned). Plant species were included as a random effect with random intercepts and random slope (6 levels, one for each species considered; see text for details). Boldface indicates significant effects.

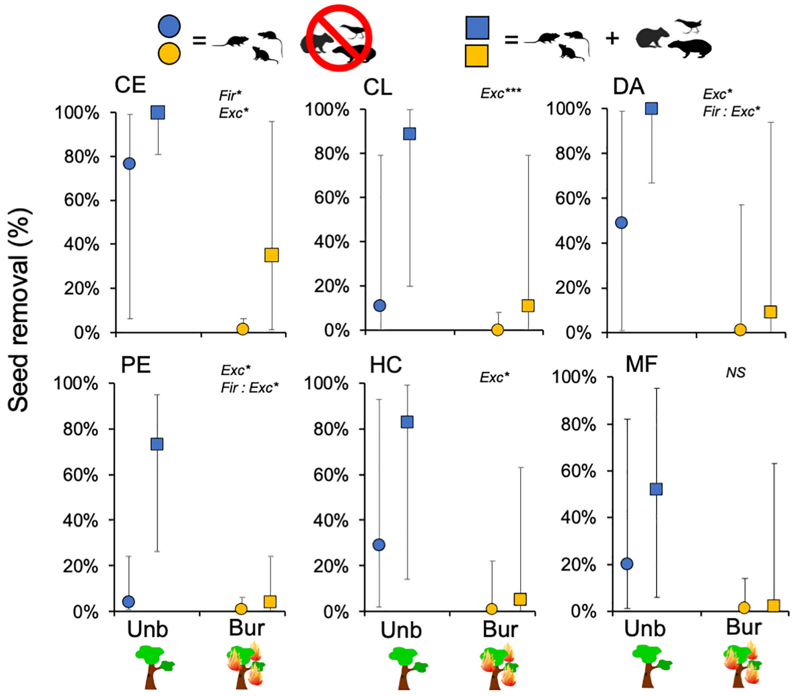

FIGURE 5 | Estimates of percentage of seeds removed (error bars = 95% confidence intervals) in relation to fire history (burned *vs.* not burned ~3 years before) and exclosure treatment (access to all vertebrates *vs.* access of small rodents only) for each of the six studied plant species (mixed-effects logistic regression). Species codes: CA, *Cariniana estrellensis*; CO, *Copaifera langsdorffii*; PE, *Platypodium elegans*; DA, *Dipteryx alata*; HC, *Hymenaea courbaril*; MF, *Mauritia flexuosa*. Significant effects of the factors (and their interaction) are indicated for each species (*$p < 0.05$, ***$P < 0.001$; see **Table 2** for complete statistical results).

and the herbaceous cover. Differences in these environmental characteristics between burned and unburned forests likely determined differences in species composition, richness, and abundance of small rodents, which influenced the rates of seed removal. Other vertebrates, larger than small rodents, played a significant role as seed removers for five of the six species. Seed removal by both groups (small rodents and other vertebrates), however, was reduced by the large-scale wildfire. The effects of fire were consistent across species, but for the two species with the largest seeds (*H. courbaril* and *M. flexuosa*) removal rates (for both groups) were extremely low in the burned forests (up to 5%).

We relied on a large-scale natural fire evaluating the responses of seed removers (small rodents and other vertebrates) to mid-term fire-induced changes in forested habitats. This kind of experiment is subject to criticism to the lack of replication in the sense that there was only one fire event. Large-scale wildfires, however, are a kind of unpredictable natural experiment that provides opportunities for the investigation of relevant ecological processes that could not otherwise be evaluated (Legge et al., 2008; Mendonça et al., 2015). Natural experiments like wildfires are relevant components of ecological research and should not be discarded based merely on a questionable dogmatic use of the pseudoreplication concept (Schank and Koehnle, 2009; Davies and Gray, 2015) which could represent the loss of opportunities to learn from large-scale disturbance events where strictly adequate replication is not feasible (Davies and Gray, 2015). In our study, we relied on a hierarchical "experimental" design using a mixed-effect modeling approach to deal with this issue. The faunal responses to large-scale fires can only be evaluated in natural "experiments" designed after the occurrence of unplanned wildfires, since small, experimental fires could not mimic a large wildfire. We acknowledge, however, that

TABLE 2 | Species-specific responses of six plant species to the effects of previous fire occurrence (burned or not burned ∼3 years before) and exclosure treatment (caged = access only to small rodents vs. uncaged = access to all vertebrate groups) on seed-removal proportion.

Plant species/Predictors	β	CI	Odds ratio	CI	*P*
Cariniana estrellensis					
(Intercept)	−4.87	−8.86 to −0.88	0.01	0.00–0.42	**0.017**
Fire (unburned)	6.05	0.42–11.68	424.92	1.52–118730	**0.035**
Exclosure (uncaged)	4.27	2.24–6.3	71.55	9.37–546.47	**<0.001**
Fi × Ex	0.12	−2.56–2.79	1.12	0.08–16.28	0.932
Copaifera langsdorffii					
(Intercept)	−6.14	−9.78 to −2.5	0	0.00–0.08	**0.001**
Fire (unburned)	4.04	−0.87–8.96	57.00	0.42–7795.90	0.107
Exclosure (uncaged)	4.04	1.99–6.1	56.96	7.29–444.96	**<0.001**
Fi × Ex	0.11	−2.51–2.72	1.11	0.08–15.19	0.937
Platypodium elegans					
(Intercept)	5.09	2.83–7.36	0.01	0.00–0.06	**<0.001**
Fire (unburned)	1.89	−1.11–4.89	6.62	0.33–132.67	0.217
Exclosure (uncaged)	1.79	0.35–3.23	5.97	1.41–25.19	**0.015**
Fi × Ex	2.40	0.51–4.29	11.01	1.67–72.75	**0.013**
Dipteryx alata					
(Intercept)	−5.00	−10.27–0.27	0.01	0.00–1.32	0.063
Fire (unburned)	4.96	−2.39–12.32	142.99	0.09–223417	0.186
Exclosure (uncaged)	2.71	0.05–5.36	14.97	1.05–212.35	**0.046**
Fi × Ex	3.36	0.09–6.63	28.82	1.10–756.63	**0.044**
Hymenaea courbaril					
(Intercept)	4.89	1.28–8.5	0.01	0.00–0.28	**0.008**
Fire (unburned)	4.01	−0.99–9.01	55.07	0.37–8178.58	0.116
Exclosure (uncaged)	1.90	0.31–3.5	6.72	1.36–33.06	**0.019**
Fi × Ex	0.59	−1.56–2.75	1.81	0.21–15.63	0.59
Mauritia flexuosa					
(Intercept)	−4.99	−8.16–−1.83	0.01	0.00–0.16	**0.002**
Fire (unburned)	3.62	−0.61–7.84	37.21	0.55–2538.70	0.093
Exclosure (uncaged)	1.05	−0.61–2.72	2.86	0.54–15.12	0.216
Fi × Ex	0.42	−1.82–2.66	1.52	0.16–14.29	0.714

Separate generalized linear mixed models were run for each of the six species. Seed-depot stations were nested within sites (4 sites for each fire treatment) which were nested within fire treatment (burned or not burned). Boldface indicates significant effects.

our approach has statistical limitations and the generalization of the conclusions that are drawn from our results must be done with care.

Fire and Small Mammals

Our results indicated that the areas that had been burned before presented a distinct species composition and a lower abundance of small mammals compared to areas that did not burn, as we expected. These differences in small mammal communities were probably associated to differences in vegetation structure, as suggested for other forested systems (Chia et al., 2016; González et al., 2021). There was a clear separation of the burnt from the unburnt forests in relation to the habitat variables measured in the field (tree diameter, canopy cover, understory plant density, herbaceous cover, and number of trees with fire scars). The previously burned forests showed an increase in understory density, herbaceous ground cover and number of trees with fire scars, as expected. This reinforces our choice and classification of forests as burned and unburned and indicates that structural differences are still evident even nearly 3 years after the fire event, reinforcing the reduced resilience of Cerrado forests in comparison to savanna formations (Coutinho, 1990; Reis et al., 2017). The increase in understory density and herbaceous cover was probably related to tree top-kill, which allows increased light to the forest interior but also lower air humidity causing dryness in the forest environment (Hoffmann et al., 2009; Prestes et al., 2020).

This increase in understory and herbaceous vegetation apparently did not result in more adequate resources which could potentially increase (or at least maintain) small mammal abundance. The average abundance of rodents in the burned forests was reduced to approximately one-sixth compared to unburned forests. This sharp reduction was probably related to the relatively small area covered by gallery forests in the study landscape (**Figure 1**), which results in low overall abundance of several forest species and limits the capacity of post-fire colonization by new individuals of forest-dweller small mammals. The burned forest sites were not occupied by non-forest specialists either. In a much larger riverine forest in the Colombian llanos, small mammal richness in burned sites

3 years after a large-scale wildfire (burning 350 ha of the forest) was lower than in unburned sites but responses varied across species. The occurrence of fire increased the abundance of the rodent *Zygodontomys brevicauda* and did not seem to impact the populations of *Oecomys* sp. whereas restricting the occurrence of the marsupial *Didelphis marsupialis* (González et al., 2021). These discrepancies with our results are probably related to the much larger forest area sampled by González et al. (2021) and consequent much higher recolonization opportunities for the small mammals (from the unburned neighboring areas) in comparison to our studied landscape.

The differences in small-mammal composition that we found were mainly due to the absence (or low number of records) of arboreal mammals in the burned areas. Some of these arboreal species were captured only in the unburned forests (i.e., *Oecomys* sp. and *R. macrurus*) or else were much less abundant in the burned forests (i.e., *G. agilis*). These arboreal species were rare or absent in the burned forests despite the high density of understory vegetation. This suggests that indirect factors, such as fire-induced reduction in canopy resources or increased predation rates (Leahy et al., 2016) could be affecting these animals. Arboreal mammals also were negatively affected by high-severity fire (like the wildfire that occurred in our study area) in Australian forests (Chia et al., 2016). In our studied gallery forests, in addition to fire-induced death of trees (Hoffmann et al., 2009) and consequent structural changes (González et al., 2021), the decline of arboreal small mammals was probably related to the potential post-fire reduction in the availability of fruits, their preferred resources (Paglia et al., 2012; Ribeiro et al., 2019). Other arboreal frugivorous rodents in the neotropics suffered a post-fire decline in abundance (or even local extinction), as reported for *Oecomys concolor* in Atlantic Forest fragments (Figueiredo and Fernandez, 2004) and *Irenomys tarsalis* in Araucaria-*Nothofagus* Chilean forests (Zúñiga et al., 2021). In neotropical savanna-gallery forests in Colombian llanos, however, the occupancy probability of *Oecomys* sp. did not differ between sites burned 3 years before and unburned sites, but the occurrence of this rodent in burned areas was related to the maintenance of an arboreal strata (González et al., 2021). Fire also negatively affected two arboreal small mammals (*G. agilis* and *R. macrurus*) in "cerradão" forests (closed woodland with arboreal cover of 50–90% and tree height mostly between 8–12; Oliveira-Filho and Ratter, 2002) burned by the same large-scale wildfire investigated in the present study. Both these species showed apparent fire-induced local extinction and were still absent or occurring in very low densities about 1.7 years after fire; Mendonça et al., 2015).

Terrestrial forest species were affected distinctly by fire. The large (∼220 g) semi-aquatic rodent *N. squamipes* occurred in both unburned and previously burned forests. This rodent is closely associated to water streams (Ernest and Mares, 1986), whose surrounding vegetation is generally less affected by fire because of its high humidity. This vegetation may confer protection and food resources for this species, which may feed on aquatic invertebrates and also on fruits and seeds (Crespo, 1982; Lessa et al., 2019). In fact, in our study all *N. squamipes* individuals were captured at stations near (≤10 m) watercourses. This species may have been responsible for most of rodent seed removal in the burned areas, which was corroborated by or results on seed consumption by *N. squamipes* in captivity. The other large terrestrial rodent captured, the frugivorous-granivorous echimyid *P. roberti*, was not captured in the burned forests, suggesting a low tolerance to this kind of disturbance. The role of *P. roberti* and other forest frugivorous rodents in burned forests could potentially be replaced by a more generalist fauna of "outsiders" small rodents, such as *N. lasiurus*, *Oligoryzomys* spp and *Calomys* spp., considering that these open-area species are able to occupy recently burned dry forests (i.e., cerradão) in the same study region (Camargo et al., 2018). This kind of Cerrado species replacement could maintain similar post-fire rates of seed removal in comparison to pre-fire patterns, especially for small seeds. In gallery forests, however, we did not detect post-fire colonization of burned forests by any open-area species.

Fire and Vertebrate Seed Removal

We evaluated rates of seed removal for six native tree species in relation to the previous (∼3 years before) occurrence of fire and kind of seed remover (small rodents *vs*. all vertebrates) and detected that overall seed removal was lower in the recently burned areas and higher for the seeds available to all vertebrates. The observed lower seed removal rates in burned forests in comparison to the unburned ones mirrored the decrease in small mammal abundance that we observed in the burned forests, corroborating the second hypothesis that we raised. Similarly, seeds accessible to all animals were removed at lower rates in sites burned 4 months earlier than in unburned sites in Australia (Tasker et al., 2011). This fire-induced decrease in seed removal also occurred in our study, albeit over a longer post-fire time frame. This decrease indicates an indirect effect of the fire factor, even almost 3 years later, on the interaction between seeds and their removal agents inside gallery forests. A direct relationship between rodent abundance and seed removal, as observed in our study, was indicated by other authors (Ostfeld et al., 1997; Schnurr et al., 2002; Demattia et al., 2004; Pearson et al., 2014). Neotropical small rodents are considered to be essentially predators of seeds in the evaluated size range (Díaz et al., 1999; Forget et al., 1999; Vieira et al., 2003; Kelt et al., 2004), which reinforces the assumption that the removal rates obtained in the treatment of partial exclusion (SMRO) in fact reflected seed predation rates.

The reduction in vertebrate seed predation in previously burned areas might be considered beneficial for post-fire recruitment of tree species in gallery forests. This is not necessarily true, however, when considering the entire plant communities associated to these forests. Vertebrates generally are non-selective seed predators and, in their absence, the relative role of other groups of relevant seed predators in the neotropics, such as insects and fungi, probably increases (Williams et al., 2021). Therefore, fire occurrence might cause a switch from generalist seed predators that do not cause strong conspecific density-dependent mortality (following the classic Janzen-Connell model; Janzen, 1970; Connell, 1971) to specific predators that attack seeds in a density-dependence manner, like fungi and insects (Terborgh, 2012). This switch might have profound medium to long-term consequences in gallery forest plant communities (Williams et al., 2021). Considering that neotropical small rodents do not prey upon all seed species in the same way (Vieira et al., 2003; Galetti et al., 2015b; also as indicated by our seed-offering experiments), a fire-induced rodent decrease and consequent seed predator release *per se* could affect plant community patterns of the forests. A reduction in predation of some plant species could cause a high dominance of these species, reducing plant diversity (Dirzo and Miranda, 1990; Putz et al., 1990). Moreover, the rodent-poor burned forests could also be more prone to be occupied by exotic plant invaders, since field experiments demonstrated that seed predation by neotropical small rodents is a source of biotic resistance to plant invasions (Pearson et al., 2014).

The results on seed-offering to captive rodents were consonant with those obtained in field. The two most-consumed seed species in captivity were also those with the highest removal rates in the partial exclosure treatment (access to small rodents only), with estimated seed removal values of 89% (*C. estrellensis*) and 49% (*D. alata*). This indicates that these species are subject to high natural predation rates and rodents potentially play a relevant role for regulating natural populations of both species. Seed removal of *C. estrellensis* was relatively high in the burned forests, being much higher (35%) than for all the other species (range 2–11%). Considering that *C. estrellensis* has the smallest seed size among the studied species (seed mass = 0.08 g), we suggest that its seeds are potentially removed by more vertebrates than the species with larger seeds. Most forest birds that feed on the ground probably are able to consume *C. estrellensis* seeds but not the seeds of other studied species (Christianini and Galetti, 2007). The guild of *C. estrellensis* seed predators include even the howler monkey *Alouatta caraya* (Oliveira-Filho and Galetti, 1996), which occurs in the study area (Schneider et al., 2011). This large spectrum of seed removal agents possible ameliorate the fire effects on *C. estrellensis* seed removal by vertebrates. These fire effects seem to be higher for the plant species with large seeds, whose spectrum of seed removal agents is more restrict (Dirzo et al., 2007; Galetti et al., 2015b; Dylewski et al., 2020).

The effects of fire and exclusion treatment on seed removal were consistent across the six plant species studied. For five of the six species, seeds were significantly more removed from the open control stations. The exception was *M. flexuosa*, but even for this species in the unburned sites removal rates in the caged stations (i.e., access to small rodents only) were about 40% of the values found for the open control stations. This overall pattern indicates a relevant role of large vertebrates as seed removers in the studied forests. High removal rates in plots accessible to all vertebrates was also reported for *H. courbaril* in Peruvian Amazon Forest (Terborgh et al., 1993) and for other forest species (see Demattia et al., 2004) in Mexican lowland forests. In our study area, the potential "large" seed-removal agents include collared peccaries, tapirs, agoutis, pacas, primates (Fonseca and Redford, 1984; Schneider et al., 2011), and frugivorous-granivorous birds (e.g., the gray-necked wood-rail *Aramides cajaneus*, the pale-vented pigeon *Patagioenas cayennensis*, and the undulated tinamou *Crypturellus undulatus*; Tubelis, 2011).

Seed removal by both vertebrate groups decreased in the previously burned forests, as indicated by the overall analysis across all species. This decrease was more accentuated for the open control stations (i.e., access to all vertebrates), with overall seed removal estimates changing from 85 to 13% across all plant species. This indicates that previous occurrence of fire reduces severely seed removal by all group of vertebrates. This reduction was still more extreme for the species with the largest seeds—*P. elegans*, *H. courbaril*, and *M. flexuosa* (2–5% of seed removal in the burned forests). Large-sized seeds are removed and consumed mainly by medium to large mammals, such as agoutis, pacas, tapirs and wild pigs (Dirzo et al., 2007; Mendieta-Aguilar et al., 2015; van der Hoek et al., 2019; Portela and Dirzo, 2020). Tapirs (*Tapirus terrestris*) and collared peccaries (*Pecari tajacu*) are probably locally extinct (Schneider et al., 2011) in the study region, with agoutis (*Dasyprocta azarae*) being by far the most common "large" mammal, as indicated by camera trapping data (EMV, unpublished).

The probable low density (or local extinction) of large frugivorous vertebrates in the burned forests are probably related to structural changes of these forests and a reduction in fruit resources. In south-eastern Amazon Forest, the occurrence of fire every 3 years caused a 50% decrease in the abundance of forest-specialist frugivorous butterflies (de Andrade et al., 2017). Moreover, available data for central Brazilian Amazon forests indicate that fruiting tree abundance is severely reduced in forest sites burned 3 years before than in unburnt forest sites and several vertebrate species (including large frugivores) declined in response to fires. One of these species with significant decline in abundance in the burned sites was an agouti species (*Dasyprocta agouti*; Barlow and Peres, 2006).

The fire-inducted decrease in seed removal by large mammals that we detected in our study may have marked effect on post-fire tree recruitment. The low removal of seeds (mainly those with the largest seed sizes) indicate that these species were probably not being dispersed adequately in such areas. Agoutis (*Dasyprocta* spp.) are the main seed dispersers of both *H. courbaril* (Hallwachs, 1986; Gorchov et al., 2004) and *M. flexuosa* (Mendieta-Aguilar et al., 2015; Acevedo-Quintero and Zamora, 2016) through scatter-hoarding. In general, it is recognized that the reduction of medium and large frugivorous seed dispersing mammals may result in less recruitment of large seed species and may eventually have negative demographic effects for species particularly dispersed by this guild (Stoner et al., 2007). A study carried out in Venezuela suggested that the regeneration of *H. courbaril* in the absence of agouti, the main disperser of this species (Hallwachs, 1986) was quite limited (Asquith et al., 1999). Other studies in neotropical forests indicated that documented changes in mammal community composition, including the loss of agouti, play a relevant role in the reduction of forest diversity (Leigh et al., 1993; Asquith et al., 1997). A decrease in local densities of *H. courbaril*, *M. flexuosa* and other large-seeded agouti-dispersed species would also affect several animal species that depend on them. The palm *M. flexuosa*, for instance, was suggested to be a "hyperkeystone" species, considering that at least 74 vertebrate species directly use this palm as a food or nest resource (van der Hoek et al., 2019).

We hypothesized that the role all vertebrates and small rodents on seed removal would be affected by the previous occurrence of fire, with a higher relative role of small rodents in comparison with the latter in burned forests. For most species, however, our results did not support this expectation, with fire reducing seed removal rates for both vertebrate groups. Only for *P. elegans*, the previous occurrence of fire declined seed removal rates relatively more in open control stations than in the caged stations (exclusive access to small rodents). This indicate that, for this species, fire not only decreases total seed removal, but also causes a shift from mixed interactions of seed predation and seed dispersal (through scatter-hoarding) to a higher relative frequency of an exclusive and primarily negative interaction (seed predation from the small rodents). In this way, for *P. elegans* fire simulates other sources of disturbances in neotropical forests, such as fragmentation (Dirzo et al., 2007; Galetti et al., 2015a).

Final Remarks

Historically, gallery forests have not suffered frequently from fire events and, for this reason, studies on the influence of fire in their associated communities are rare. The present study was an important opportunity to assess the effects of fire on the composition of non-volant small mammal communities as well as their role as seed removal agents. We recommend that future studies should evaluate the fate of seeds removed in gallery forest environments disturbed by fire, so that it would be possible to discern between predation or dispersal processes. Furthermore, the fire effects on community composition of large mammals in this forest type should also be investigated.

We investigated the mid-term effects (∼3 years) of a large wildfire on gallery forests of the Cerrado (neotropical savanna) and showed that these effects include a reduction in small mammal richness and abundance (affecting mainly the arboreal frugivorous species). We conclude that the observed decline in small rodent seed predation in the burned forests may have marked medium- and long-term effects on plant communities in gallery forests. These potential effects include changes in community composition, species coexistence, and diversity.

Fire also caused a decline in seed removal by large mammals. These animals (mainly the agouti *D. azarae*) provide dispersal services that generally are not performed by small vertebrates, mainly for the large-seeded species. The maintenance of such services and consequently of the trees that depend on them may be jeopardized by the burning of gallery forests. We believe that the occurrence of rare and not very extensive wildfires in such forest type probably do not affect the occurrence of small and large mammals (nor their roles as seed predators and seed dispersers) at a landscape scale, if there is enough time for forest regeneration and unburned sources for mammal recolonization. Fire events, however, have been increasing in frequency and intensity in the Cerrado because of human activities and climate changing (Pivello et al., 2021), being capable of destroying otherwise resistant Gallery Forests (Redford and Fonseca, 1986). This is a serious threat considering that these forests are fire-sensitive ecosystems (Pivello et al., 2021) and keystone habitats that play a crucial role in maintaining mammalian diversity in the Cerrado (Redford and Fonseca, 1986). This role is not restricted to exclusive forest mammals. Even though covering a small total area within the landscape (about 5% of the entire Cerrado area; Cássia-Silva et al., 2020), gallery forests are used to some extent (obligately or opportunistically) by 84% of 31 small mammal genera (marsupials and rodents) reported to occur in the Cerrado, including several genera that occur primarily in typical savanna environments (Redford and Fonseca, 1986).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by Committee on Animal Research and Ethics (CEUA, Universidade de Brasilia—UnB), license number 44372/2012.

AUTHOR CONTRIBUTIONS

TC collected data in the field. EV and TC performed statistical analysis. Both authors contributed to the conception and design of study, wrote the manuscript, and contributed equally to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.793947/full#supplementary-material

Supplementary Video 1 | This video shows a small rodent (probably *Hylaeamys megacephalus*) entering a semipermeable exclosure with seeds in its interior during the field experiment. Inside the cage there was another rodent of the same species.

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Habitat Specificity Modulates the Response of Small Mammals to Habitat Fragmentation, Loss, and Quality in a Neotropical Savanna

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Landscape conversion of natural environments into agriculture and pasture are driving a marked biodiversity decline in the tropics. Consequences of fragmentation might depend upon habitat amount in the landscape, while the quality of remnants can also affect some species. These factors have been poorly studied in relation to different spatial scales. Furthermore, the impacts of these human-driven alterations may go beyond species loss, possibly causing a loss of ecosystem function and services. In this study, we investigated how changes in landscape configuration (patch size and isolation), habitat loss (considering a landscape gradient of 10, 25, and 40% of remnant forest cover), and habitat quality (forest structure) affect small mammal abundance, richness, taxonomic/functional diversity, and species composition in fragmented landscapes of semideciduous forests in the Brazilian Cerrado. Analyses were performed separately for habitat generalists and forest specialists. We live-trapped small mammals and measured habitat quality descriptors four times in 36 forest patches over the years 2018 and 2019, encompassing both rainy and dry seasons, with a total capture effort of 45,120 trap-nights. Regression analyses indicated that the effect of landscape configuration was not dependent on the proportion of habitat amount in the landscape to determine small mammal assemblages. However, both patch size and habitat loss impacted different aspects of the assemblages in distinct ways. Smaller patches were mainly linked to an overall increase in small mammal abundance, while the abundance of habitat generalists was also negatively affected by habitat amount. Generalist species richness was determined by the proportion of habitat amount in the landscape. Specialist richness was influenced by patch forest quality only, suggesting that species with more demanding habitat requirements might respond to fragmentation and habitat loss at finer scales. Taxonomic or functional diversity were not influenced by landscape structure or habitat quality. However, patch size and habitat amount in the landscape were the major drivers of change in small mammal species composition in semideciduous forests in the Brazilian savanna.

Keywords: Cerrado, landscape structure, forest structure, rodents, marsupials, functional diversity

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INTRODUCTION

Habitat loss and fragmentation are the main drivers of biodiversity decline on Earth (Pardini et al., 2010; Haddad et al., 2015; Hanski, 2015; Laurance et al., 2018). In the tropics, these landscape alterations result mostly from the conversion of natural environments into agriculture and pasture (Fearnside, 2001; Gibbs et al., 2010; Peres et al., 2010; Françoso et al., 2015; Strassburg et al., 2017). These human-driven changes may affect species abundance, richness, and diversity (Andren, 1994; Fahrig, 2003; Laurance et al., 2011; Hanski, 2015; Melo, 2015; Bovendorp et al., 2019). Additionally, ecological traits might be filtered out, which might drive communities to biotic homogenization (Olden et al., 2004; Gámez-Virués et al., 2015; Melo, 2015; Almeida-Gomes et al., 2019), leading to changes in ecosystem function and forest dynamics (see Laurence et al., 2000; Haddad et al., 2015; Laurance et al., 2018). Therefore, understanding the impacts of habitat conversion not only on taxonomic diversity, but also on functional diversity (i.e., the degree of functional difference among species in a community) (Petchey and Gaston, 2006) allows a broader comprehension of the consequences of species loss on ecosystem functioning and stability (Petchey and Gaston, 2006). Conservation strategies should be more effective in maintaining ecosystem services if they also consider the functional dimension of biodiversity (Cadotte et al., 2011; Freitas and Mantovani, 2018).

Habitat amount in the landscape is an important predictor of species persistence in altered landscapes (Andren, 1994; Fahrig, 2003, 2013; Melo et al., 2017). However, the effects of fragmentation may vary depending on landscape context (Andren, 1994; Pardini et al., 2010; Villard and Metzger, 2014). In landscapes with high habitat cover, migration among patches are elevated enough to maintain high overall species abundance and richness, because of the proximity between fragments, irrespective of patch size (Pardini et al., 2010). As habitat loss advances, the relative importance of patch size and isolation to explain species loss and population declines increases (Andren, 1994; Villard and Metzger, 2014). Consequently, the effects of landscape configuration on species richness and abundance should be evident when there are intermediate amounts of habitat in the landscape (Pardini et al., 2010; Martensen et al., 2012; Villard and Metzger, 2014).

In severely eroded landscapes, however, connectivity is jeopardized enough that metapopulations can no longer persist, due to high extinction and low colonization rates (Lande, 1987; Andren, 1994). Under this condition, even large patches can present local extinctions due to increasing isolation, which renders them vulnerable to stochastic events. Any additional loss of native cover at the landscape scale might have greater impact on extinction and colonization probabilities (With and King, 1999; Fahrig, 2003). Therefore, no relationship between species richness and patch size would be expected (Pardini et al., 2010).

Within these diverse spatial dynamics, the interaction between patch and matrix can influence the ecological consequences of landscape alterations for different species (Prevedello and Vieira, 2010; Newmark et al., 2014; Wilson et al., 2016). Also, deterioration of patch habitat quality resulting from landscape conversion may contribute to species loss and changes in species composition (Tabarelli and Gascon, 2005; Carrete et al., 2009; Delciellos et al., 2016; Zimbres et al., 2017; Hannibal et al., 2020), because habitat complexity and heterogeneity are well known to influence biodiversity (Fahrig et al., 2011; Lesak et al., 2011; Ke et al., 2018; Laurance et al., 2018). Despite the important role of habitat quality in regulating spatial dynamics in fragmented landscapes and influencing species distribution patterns, few studies have investigated this subject in comparison to classical spatial approaches (Mortelliti et al., 2010). Moreover, knowledge on this matter can improve considerably the effectiveness of management strategies applied to the conservation of remnants, their diversity, and the ecosystem services provided by them (Tabarelli and Gascon, 2005). This is especially critical for the Brazilian environmental policies, because most of the protected areas in the country consists of legally required forest areas set aside within private landholdings (Galleti et al., 2010).

Non-flying small mammals (Rodentia and Didelphimorphia) are abundant, diverse, and perform key roles in the ecosystems as seed/seedling predators, seed dispersers, prey for many predators, and secondary consumers (Brown et al., 2001; Bisceglia et al., 2011; Ribeiro et al., 2019). Additionally, they respond to microhabitat structure (Kajin and Grelle, 2012), to resource diversity/availability (Bergallo and Magnusson, 1999; Previtali et al., 2009; Camargo et al., 2019a), and are sensitive to environmental and landscape changes (Pardini et al., 2010; Melo et al., 2017; Hannibal et al., 2018). These characteristics make them potential indicators of environmental quality (Bonvicino et al., 2002), and an ideal group to assess human-driven landscape impacts on biodiversity.

In this study, we investigated how changes in landscape configuration (i.e., patch size and isolation), habitat loss (considering a gradient of 10, 25, and 40% of remnant habitat amount), and habitat quality (i.e., forest structure) affect small mammal abundance, richness, taxonomic/functional diversity, and species composition in fragmented landscapes of semideciduous forests in the Brazilian Cerrado. We expected the effect of patch size on community metrics to be dependent on the landscape context in terms of overall habitat amount. In landscapes with intermediate levels of habitat amount, patch size effects should be stronger, especially for forest-dependent species (Pardini et al., 2010; Villard and Metzger, 2014; Melo, 2015). Yet, in more degraded landscapes (10% of habitat amount) and in more conserved ones (40%), we expected to find no patch size effects on abundance, richness, and diversity, but only a positive effect of habitat amount. On the other hand, we predicted that generalist species should not respond to patch size, neither to habitat amount in the landscape, or be affected by patch size alone in the most degraded landscape (10%) (Pardini et al., 2010). Regarding habitat quality (here represented by forest structure features), we foresaw that more conserved patches (i.e., with higher structural complexity and heterogeneity) should harbor more species, and with higher abundance, mainly for forest specialists. Therefore, assemblages in more complex forests should be more diverse taxonomically and functionally (Zimbres et al., 2017).

Finally, we expected species composition to vary across the landscape structure gradient, also according to changes in habitat quality (i.e., forest structure). Rare species, forest specialists, with higher sensitiveness to environmental alterations would be more associated with larger patches and/or landscapes with higher levels of habitat amount, as well as to more structurally complex forests (Melo, 2015; Hannibal et al., 2020). On the other hand, tolerant and generalist species would be more associated with smaller and isolated patches, lower habitat amount in the landscape, and low habitat quality (Melo, 2015).

MATERIALS AND METHODS

Study Area

We conducted the study in the Brazilian Cerrado, a biodiversity hotspot (Myers et al., 2000). This neotropical savanna is one of the richest savannas in the world (Klink et al., 2005; Ribeiro and Walter, 2008), and presents high environmental heterogeneity, comprising different vegetation physiognomies such as open grasslands, typical savannas, and forests (Oliveira-Filho and Ratter, 2002; Ribeiro and Walter, 2008). Seasonal forests were once probably the most extensive forest type within this biome (Oliveira-Filho and Ratter, 2002). Since it occurs on highly fertile soils, and harbors economically valuable plant species, it was the first vegetation physiognomy to be converted into crop fields and pastures, also being exploited by logging activities (Murphy and Lugo, 1986; Oliveira-Filho and Ratter, 2002; Miles et al., 2006). It is still a poorly studied vegetation type, and has been neglected in terms of conservation efforts (Scariot and Vieira, 2006; Prieto-Torres et al., 2021).

Our study sites were located in remnants of semideciduous seasonal forests in a highly deforested portion of the Cerrado, in Central Brazil. The study areas comprised three landscapes of ∼15,000 ha with different levels of remnant habitat amount (∼ 10, 25, and 40%). In each landscape, we sampled 12 forest patches (totaling 36 sampling sites) (**Figure 1**). Remnants ranged from 2.41 to 1440 ha (**Supplementary Table 1**). Sampling site choice was based on (1) the highest variation in patch size possible within each landscape; (2) ease of access; (3) landowners' permissions. Sampling patches were located in the municipalities of Abadiânia (16°2′51″ S 48°51′44″ W), Jesúpolis (15°57′05″ S 49°22′26″ W), Jaraguá (15°44′31″ S 49°20′6″ W), Ouro Verde de Goiás (16°13′13″ S 49°11′36″ W), Pirenópolis (15°53′06.40″ S 49°10′46.29″ W), and São Francisco de Goiás (15°55′51″ S 49′15′2″ W), in the central portion of the state of Goiás, Brazil. In this region, the matrix is composed mainly of pasture, but there are also agricultural areas (such as crop fields and/or banana plantations), and few patches of native savanna vegetation. Sampling sites were located in the Legal Reserves of private farms, which are natural vegetation areas all landowners are legally obliged to set aside. Also, there were three sites adjacent to conservation units (Reserva Particular de Patrimônio Natural Vaga Fogo Farm, Pirenópolis – GO, and Parque Estadual da Serra de Jaraguá, Jaraguá – GO).

The climate is classified as Aw according to Köppen, with two well defined seasons (hot/wet summers from October to March, and dry/cold winters from April to September). To minimize differences in species composition between sampling sites, maximum distance between landscapes did not exceed 100 km, and were located in the same river basin (Basin of Tocantins-Araguaia river).

Small Mammal Survey

In each of the 36 sampled patches, we established a trapping line of 200 m, located 30 m from patch edges to minimize edge effects. Each line had 20 trap stations, placed every 10 m, with four live traps each, where half were set on the ground, and half in the understory (1.5 m to 3 m height), totaling 80 traps per patch. Every station had a Tomahawk® (300 × 160 × 160 mm) and a small Sherman® (250 × 80 × 90 mm) on the ground, and a large Sherman (300 × 80 × 90 mm) and a small one in the understory, except for the first and last trap stations, where we replaced a Tomahawk trap by a large Sherman. Understory traps were strapped with a wire onto wooded vines or more horizontal trunks of tree trunks that were connected to the forest canopy, avoiding isolated trees. The study was conducted over the years 2018 and 2019, in the following periods: rainy-dry season (April to June 2018), dry-rainy season (August to October 2018), rainy (February to April 2019), and dry season (June to August 2019). Captures occurred during four consecutive nights per field campaign, resulting in an effort of 1,280 trap-nights per patch and 45,120 trap-nights in total.

Traps were baited with a mixture of peanut butter, corn powder, sardine, and banana. Captured animals were identified and marked with numbered ear-tags. They were released in the same trap location where they were captured. Voucher specimens were collected and will be held in the Mammal Collection of the Department of Zoology, University of Brasília (UnB, Brasília, Brazil). All procedures followed the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists, 2016).

Landscape Structure

Landscape types were categorized based on the 2016 land use and land cover map from the MapBiomas[1] project, collection 4.0, which classifies Landsat satellite imagery at a 30-m resolution. The temporal mismatch between the land cover map from MapBiomas and the field campaigns should not be important, as the study sites are within a relatively consolidated landscape in terms of human occupation. Landscape choice was based on the proportion of five land cover classes: forest, savanna, agriculture, pasture, and mosaic of agriculture and pasture.

Landscape structure was evaluated as: patch size (ha); mean patch isolation (as the mean distance to all nearest neighbor patches in a 1km radius buffer); and proportion of habitat amount available in each landscape context [10, 25, and 40% of natural cover (forest plus savanna) as shown in **Figure 1**]. These metrics were calculated using the Patch Analyst extension in ArcGis 10.2.

Habitat Quality

We considered patch quality as habitat properties that might have an impact on population parameters such as survival

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[1] http://mapbiomas.org

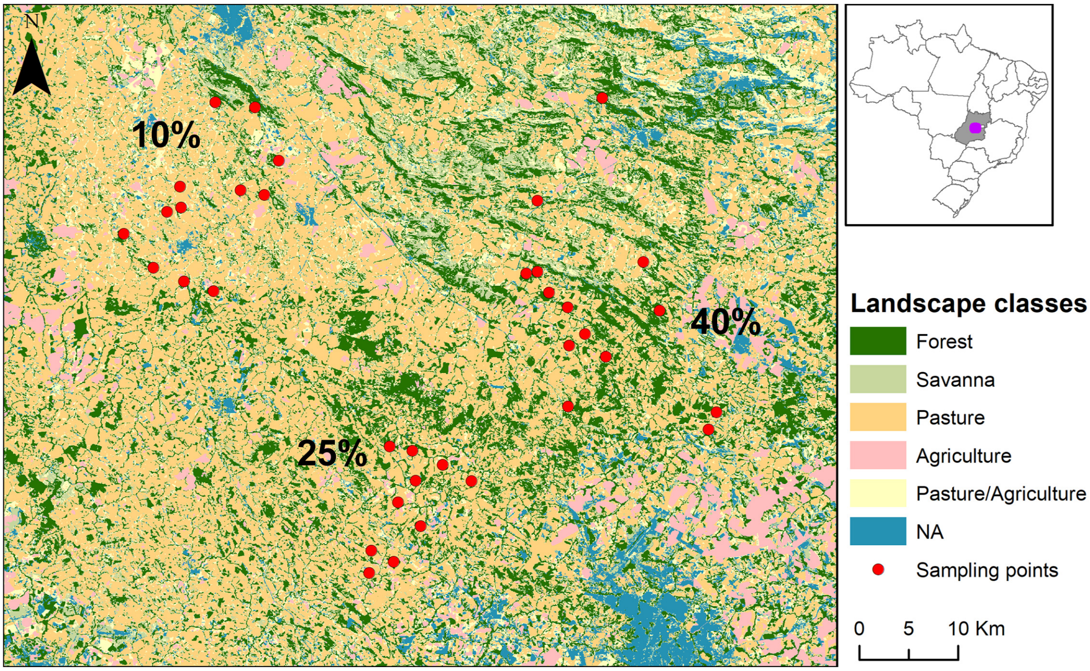

FIGURE 1 | Landscapes of 15,000 ha with 10, 25, and 40% of habitat amount (including both forest and savanna), and the sampled patches (red dots) in central state of Goiás, Brazil (highlighted in gray in the inset map). Patches located in the western portion of the map are within the landscape with 10% of remnant habitat amount; southern patches correspond to the landscape with 25%; and the eastern patches are in the landscape with 40% of habitat amount.

and fecundity (Mortelliti et al., 2010). To that end, we selected environmental variables revealed by other studies as important to small mammal occurrence and habitat use, which can potentially affect population parameters and individual condition, influencing species coexistence (Pardini et al., 2005; Ribeiro, 2015; Delciellos et al., 2016, 2018; Camargo et al., 2018; Hannibal et al., 2018, 2020). These variables describe habitat heterogeneity and forest complexity.

At each patch,we sampled descriptors of habitat quality in ten 4 × 4-m plots located every 20 m along the 200-m transect line. Each plot corner was marked by a colored flagging tape for the plot to be re-visited during the study. To evaluate forest structure, we measured the following variables inside each plot: (1) Canopy cover, as the proportion of closed pixels from a photograph taken with a digital camera in the center of each plot, using the software Image J. We took one picture per season and used mean values per patch; (2) Mean number of vines; (3) Mean tree height (m) of the closest four trees from the plot center, with circumference $\geq$ 16 cm at 30 cm height - estimated with a 3-m pole; (4) Basal area (m^2), estimated from the diameter at breast height (DBH) from the same four previously measured trees; (5) Understory clutter (up to a 3-m height) (%), estimated with a graduated 3-m pole (with a graduation of 10 cm) following Martins et al. (2017); (6) Litter volume (cm^3), estimated from litter material sampled in a 50 × 50-cm quadrat inside each plot (located in its superior left corner), following Santos Filho et al. (2008). We placed the collected litter inside a translucid graduated cylindric box (with a diameter of 28.2 cm), and pressed down the material with a 1-kg weight, thus indicating the correspondent litter height on a scale of 120 mm (**Supplementary Figure 1**). Litter height (h) was then used to estimate cylinder volume according to $V = \pi. (14.1)^2.h$.

Cattle ranching is the main human activity in the study region, so we also estimated (7) Cattle intrusion to measure human-driven habitat alteration in forests. We classified intrusion level as an ordinated variable (0–4) based on incidence of footprints, cattle trampling, and dung presence in a 15-m radius around each plot center. For this variable we used median plot values for each patch, while we used mean values for all the other variables.

Functional Traits

To assess species functional responses to habitat loss and fragmentation, as well as to habitat quality, we used morphological and behavioral traits related with habitat use and trophic habits, which might influence species tolerance to landscape alterations (**Supplementary Table 2**). We measured the following quantitative morphological traits in the field: (1) Tail length (mean tail length/mean body length), which is related to vertical use of space: longer tails are associated to more arboreal habits (Eisenberg and Wilson, 1981); (2) Hind foot width (mean width/mean length of hind foot), which is related with locomotion habits, and consequently with use of space: short and wider hind feet are associated with more arboreal habits, while longer and straight hind feet indicate more cursorial habits (Camargo et al., 2008; Vieira and de Camargo, 2012); (3) Body weight (g), a feature related with food resource use (influencing prey size consumed), metabolic costs (MacMillen, 1983), travel speed (Hirt et al., 2017), dispersal distance (Whitmee and Orme, 2013), trophic niche partitioning (Andreas et al., 2013), foraging behavior, and predation risk (Kotler and Brown, 1988);

(4) Arboreality index (number of captures in understory/total number of captures), which measures the vertical use of space (Camargo et al., 2019b). As categorical variables, we classified the species based on information available in the literature according to: (5) habitat specificity (forest specialists – species restricted to forest environments, or habitat generalists – species that inhabit forests as well as open areas, such as grasslands, savannas, and crop fields) following Bonvicino et al. (2002), Marinho-Filho et al. (2002), Pardini (2004), Bezerra et al. (2009), Cáceres et al. (2010), Oliveira and de Bonvicino (2011), Rossi et al. (2011), Gomes et al. (2015), and Ribeiro (2015) (**Supplementary Table 2**); and finally the multichoice binary variable (6) Diet – representing a combination of the following trophic guilds: insectivore, frugivore, granivore, and omnivore (Paglia et al., 2012; Shiels et al., 2014; Riofrío-Lazo and Páez-Rosas, 2015).

Data Analyses

Community Metrics

We evaluated species richness [with Chao1 estimator (Colwell et al., 2012)], and abundance (as the total number of individuals captured in each patch) separately for forest specialists and habitat generalists. Considering all species together, we estimated taxonomic species diversity with the true diversity Shannon Index (exp(H′))] (Jost, 2006), and functional diversity (FD) was evaluated as the Rao's quadratic entropy (Q). It measures functional distance between pairs of individuals based on the selected functional traits, and incorporates species abundances (Botta-Dukát, 2005), besides being weakly influenced by species richness (Laliberté and Legendre, 2010; Pavoine and Bonsall, 2011; Dias et al., 2013). We used Gower distance to estimate FD, since we had continuous, categorical, and binary traits (Podani and Schmera, 2006; de Bello et al., 2010). Taxonomic metrics were calculated using the *vegan* package (Oksanen et al., 2019) in R, while functional diversity was estimated with the *FD* package (Laliberté et al., 2014).

Community Metrics and the Effects of Fragmentation and Habitat Loss

To evaluate the relative effects of patch size and patch isolation according to landscape habitat amount, we performed regression analyses with generalized linear models (GLMs) using the lme4 package (Bates et al., 2015). GLMs were used to accommodate residual deviations from normality. Also, according to the response variables evaluated and model residual dispersion, we used different distribution families (Gaussian, Gamma, Poisson, and Negative Binomial) (Zuur et al., 2009). To determine which variables influences our response variables the most, nested models were compared by likelihood ratio tests (LRT). The significance of explanatory variables was given by Deviance and p-values, based on χ^2 tests. For all global models, we investigated spatial autocorrelation in the model residuals with Moran's I associated with bubble plots from the *sp* package in R (Pebesma and Bivand, 2005). Also, we checked for multicollinearity between predictors using the variance inflation factor (VIF) in all global models (Zuur et al., 2007). During model fitting, we log-transformed patch size to improve the homoscedasticity of residuals (Zuur et al., 2007). Also, predictors were standardized (scaled to the z-score) to ensure variables were at the same scale. We tested for overdispersion with Pearson residuals in all global models and used Negative Binomial GLM to correct it whenever needed. We performed model validation by visual inspection of model residuals following Zuur et al. (2009).

Community Metrics and Habitat Quality

We evaluated the effects of habitat quality in community metrics following the same protocol described above using GLM. However, we first performed a principal component analysis (PCA) to reduce the data dimensionality of forest structure variables (Borcard et al., 2011). We used scores from PC1 and PC2 (summarizing > 50% of variable variation between sampling sites) as predictors in GLM models. Before running the PCA, we checked for multicollinearity between habitat variables, excluded those with Pearson correlations > 0.5, and scaled variables to the z-score.

Species Composition, Landscape Structure, and Habitat Quality

To evaluate whether changes in species composition were explained by the gradients of fragmentation and habitat loss, as well as by habitat quality, we applied a redundancy analysis (RDA) using the *vegan* package (Oksanen et al., 2019). We used a species abundance matrix with Hellinger transformation (Borcard et al., 2011) as the response variable, while patch size, patch isolation, proportion of habitat amount in the landscape, and PC1 and PC2 were input as scaled predictors. Moreover, global significance of the RDA model, significance of RDA axes, and significance of model terms (predictors) were tested with permutation tests based on 1000 randomizations (Borcard et al., 2011). Before running the model, we tested for spatial autocorrelation between species composition and geographic coordinates with Mantel correlograms based on 999 randomizations.

All analyses were conducted in R version 3.6.2 (R Core Team, 2019).

RESULTS

With a capture success of 4.56%, we registered 1323 individuals, recaptured 735 times. Captures belonged to 15 species, five marsupial and 11 rodent species (**Supplementary Table 1**). The most abundant species in the study were the marsupials *Gracilinanus agilis* (*n* = 840 individuals, 63% of total captures) and *Didelphis albiventris* (*n* = 134, 10%), followed by the rodents *Oecomys cleberi* (*n* = 121, 9.1%), and *Rhipidomys macrurus* (*n* = 70, 5.2%) (**Supplementary Table 1**). The rarest species were the exotic european rodent *Rattus rattus* (*n* = 1) and *Oligoryzomys nigripes* (*n* = 1).

Regression models were not overdispersed, and most of them presented no spatial autocorrelation according to Moran's I test (**Supplementary Table 3**). However, whenever we detected spatial autocorrelation in model residuals, we did a visual inspection of residual dispersion (Zuur et al., 2009), associated with the visualization of bubble plots of the model's Pearson residuals and site coordinates. This led us to conclude that correlations were not linked directly to the spatial variation of the measured variables themselves, since there was no clear spatial pattern detected, overall small correlation values, and only a few sites presenting higher values. Correlations were thus considered second order correlations (stochastic or purely random) (Borcard et al., 2011). Therefore, we did not consider them important enough to compromise the global model, so we proceeded with the analyses.

Community Metrics and the Effects of Fragmentation and Habitat Loss

Regarding habitat generalist abundance, we found a negative effect of patch area ($\beta_{\text{log(patch area)}} = -0.44 \pm 0.09$; df = 33; $p = 1.022 \times 10^{-5}$, **Figure 2A** and **Supplementary Table 4**) and a slighter significant negative effect of habitat amount in the landscape ($\beta_{\text{landscape}} = -0.24 \pm 0.09$; df = 33; $p = 0.019$, **Figure 2B** and **Supplementary Table 4**). In other words, generalist species were more abundant in smaller patches and in landscapes with lower proportion of habitat amount. Concerning the abundance of forest specialists, GLM revealed only a negative effect of patch area irrespective of landscape habitat amount ($\beta_{\text{log(patch area)}} = -0.47 \pm 0.19$; df = 34; $p = 0.007$, **Figure 2C** and **Supplementary Table 4**).

In relation to estimated species richness, we found a positive effect of landscape habitat amount for habitat generalists, indicating more conserved landscapes presented more species regardless of patch size ($\beta_{\text{landscape}} = -0.047 \pm 0.02$; df = 34; $p = 0.043$, **Figure 2D** and **Supplementary Table 4**). For forest specialists, we failed to detect any effect of landscape structure in estimated species richness (**Supplementary Table 4**).

Moreover, regression models indicated that variations in species diversity or in functional diversity were not explained by landscape structure (**Supplementary Table 4**).

Community Metrics and Habitat Quality

Raw variables describing habitat quality are shown in **Supplementary Table 1**. Considering forest structure, here used as habitat quality features, the only variable excluded from the dataset used in the PCA analyses due to multicollinearity was cattle intrusion level, since it was highly correlated with understory clutter ($r = -0.75$). We compared the explanatory power of the PCA axes with and without the variable cattle

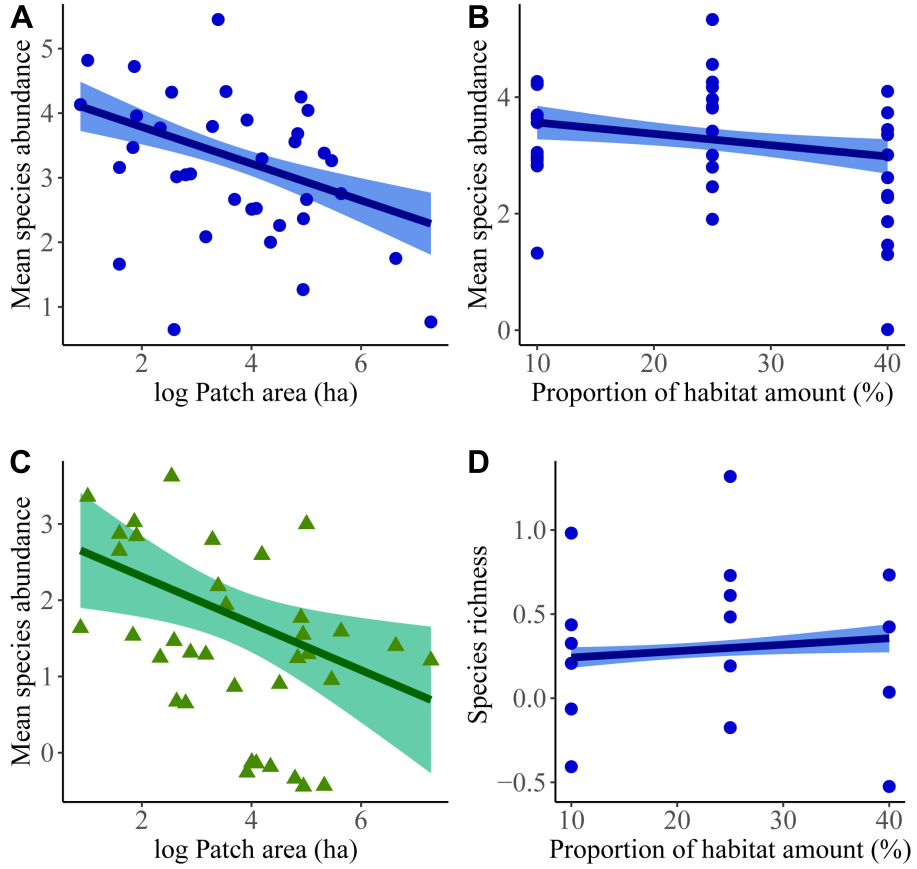

FIGURE 2 | Final regression models revealing the effects of landscape structure on small mammal community metrics in semideciduous forest patches in the Brazilian Cerrado, including: patch area **(A)** and proportion of habitat amount in the landscape **(B)** for the abundance of habitat generalists; the effect of patch area **(C)** for forest specialists, and the effect of proportion of habitat amount in the landscape **(D)** for generalist estimated species richness (Chao 1). Habitat generalists are represented in blue, forest specialists are shown in green.

intrusion, and concluded that excluding it improved explanatory power. The first component of PCA (PC1) explained 29.55% of data variation, while the second (PC2) explained 23.45%. PC1 was more related to basal area and tree height (loading values ≥ 0.5), while PC2 was more related with canopy cover (**Supplementary Figure 2** and **Supplementary Table 5**). Therefore, PC1 axis represented a gradient of sites with shorter trees with lower basal area toward patches with taller trees with larger diameters. On the other hand, PC2 denoted a gradient of more open forests to more closed-canopy forests (**Supplementary Figure 2**).

Among all community metrics evaluated (abundance of generalist and specialist species, estimated richness for generalist and specialist species, species diversity, and FD), we only detected an effect of habitat quality on the richness of forest specialists. The number of forest specialists was positively associated with PC2, indicating that patches with higher canopy cover harbored more specialist species ($\beta_{PC2} = 0.25 \pm 0.10$; df = 34; $p = 0.018$, **Figure 3** and **Supplementary Table 6**).

Species Composition, Landscape Structure, and Habitat Quality

We found no spatial autocorrelation between species composition and the sites' geographic coordinates. The RDA representing the relationship between species composition, landscape structure, and habitat quality explained 26% of the variation of species abundance across sites (*adjusted* $R^2 = 0.13$; $p = 0.001$). In total, the first two axis explained 84% of data variation (RDA1 explained 55%, and RDA2, 29%). However, only the RDA1 axis was significant ($p = 0.009$), and among the explanatory variables, only patch area ($p = 0.007$), patch isolation ($p = 0.018$), and landscape habitat amount ($p = 0.006$) were significant.

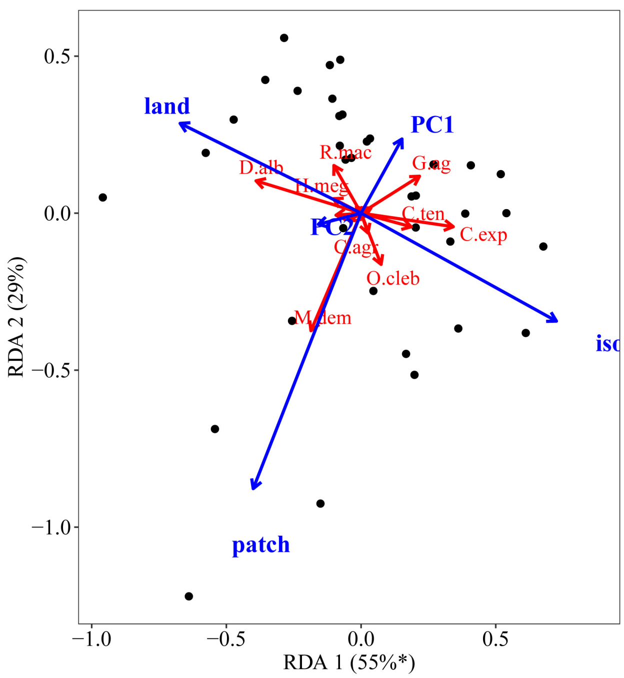

FIGURE 4 | RDA triplot (Scaling 2 method – correlation plot) showing the relationship between small mammal species composition, landscape structure [patch area (patch), patch isolation (iso), and proportion of habitat amount in the landscape (land)], and habitat quality (PC1 and PC2 corresponding to the first and second axis of a principal component analysis of six forest structure variables used to describe habitat quality) in semideciduous forest patches in the Brazilian Cerrado. Species are shown in red: *Calomys expulsus* (C.exp), *C. tener* (C.ten), *Cryptonanus agricolai* (C.agr), *Didelphis albiventris* (D.alb), *Gracilinanus agilis* (G.ag), *Hylaeamys megacephalus* (H.mega), *Marmosa demerarae* (M.dem), *O. cleberi* (O.cleb), and *Rhipidomys macrurus* (R.mac). Sampling sites are represented by black dots.

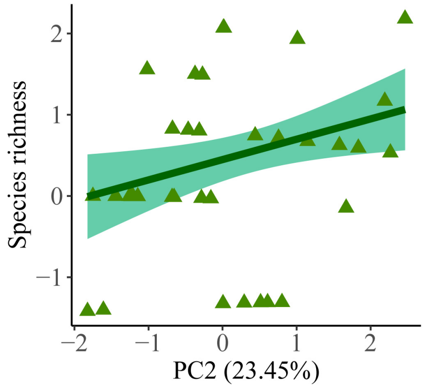

FIGURE 3 | Final regression model revealing the effect of habitat quality in small mammal estimated species richness (Chao 1) for forest specialists in semideciduous forest patches in the Brazilian Cerrado. PC2 corresponds to the second axis of a principal component analysis of six forest structure variables used to describe habitat quality.

Evaluating the RDA triplot (**Figure 4**) together with the significance of axes and predictors, we observed that both evaluated landscape structure variables (in RDA1, longer blue arrows with greater projections on this axis) were much more important to explain the variation in species composition of the sampling sites than habitat quality features. From negative to positive values of the RDA1 axis, a clear gradient of patch size, isolation and habitat amount emerged: from larger patches, inserted in landscapes with higher amounts of habitat, toward smaller and isolated patches located in more degraded landscapes. Additionally, we could also observe that there were species clearly correlated with these explanatory variables (indicated by longer red arrows with greater right-angled projections on the RDA1 axis): *Didelphis* was associated with higher amounts of forest cover in the landscape. The marsupial *M. demerarae* was highly related to larger patches, irrespective to forest cover in the landscape. On the other hand, *G. agilis* showed great association with smaller patches, independently of habitat amount. The generalist rodents *C. expulsus* and *C. tener* were highly associated with more deforested landscapes and with isolated patches, but not with patch size. *Oecomys cleberi* was also related with less habitat amount in the landscape. The other species were gathered together in the center of the plot, apparently not influenced by the evaluated predictors. The following species were omitted for obtaining a better visual aspect in the plot, since they displayed no correlation with evaluated predictors: *M. murina*, *Oecomys catherinae*, *Oligoryzomys mattogrossae*, *O. moojeni*, *O. nigripes*, and *Rattus rattus*.

DISCUSSION

Contrary to our expectations, we did not find any patch size effects depending on landscape habitat amount on abundance, richness, or taxonomic and functional diversity, regardless of the level of habitat specificity. However, habitat generalists and forest specialists responded differently to the isolated effects of patch size and habitat amount, and only specialist richness was affected by habitat quality. Furthermore, small mammal diversity metrics did not respond to either landscape structure or habitat quality.

Contradicting our hypothesis, the abundance of habitat generalists and forest specialists responded negatively to patch size, indicating that smaller patches held higher overall small mammal abundance. However, only generalists responded to the proportion of habitat amount in the landscape, being more abundant in more deforested landscapes, according to the findings of Pardini et al. (2010) for generalists in the Atlantic Forest. For habitat generalists, this pattern was also found by Melo (2015) in woodland savannas in the Cerrado. As for the abundance of forest specialists, she only found a negative effect of patch size in intermediate landscapes (30% of habitat amount), while specialists were more abundant according to higher forest cover in the landscape. In the Amazon, an increase of small mammal abundance with the reduction of forest area was also registered (Palmeirim et al., 2020).

The overall increase in species abundances (for generalists and forest specialists), which we found in smaller patches, might be linked to several ecological processes. First, to some extent, we believe that an ecological release from predators such as medium-sized mammals, raptors, owls and snakes, might be taking place. These are important predators of small mammals, and can suffer negatively with fragmentation and habitat loss (Carrete et al., 2009; Fenker et al., 2014; Rocha et al., 2018). Additionally, there might be a competition release effect due to the defaunation of large seed-predator mammals (Dirzo et al., 2014; Galetti et al., 2015a). It has been observed that defaunated forests showed an increase in the abundance of small seed-predators, specially rodents (Galetti et al., 2015b). Moreover, but to a lesser extent, forest invasion by matrix-tolerant species (for example, belonging to the genus *Calomys*) can contribute to the observed increase in abundance of habitat generalists in smaller fragments and in more eroded landscapes, which is probably linked to higher edge effects (Pardini, 2004; Santos-Filho et al., 2008). Also, in our study, a major increase in abundance of habitat generalists, mainly in smaller patches, might be an effect of a higher abundance of the dominant species *Gracilinanus agilis,* which represented almost 64% of all captures.

Finding no patch size or isolation effects either for forest specialist or generalist species richness, but identifying an effect of habitat amount at the landscape scale (even though for generalist species only) suggests that landscape vegetation cover is a better predictor of species richness than patch size and patch isolation. This landscape effect was proposed by Fahrig (2013) in the Habitat Amount Hypothesis, later tested and confirmed by Melo et al. (2017) for overall small mammal richness in woodland savannas in the Brazilian Cerrado, as well as for other animal groups (Garmendia et al., 2013; Ikin et al., 2014; Arroyo-Rodríguez et al., 2016). Landscape-scale responses might vary among ecosystems, with the level of habitat specificity of the studied species (Pardini et al., 2010; Melo, 2015), with the quality of the matrix habitat, an important feature of landscape-mediated processes, which can severely impact animal movements across the landscape, and influence colonization/extinction rates among patches (Palmeirim et al., 2020).

In fragmented landscapes, higher amounts of habitat should reduce overall patch isolation (Pardini et al., 2010), increasing inter-patch connectivity, and favoring movements of certain species between patches (Vieira et al., 2009). In this context, matrix type and finer-scale matrix elements such as scattered trees should play an important role in determining which species can succeed in moving through the matrix between patches (Prevedello and Vieira, 2010; Garmendia et al., 2013; Muanis, 2017). Structurally simplified matrices, such as the dominant pasture matrix in our study, might be more impermeable for forest specialists than for habitat generalists, since matrix type effects depend on species-specific habitat requirements, and matrix quality is linked to patch structure similarity (Prevedello and Vieira, 2010; Arroyo-Rodríguez et al., 2016). In this sense, our findings on the relationship between generalist species richness and habitat amount should be expected. Moreover, the lack of an effect of habitat amount for specialists, contrary to the findings from other studies (Pardini et al., 2010; Melo, 2015), also indicates that in our study system there might be more important factors influencing species richness than spatial structure; or there might be other non-evaluated landscape predictors of biodiversity such as landscape heterogeneity. In highly fragmented savanna landscapes immersed in agricultural mosaics, landscape heterogeneity was a better preditor of taxonomic diversity than habitat amount for non-breeding birds (Ke et al., 2018).

In altered landscapes, habitat conditions inside patches (i.e., patch quality) might be equally or more important than spatial structure of the landscape to determine assemblages (Ikin et al., 2014; Delciellos et al., 2016; Zimbres et al., 2017; Palmeirim et al., 2020), since habitat quality features may be more closely related to the consequences of fragmentation on ecosystems (Ikin et al., 2014). This way, habitat degradation resulting from fragmentation can have a more important deleterious effect on species persistence in fragments, reducing species richness, mainly of forest specialists (Zimbres et al., 2017).

Indeed, in our study, habitat quality features predicted specialist species richness, indicating that forests with higher canopy cover harbored more species. A more closed canopy cover suggests higher levels of forest integrity, or more structured forests. Fragmentation leads to the mortality of large trees (as a consequence of increased desiccation at edges, associated with secondary causes such as more frequent fire events and logging activity), which can reduce canopy cover, the presence of emergent species, volume of trees, and consequently forest structural complexity (Laurence et al., 2000). Structural complexity offers more opportunities for species coexistence, leading to vertical niche stratification of small mammals, increasing species turnover among forest strata, and consequently enhancing richness (Camargo et al., 2018). Our findings reinforce the relative importance of patch forest quality compared to spatial structure for maintaining specialist species, which require more complex forests to persist in a fragmented landscape.

We failed to detect any effects of landscape structure or habitat quality on taxonomic or functional diversity. Responses of animal diversity to landscape structure are rather idiosyncratic: several studies identified positive patch size effects for small mammal taxonomic (Melo, 2015; Bovendorp et al., 2019) and functional diversity (Melo, 2015; Zimbres et al., 2017; Bovendorp et al., 2019), while others failed to find these effects on the same diversity dimensions (Palmeirim et al., 2020; Sancha et al., 2020; Smith et al., 2020). In much the same way, forest cover (i.e., habitat amount in the landscape) did not affect functional diversity of Atlantic forest small mammals (Sancha et al., 2020), while being an important predictor for forest-dependent frog species in the same biome (Almeida-Gomes et al., 2019). Bovendorp et al. (2019) suggested that, besides species-area effects, ecological interactions of predation or competition represented by the occurrence of medium and large-sized mammals should contribute to the retention of species and functional diversity of small mammal communities in the Atlantic Forest. On the other hand, small mammal functional diversity might be better predicted by non-evaluated landscape metrics more adequate for the spatial scale of response of small vertebrates, such as landscape heterogeneity. Conversely, temperature variables, rather than landscape structure, may determine functional diversity for small vertebrates (Sancha et al., 2020).

Finally, small mammal species composition has been strongly influenced by fragmentation and habitat loss, leading to marked species turnover with the reduction of specialist species and increased dominance of generalist species (Vieira et al., 2009; Pardini et al., 2010; Banks-leite et al., 2012; Garmendia et al., 2013; Melo, 2015; Palmeirim et al., 2020). Habitat quality inside patches related to landscape alterations have also been indicated as important predictors of change in species composition (Melo, 2015; Delciellos et al., 2016; Hannibal et al., 2018, 2020). However, our results showed that landscape structure variables (patch size, isolation, and proportion of habitat amount in the landscape) were the major drivers of changes in small mammal species composition relative to habitat quality features in semideciduous forests in the Brazilian savanna.

Surprisingly, *Didelphis albiventris* was the only species associated with higher amounts of forest cover in the landscape. Even though the genus *Didelphis* is considered a habitat generalist, apparently it also depends on higher forest cover at the patch (Santos-Filho et al., 2008) or landscape scale. In addition, *D. marsupialis* showed declining occupancy probability in more degraded forests in the Amazon Forest (Zimbres, 2016). These results suggest that even common and generalist species might have minimum habitat requirements to persist in human-modified landscapes.

Marmosa demerarae, one of the rarest species in our study, on the other hand, was related to large patches, irrespective of the surrounding proportion of habitat amount. In the Atlantic Forest it was associated with forest edges and to a secondary forest matrix (Pardini, 2004), and reproductive males were able to travel among patches across a matrix composed by tall grasses, shrubs, and scattered trees (Pires et al., 2002). On the other hand, Santos-Filho et al. (2008) registered high abundance of this species in the interior of forest patches, while it was never captured in the pasture matrix. Matrix use is thus apparently highly dependent on matrix quality, which explain these variations in abundance and responses to edge effects and matrix permeability found in other studies. Our results indicated that *M. demerarae* is a sensitive species to fragmentation in the Brazilian Cerrado, and this sensitiveness might be affected by the quality of the surrounding matrix.

Conversely, *G.agilis*, the dominant species in our study, was strongly associated with smaller patches, independently of landscape vegetation cover. This abundant and generalist species has been indicated to be less susceptible to habitat fragmentation, not suffering from edge effects (Santos-Filho et al., 2008), and responding negatively to patch size (Cáceres et al., 2010). Also, it has been positively associated with the number of lianas, a proxy for forest disturbance (Campbell et al., 2015; Hannibal et al., 2018).

The rodents *C. expulsus* and *C. tener* were more associated with deforested landscapes and patch isolation, but were not influenced by patch size. In the Cerrado, the genus *Calomys* include common inhabitants of open areas such as grasslands and savannas (Marinho-Filho et al., 2002). However, they can also be equally present in forest edges and inside forest patches in fragmented landscapes, as well as in the pasture matrix (Santos-Filho et al., 2008). They have been positively associated with environmental disturbances such as fire (Vieira, 1999), and also with lower forest NDVI, indicating a relationship with lower levels of forest integrity (Hannibal et al., 2018).

Lastly, *Oecomys cleberi* was negatively associated to forest cover in the landscape. Thus, this species might be sensitive to small patches but may tolerate some level of forest disturbance at larger scales. In fact, *Oecomys* genus apparently is less affected by edge effects (Santos-Filho et al., 2008), but still not be able to use pasture matrix, which might represent a barrier to dispersal. The genus apparently includes species that are dependent on resources available inside resident patches. Additionally, the congener *O. bicolor* was positively related to canopy cover and to NDVI (Hannibal et al., 2018) in semideciduous forests in the Cerrado, indicating demands for better conditions of forest structure, which is usually not the case for smaller patches (Laurence et al., 2000).

The above mentioned results suggest that species responses to landscape changes may not only be necessarily guild-specific or associated to the degree of habitat specialization of the taxa, but be species-specific, being mediated by other ecological and behavioral traits (Caruso et al., 2016; Heim et al., 2019) related to reproduction, life-cycle, body size and dispersal hability (Blanchet et al., 2010; Farneda et al., 2015; Lecoq et al., 2021).

Contradicting our expectations, the results of this work indicated that the effect of landscape configuration did not depend on the proportion of habitat amount in the landscape to determine small mammal assemblages, as found in other studies in the Brazilian Cerrado (Melo, 2015) and in the Atlantic Forest (Pardini et al., 2010). However, both landscape structure characteristics analyzed impacted different aspects of assemblages and in distinct ways. Reduction in patch size was mainly linked to an overall increase in small mammal abundance, while habitat generalist species richness was determined by habitat amount in the landscape. This result reinforces that habitat amount should be a better predictor of species richness than patch size, as proposed by Fahrig (2013) and confirmed to taxa such as small mammals (Melo et al., 2017) and birds (De Camargo et al., 2018). On the other hand, specialist richness was only influenced by forest quality inside patches, suggesting that species with higher habitat requirements might respond to fragmentation and habitat loss at finer scales. In this sense, our study demonstrated the importance to address habitat quality changes in landscape research (Delciellos et al., 2016), in order to better understand the consequences of fragmentation and habitat loss in ecosystems, which will depend on the species in question and their habitat requirements. Lastly, we failed to detect any effect of either landscape structure or habitat quality on the other diversity dimensions.

In the face of current high rates of deforestation and conversion of natural landscapes into croplands and pastures in the Brazilian Cerrado (Alencar et al., 2020), associated with low levels of compliance with environmental legislation (Fearnside, 2001; Strassburg et al., 2017), it is essential to generate guidelines and more effective policies for conservation and restoration plans focused on landscape remnants in the world's richest savanna (Faleiro et al., 2013). In this context, our study showed that landscapes with higher vegetation cover should be more effective for protecting habitat generalist species, while preserving the integrity of remnants should benefit forest specialists. Therefore, we suggest that landscape management actions prioritize setting aside and/or restoring existing legal reserves in a way that maximizes forest cover at the landscape scale. This should be planned and executed by coordinating efforts among landholders, as also suggested by Zimbres et al. (2017). Additionally, we reinforce that conserving biodiversity requires the restoration and maintenance of habitat quality of forest remnants, which has been neglected by current environmental policies. Among the management actions that should contribute to more structurally sound forests within reserves are: avoiding cattle intrusion, protecting remnants from wildfires, and avoiding selective logging (Gerwing, 2002; Vieira and Scariot, 2006; Piana and Marsden, 2014).

Furthermore, we propose that future studies should investigate the impacts of shifting species interactions (predators and competitors) on the community dynamics, since defaunation is apparently a strong driver of change in abundance and diversity of small mammals in altered landscapes (Galetti et al., 2015b; Bovendorp et al., 2019), which in turn has profound consequences in ecosystems (Dirzo et al., 2014; Soares et al., 2015; Marjakangas et al., 2020). We also suggest evaluating the effects of the matrix structure, quality, and landscape heterogeneity (Fahrig et al., 2011; Reynolds et al., 2017; Ke et al., 2018) in the studies seeking to better understand the dynamics of species and populations surviving in fragmented landscapes.

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

The animal study was reviewed and approved by Committee of Ethics and Animal Use from the Universidade de Brasília (18/2018 CEUA-UnB).

AUTHOR CONTRIBUTIONS

IM conceived and designed the study, conducted data collection and data analysis, and drafted the manuscript. BZ contributed to the study design, performed spatial analysis, and contributed to the writing of the manuscript. JM-F contributed to the study design and supervised the work. All authors critically revised the manuscript.

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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.2021.751315/full#supplementary-material

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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 (α-diversity) but high species turnover (β-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

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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 (α-diversity, the number of species in a given site), and species turnover (β-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; Françoso 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 β-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 (Françoso 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 β-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 researches 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 Mendonça 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^2 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*"

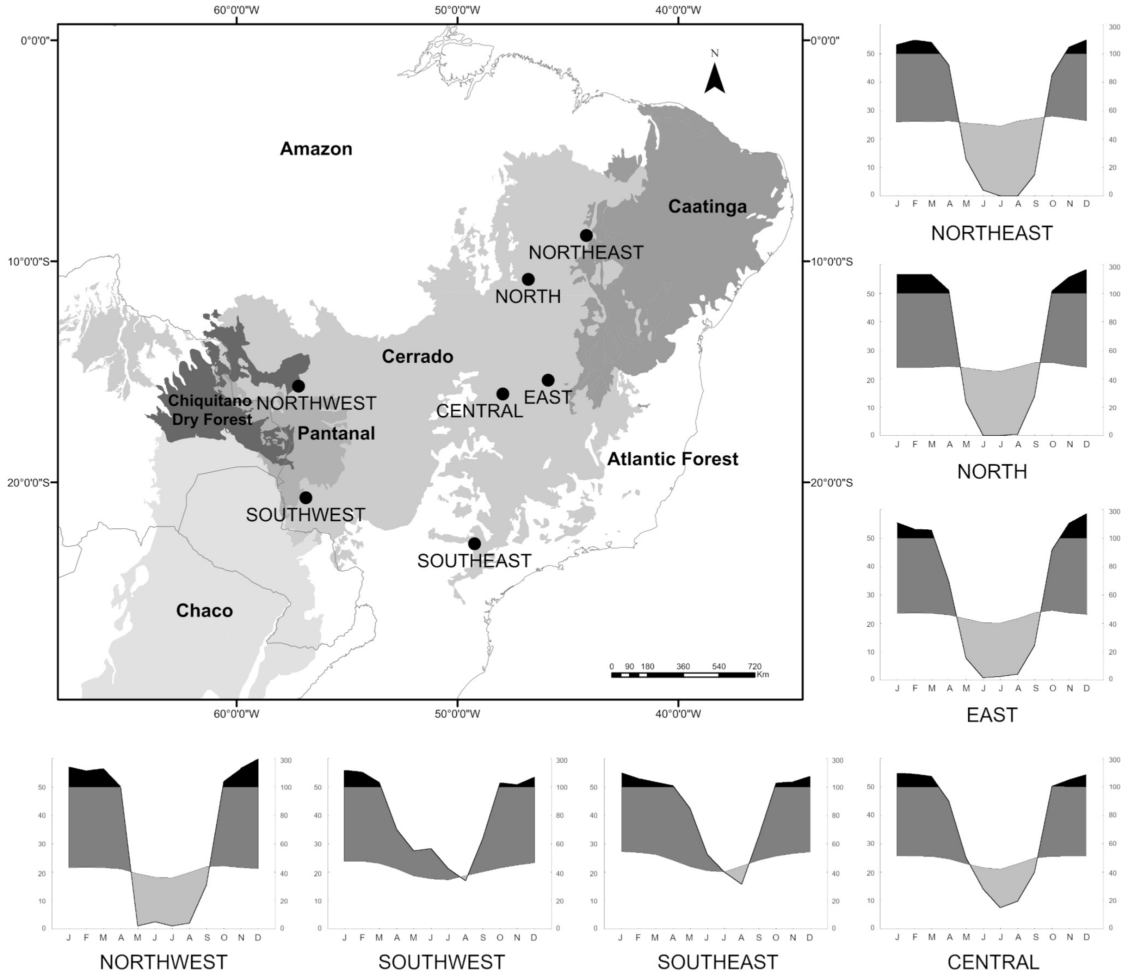
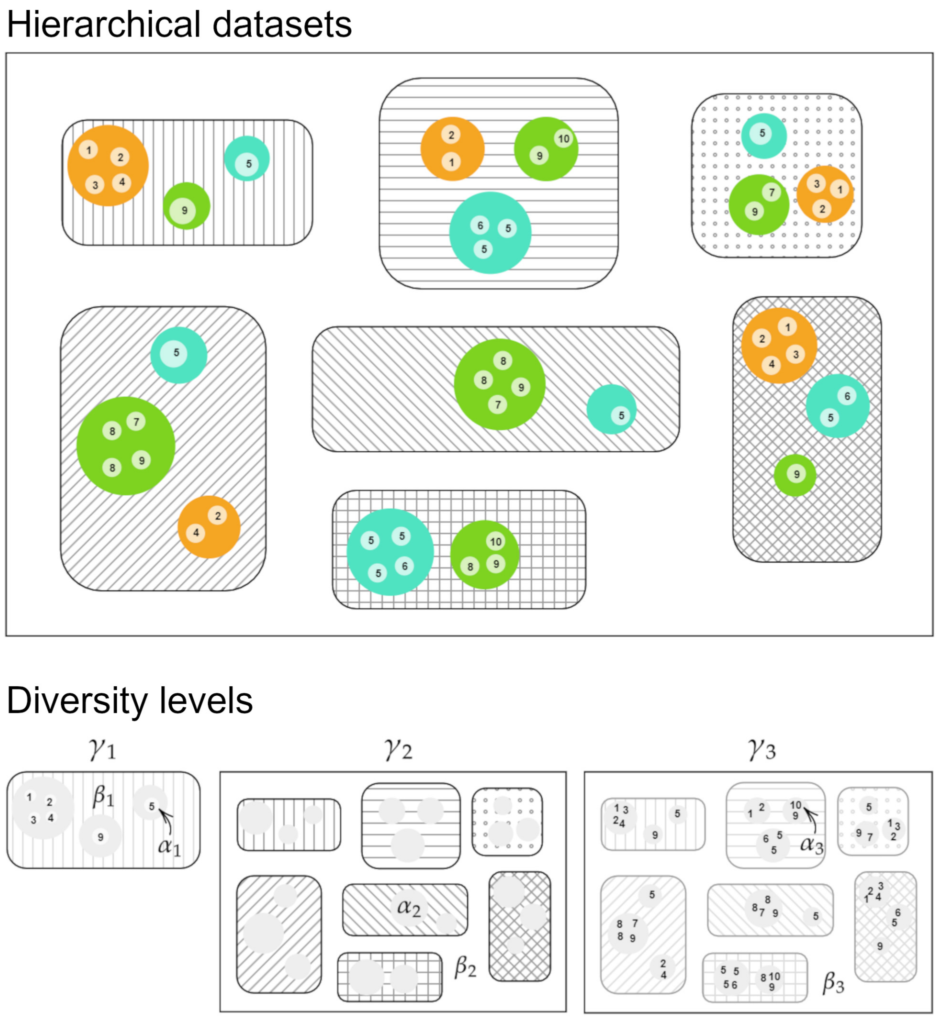


FIGURE 1 | The seven localities surveyed across the Cerrado biome. Limits of the Cerrado and neighboring biomes in gray tones based on the ecoregion approach of Dinerstein et al. (2017). Climatic diagrams showing variations in annual temperature (left vertical axis) and rainfall regime (right vertical axis) within each locality surveyed in the Cerrado. In black, periods of rainfall above 100 mm; in dark gray, periods of rainfall above the temperature line, both periods usually associated with the rainy season; in light gray, periods of water deficiency, associated with the dry season. 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 2 | The three main habitat types surveyed within the Cerrado. Grassland [left, "campo sujo (CS)" at the Santa Bárbara Ecological Station], Savanna [center, "cerrado *sensu stricto* (CE)" at the Santa Bárbara Ecological Station], and Forest [right, "cerradão (CD)" at the Santa Bárbara Ecological Station].

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


Hierarchical datasets

Diversity levels

FIGURE 3 | A schematic figure showing the hierarchical datasets: sites (45 points), habitats (10 numbers), habitat types (3 circles), and localities (7 squares) and their relationship with each diversity level analyzed in this study, where α_1; α_3 = mean species richness at sites, β_1 = species richness across sites at localities, γ_1; α_2 = mean species richness at localities, β_2 = species richness across localities; β_3 = species richness across sites at the entire sample, γ_2; γ_3 = species richness of the entire sample.

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 α-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 β-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, SF, 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: γ-diversity = α-diversity + β-diversity (Loreau and Hector, 2001; Veech et al., 2002; Chao et al., 2012) to investigate the contribution of species richness (α-diversity) and species turnover (β-diversity) across scales, i.e., within and across sites, habitats, and localities. α-diversity (α_1) was treated as the mean observed and extrapolated number of species recorded in each site, β-diversity (β_1) as the species richness found across sites (or habitats), and γ-diversity (γ_1) as the mean number of species in a given locality. α-diversity (α_2) was treated as the mean observed and extrapolated number of species recorded in each locality ($\alpha_2 = \gamma_1$), β-diversity (β_2) as the species richness found across localities, with γ-diversity (γ_2) as the observed and estimated number of species found in the entire sample. α-diversity (α_3) was also treated as the mean observed and extrapolated number of species recorded in each site ($\alpha_3 = \alpha_1$), β-diversity (β_3) as the number of species recorded across all sites (or habitats) encompassing all localities, with γ-diversity (γ_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 β-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 − 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 ± SD = 5.44 ± 2.56, **Table 1**), with the estimated richness ranging from 2.00 to 15.71 (mean ± SD = 7.28 ± 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 ± SD = 17.60 ± 12.81), with sampling coverage varying accordingly, from 0.00 to 1.00 (mean ± SD = 0.82 ± 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 ± 1.00 (in the areas of "CC") to 6.67 ± 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 ± SD = 4.53 ± 2.07 for grasslands; mean ± SD = 5.69 ± 3.01, for savannas; and mean ± SD = 6.06 ± 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 ± SD = 27.73 ± 6.31) and savannas (mean ± SD = 30.48 ± 5.79), with forests showing a somewhat higher richness (mean ± SD = 39.69 ± 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 (*Necromys 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 ± SD = 16.00 ± 3.56), with the estimated richness ranging from 13.50 to 23.92 species (mean ± SD = 18.19 ± 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.

		Locality									
		CENTRAL	**EAST**	**SOUTHEAST**	**NORTHWEST**	**SOUTHWEST**	**NORTH**	**NORTHEAST**	**Habitat**	**Habitat type**	**Total**
	Site	**SC - N - SR**	**SC - N - SR**	**SC - N – SR**	**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 *sensu stricto* (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 *sensu stricto* (CE)		1.00 - 14 - 3					0.93 - 24 - 10			
	Cerrado *sensu stricto* (CE)							0.95 - 40 - 11			
	Rocky Cerrado (RC)						0.91 - 11 - 2		0.88 - 32 - 10		
	Carrasco (CAR)		0.80 - 15 - 5					1.00 - 6 - 3			
Forests	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.

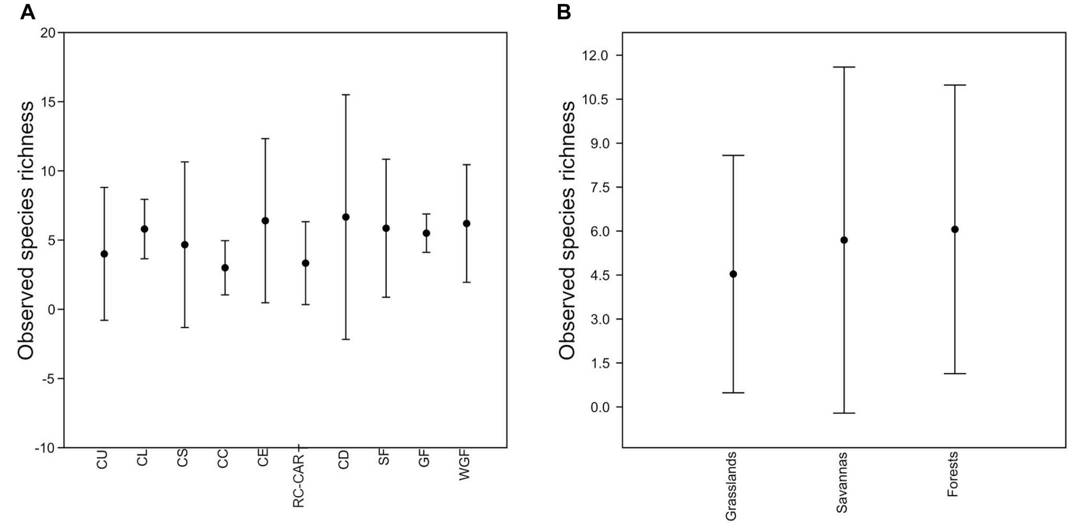


FIGURE 4 | Mean observed species richness across the different habitats **(A)** and the three main habitat types **(B)** based on the 45 sites surveyed within the Cerrado. Point = mean, lines = SD, CU = "campo úmido," CL = "campo limpo," CS = "campo sujo," CC = "campo cerrado," CE = "cerrado *sensu stricto,*"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

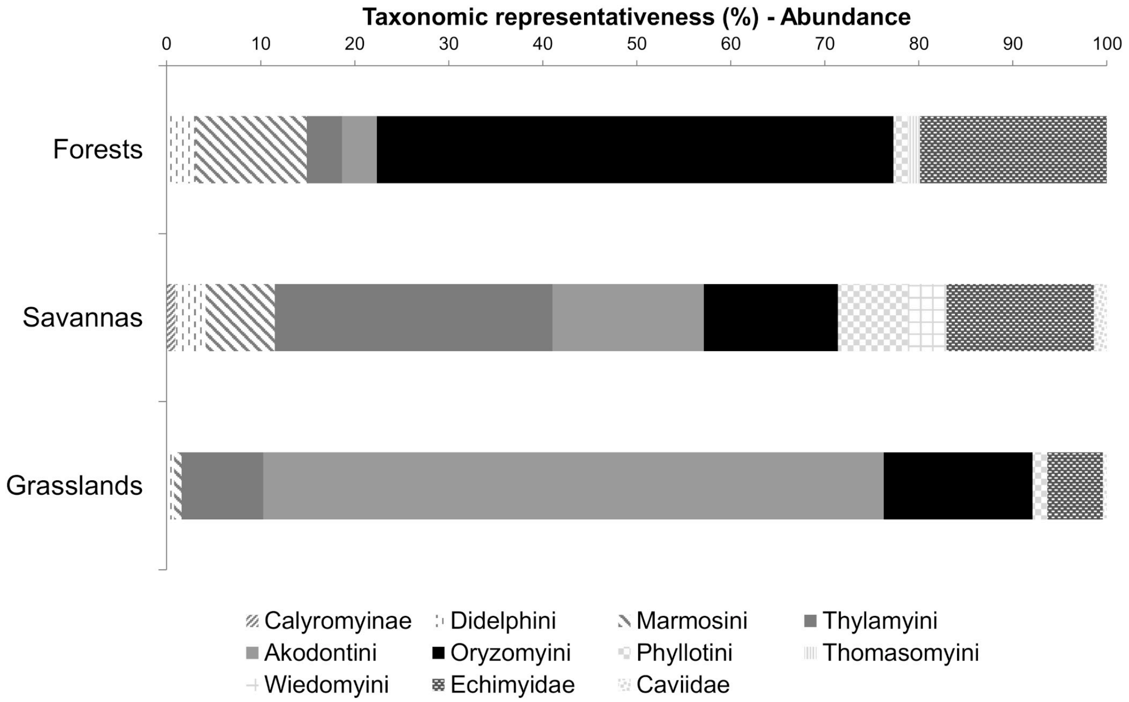


FIGURE 5 | Percentage of taxonomic groups based on the number of individuals surveyed at the three main habitat types across the 45 sites in the Cerrado.

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

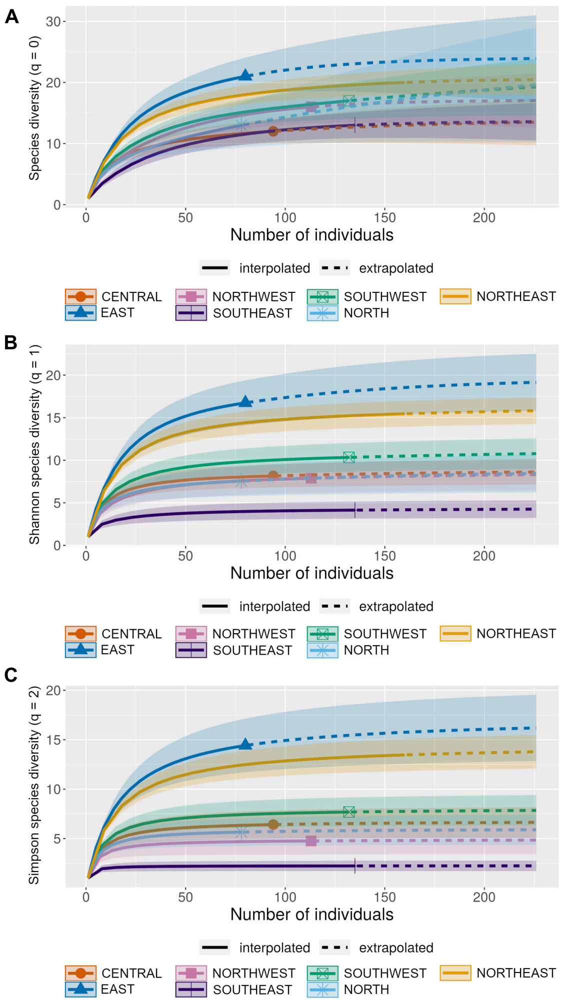


FIGURE 6 | Rarefaction and extrapolation curves based on abundance data for each locality surveyed in the Cerrado. The sample-based curves were generated on the online iNEXT platform (Hsieh et al., 2016). **(A)** Observed species richness (*q* = 0), **(B)** observed Shannon index (*q* = 1), and **(C)** observed Simpson index (*q* = 2). 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.

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 α- and β-Diversity Across Scales

Observed and estimated mean α_1-diversity (at sites; varying from 2 to 11 species) represented a small portion (34–40%) of γ_1-diversity (at localities; varying from 12 to 21 species), with β_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 β_2-diversity (72.4–70.9%—species turnover across localities) and β_3-diversity (90.6–88.4%—species turnover across habitats and localities, all sites) was even greater compared to α_2-diversity (27.6–29.1%—species richness per locality) and α_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 (β_2; **Supplementary Figure 5**), which

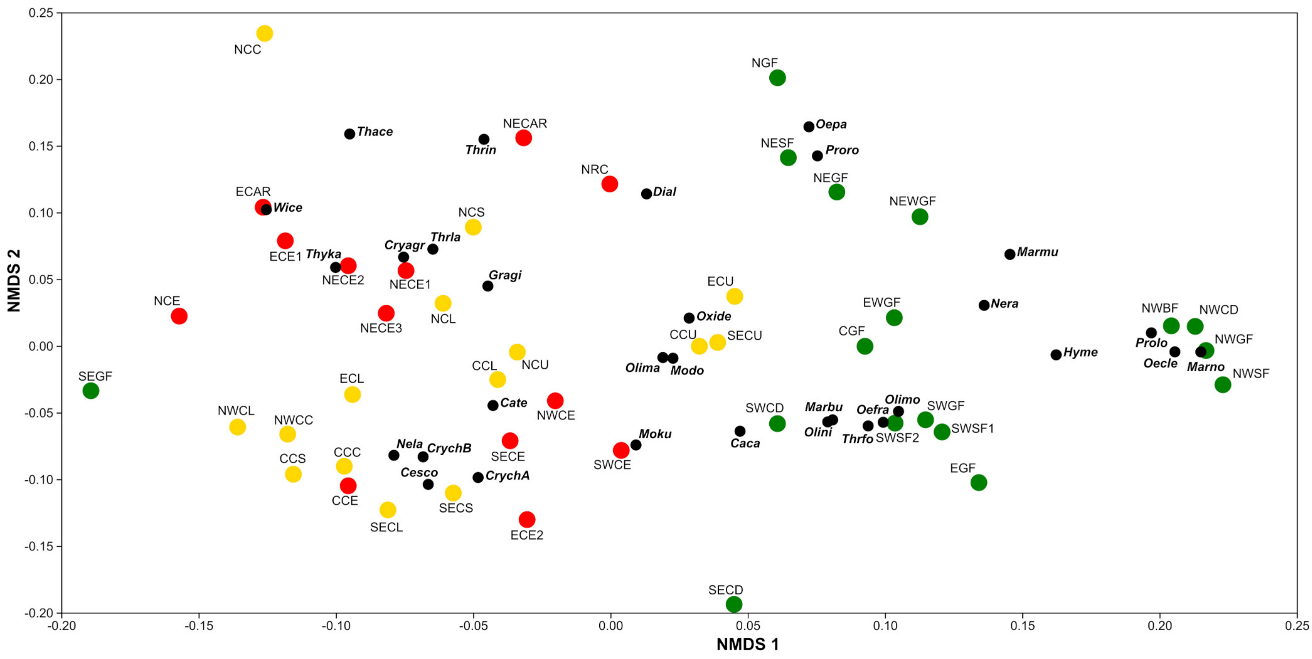


FIGURE 7 | A non-metric multidimensional scaling (NMDS) ordination plot based on a Bray–Curtis similarity matrix, considering the capture success of species with at least five captures across the 45 sites surveyed in the Cerrado. Sites in color, with forests represented by green circles, savannas by 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*, Marmu = *Marmosa murina*, Marno = *Marmosops noctivagus*, Modo = *Monodelphis domestica*, Moku = *Monodelphis kunsi*, Nela = *Necromys lasiurus*, Nera = *Nectomys rattus*, Oecle = *Oecomys cleberi*, Oefra = *Oecomys franciscorum*, Oepa = *Oecomys paricola*, Olima = *Oligoryzomys mattogrossae*, 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 mattogrossae* 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 kunsi*, 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, α-diversity at sites (α_1) has been properly accessed 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 megacephalus*, 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. kunsi*, 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 α- and β-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 α-diversity at sites ($\alpha_1 = 40\%$; $\alpha_3 = 10\%$) and at localities ($\alpha_2 = 30\%$), β-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 β-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 β-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; Françoso 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 ∼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 β-diversity, which is proving to be typical of the biome (Nogueira et al., 2011; Valdujo et al., 2013; Françoso et al., 2020; Ribeiro et al., 2020). In fact, 113 native small mammals were recorded along the 446 sites in the review of Mendonça 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; Françoso et al., 2016, 2020; Amaral et al., 2017), stressing the importance of β-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; Mendonça 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 β-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 β-diversity found across localities, as previously widely distributed taxa are currently represented by distinct restricted-range species [e.g., former concepts of *Oligoryzomys fornesi* (Weksler 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.

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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Differential Responses of Small Mammals to Woody Encroachment in a Semi-Arid Grassland

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Encroachment by woody invasive plants is a major threat to grasslands and savannah ecosystems worldwide. Rodents, being primary consumers, are likely to be the first to respond to changes in the structure and composition of native vegetation. We examined the effect of an invasive shrub *Prosopis juliflora* (hereafter Prosopis) on the native rodent community of an arid grassland system of Western India. Our sampling plots were divided into five categories representing different stages of Prosopis invasion and other land cover types. These consisted of restored native grassland, agriculture fallow, open brushland, sparse-Prosopis plots, and Prosopis-dominated plots. We also examined the impact of woody invasion on the response of native rodents toward moonlight and temperature. As hypothesized, we found a significantly higher abundance of rodent species in the native grassland habitat compared to sparse-Prosopis habitats. However, there was no significant difference in rodent abundance and diversity between the grassland and Prosopis-dominated habitats. Thus, species richness and abundance of rodents were the highest in the restored grasslands and dense Prosopis thickets, and the lowest in the sparse Prosopis, potentially showing a "U" shaped response to Prosopis invasion. We observed a species-specific effect of Prosopis on the activity of *Tatera indica, Bandicota bengalensis*, and *Millardia meltada*. Habitat type mediated the effect of different environmental factors (moonlight and temperature) on the activity of the most commonly ocurring species *T. indica* while activity of *M. meltada* showed a weak association with environmental factors. *B. bengalensis* was the most generalist species showing similar activity across all habitat types. Thus, the impact of Prosopis invasion on the rodent community was uneven, and depended on species as well as on local environmental characteristics.

Keywords: woody encroachment, dry grassland, savanna ecosystem, rodents, *Prosopis juliflora*

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INTRODUCTION

Dry grasslands and savannah ecosystems across the world have been negatively affected due to the rapid expansion of woody invasive species (White et al., 2000; Ratajczak et al., 2012; Murphy et al., 2014; Stevens et al., 2016). An increase in woody cover in these landscapes has been attributed to a range of environmental and anthropogenic factors such as fire suppression, change in herbivore community, and an increase in atmospheric temperature and CO_2. Deliberate introduction of non-native species by humans remains a leading cause of the increase in woody cover in many parts of the world (Archer et al., 2001; Popp et al., 2007; Auken, 2009; Ratajczak et al., 2012). Introduced species often spread out of control and can have large-scale impacts on native ecological communities. Once established in a new ecosystem, such species alter the composition of the native vegetation community either by outcompeting native plants in resource acquisition (Dyderski and Jagodziński, 2019) or by secreting toxic metabolites in the soil which inhibit the growth of native vegetation under their cover (Kaur et al., 2012). Examples of such successful invasion and establishment include *Rhododendron ponticum* in northern Europe (Tyler et al., 2006), *Prosopis glandulosa* in South Africa (Wild, 2018), and *Lantana camara* and *P. juliflora* in India (Kaur et al., 2012; Sundaram and Hiremath, 2012).

Invasion driven changes in species composition and the structure of native vegetation communities can affect native fauna through direct or indirect pathways (Stanton et al., 2018). While changes in plant species composition can alter food availability, the structural complexity of vegetation defines the perceived predation risk in the landscape (Prugh and Golden, 2014). For example, non-palatable invasive species can alter the availability of food resources for herbivores and other primary consumers (Mogashoa et al., 2020; Nerlekar et al., 2021). Bush encroachment can also either increase predation risk by providing enhanced cover for predators (Chen et al., 2021), or, decrease predation risk by providing escape cover for prey, particularly small mammals (Ceradini and Chalfoun, 2017; Jayadevan et al., 2018). As primary consumers, small mammals such as rodents are likely to be the first to respond to these changes in vegetation composition and structure. Open grassland habitats may be rich in food due to the high availability of palatable grasses and seeds but also riskier due to higher visibility for predators, compared to habitats with thick shrub cover. Therefore, rodents have to balance their use of open grasslands to take advantage of high food availability by adjusting their activity time to minimize their detection by predators (Guiden and Orrock, 2019), or select habitats with protective cover (Malo et al., 2013; Loggins et al., 2019a,b).

These impacts of bush encroachment do not apply to all species evenly and can vary with species within a guild (Kluever et al., 2019). For example, structural changes in sagebrush steppe due to invasive cheatgrass *Bromus tectorum* reduced the abundance and foraging efficiency of small mammals due to increased vegetation cover (Ostoja and Schupp, 2009; Bachen et al., 2018). On the other hand, invasive *Rhododendron ponticum* in southern England reduced predation risk for wood mice *Apodemus sylvaticus* thus increasing their abundance under its protective cover (Malo et al., 2013). Similarly, the abundance of deer mice *Peromyscus maniculatus* in the Great Basin Desert was negatively correlated with the intensity of cheatgrass cover. But in the same community, the abundance of Ord's kangaroo rat *Dipodomys ordii* initially increased with rising cheatgrass cover up to a threshold before it started to decline (Kluever et al., 2019). Thus, woody invasion can alter resource abundance for some species, but can also reduce predation risk for others, and this differential response can be seen even within the same ecosystem, depending on the species of rodents.

The presence of invasive woody species can also alter how small mammals respond to abiotic factors such as moonlight and temperature. In open habitats, rodent activity tends to be lower, since bright moonlight increases risk due to better visibility for predators (Kotler et al., 2010; Jayadevan et al., 2018). However, encroachment of invasive woody species in open habitats mediates the effect of moonlight on the activity pattern of nocturnal rodents by reducing light penetration and consequently lowering the risk of predation (Guiden and Orrock, 2019). Similarly, woody vegetation can also mediate the effect of temperature on the activity of rodents by altering the micro climatic condition under its cover. Woody encroached areas can provide a micro-climate up to 2°C warmer at night compared to open grassland habitats (He et al., 2010). The warmer climate has been associated with significantly higher activity of desert rodent community (O'Farrell, 1974) as lower night-time temperature imposes a higher thermoregulatory cost to desert rodent communities (Ghosh et al., 1979).

Finally, structural changes induced by bush encroachment can also mediate interspecies interactions between two competitive species and alter their activity and habitat use in a landscape. For example, increased woody canopy cover in North and Central Florida favors gray squirrels *Sciurus carolinensis* resulting in reduced fox squirrel *S. niger* occupancy in these areas due to interspecific competition (Sovie et al., 2020). The dominant species can replace sub-ordinate species from habitats with high resource availability thus changing their habitat selection (Brown and Munger, 1985). For example, the rodent *Dipodomys spectabilis* was found to dominate patches with high food availability, resulting in a reduction in the abundance of the smaller species *D. merriami* and *D. ordii.* The experimental removal of *D. spectabilis* from the patch released the smaller species from competition, thus increasing their abundance (Brown and Munger, 1985).

In this study, we aimed to understand the response of a rodent community to a change in vegetation structure due to the encroachment of a woody invasive species in a semi-arid grassland ecosystem. Introduction of the South American *P. juliflora* (hereafter Prosopis) has been a major driver of change in vegetation structure of the Banni landscape in western India, along with the recent expansion of area under agriculture. Previous studies have shown reduced growth and productivity of native grasses and other vegetation under Prosopis cover (Kaur et al., 2012; Nerlekar et al., 2021). A recent study in the landscape showed a high abundance of generalist rodents under dense Prosopis cover compared to sparse Prosopis cover (Jayadevan et al., 2018). However, the response of the native rodent community toward other natural and agricultural habitats as well as restored native grasslands in relation to Prosopis, as well as how Prosopis invasion can mediate the effect of moonlight and temperature on rodent activity, remain unknown.

These restored grasslands plots support significantly higher cover of palatable grasses compared to Prosopis patches (Nerlekar et al., 2021). These grass species are a major food source for the generalist rodent community in the landscape (Prakash and Singh, 2005; Jayadevan et al., 2018). Therefore, we hypothesized that rodent species diversity and abundance would be the highest in these restored patches of grasslands compared to Prosopis encroached areas. We expected that agricultural fields would also support high rodent abundance due to increased food availability in the form of agricultural produce but lower species richness as shown in previous studies (Fraschina et al., 2014; Mamba et al., 2019). We hypothesized that native brushland would support more specialist rodent species due to the unique nature of the arid and highly saline soil with halophytic vegetation. We assessed the activity of rodent species under these different habitat types, and their interaction with abiotic factors such as temperature, and moonlight. Finally, we hypothesized that in areas where multiple species co-occur, potential intraguild interaction could also affect the activity of these species.

MATERIALS AND METHODS

Study Area

The Banni grassland ecosystem is situated at the northern border of Kutch district in Gujarat, India (23° 19′ to 23° 52′ N latitude and 68° 56′ to 70° 32′ E longitude) encompassing an area of ∼ 2500 sq km. Climatically the region falls under the hot arid region of Western India with an annual average rainfall of ∼300 mm. The short rainy season lasts between June to September, resulting in seasonal flooding in low-lying areas.

The native vegetation of Banni is typically grass-dominated along with halophilic vegetation in high saline areas. Physiognomically this area is classified as a *Dichanthium-Cenchrus-Lasiurus* type of grassland (Dabadghao and Shankarnarayan, 1973). Complex social-ecological interactions have shaped the land cover type of the landscape. Prosopis was first introduced during the time of the erstwhile rulers of Kutch, the *Maharao,* in colonial India, but large-scale plantation occurred only in the early 1960s following the first national forest policy of independent India (Ramya Ravi *unpublished*). The introduction was aimed at reducing soil salinity and providing fuelwood and alternate livelihoods to local pastoralists. Owing to its fast growth and drought tolerance, the invasive shrub has converted large parts of the once open grasslands into dense woodland. Over time, the local communities have begun harvesting Prosopis to make charcoal and have also cleared patches of it for the cultivation of seasonal crops such as castor, cluster beans, and yellow mustard. Other natural vegetation consists of patches of saline open brushland of *Suaeda fruticosa* and salt-tolerant grasses such as *Aeluropus lagopoides* and *Urochondra* sp.

Indian gerbil (*Tatera indica*), soft furred field rat (*Millardia meltada*), sandy-colored metad (*M. gleadowi*), and Indian field mouse (*Mus booduga*) are some of the generalist rodent species reported from the landscape (Jayadevan et al., 2018). The major predators of rodents include several species of large owls, snakes, the Bengal monitor lizard (*Varanus bengalensis*), and mammalian mesopredators such as the golden jackal (*Canis aureus*), desert fox (*Vulpes vulpes pusilla*), Indian fox (*V. bengalensis*), jungle cat (*Felis chaus*), and desert cat (*Felis silvestris ornata*).

Sampling Design

We defined our sampling plots into five categories, each representative of different stages of Prosopis invasion and land cover types (**Figure 1**). These categories are (i) Grassland plots- native grassland plots maintained free of Prosopis for grazing and fodder after its mechanical removal by the local communities. Vegetation in these plots is mainly dominated by palatable grasses such as *Dichanthium annulatum* and *Eleusine compressa*. Many of these plots are around 40-years old, range in size from 0.54 hectares to 42 hectares and may be representative of native grassland vegetation before the Prosopis invasion. (ii) Prosopis-dominated plots – dense thickets of Prosopis (51–100% Prosopis cover) representing a high invasion of the shrub. (iii) Sparse Prosopis plots- areas with less than 50% cover mixed with native vegetation. These habitats are relatively more open compared to Prosopis dominated habitats. (iv) Agriculture fallow – these are open fallow agricultural land left after harvesting of crops such as castor, cluster beans, and yellow mustard and (v) Saline open brush – these open brushlands are dominated by *Suaeda fruticosa* and salt-tolerant grasses such as *Aeluropus lagopoides*, *Urochondra spp.* in saline areas. Percentage Prosopis cover for each 50 × 50 m plot was calculated from a classified sentinel-2 image with a spatial resolution of 10 m for both sampling years (2017–2018 and 2019–2020). The land cover classification was based on spectral properties of sentinel-2 bands using "SmileCart" classifier in Google Earth Engine. We overlaid our 50 × 50 m sampling grids on the classified image counted the number of Prosopis pixels to obtain the percentage Prosopis cover in each sampling site. The difference in mean Prosopis cover between Prosopis dominated and sparse Prosopis plots are shown in **Figure 1D**.

Our sampling schema consisted of a matched pair of a Prosopis thicket closest to a selected grassland enclosure (<250 m to 1 km), to control for changes in climatic, soil condition, elevation, and other anthropogenic factors (in 2017–2018 and 2019–2020). The minimum distance between the closest plots was well above the daily distance traveled (60.38 ± 09.3 m) by the most commonly found species of the rodent community; *T. indica* (Prakash and Singh, 2005). The sparse Prosopis plots were sampled in areas that are either recently invaded or where Prosopis is regenerating after a recent lopping cycle (in 2017–2018 and 2019–2020). Agriculture plots were sampled only in 2019–2020 in recently cultivated fields after crops were harvested. Open brush plots represent the area occupied by the sparse cover of *Suaeda* brush and bare soil with short ephemeral vegetation. Thus, we sampled a total of 43 sites; 9 in the sampling year 2017–2018 (3 grasslands, 3 Prosopis dominated, and 3 sparse Prosopis) and 34 in the sampling year 2019–2020 (8 grasslands, 7 Prosopis dominated, 6 sparse Prosopis, 7 agriculture fallow, and 6 open brushlands). The selection of these plots was based on spatial representation, as well as the willingness of local pastoralists to allow us access for sampling (**Table 1**).

Data Collection

We sampled rodent abundance and diversity in a 50 × 50 m plot at each sampling site. We used high-density Sherman live trap grids (10 m spacing) and moderate sampling duration (4 nights) following (Smith et al., 2017) to determine the rodent species composition at each sampling plot. We divided each 50 × 50 m plot into 25 sub-cells of 10 × 10 m and one Sherman trap

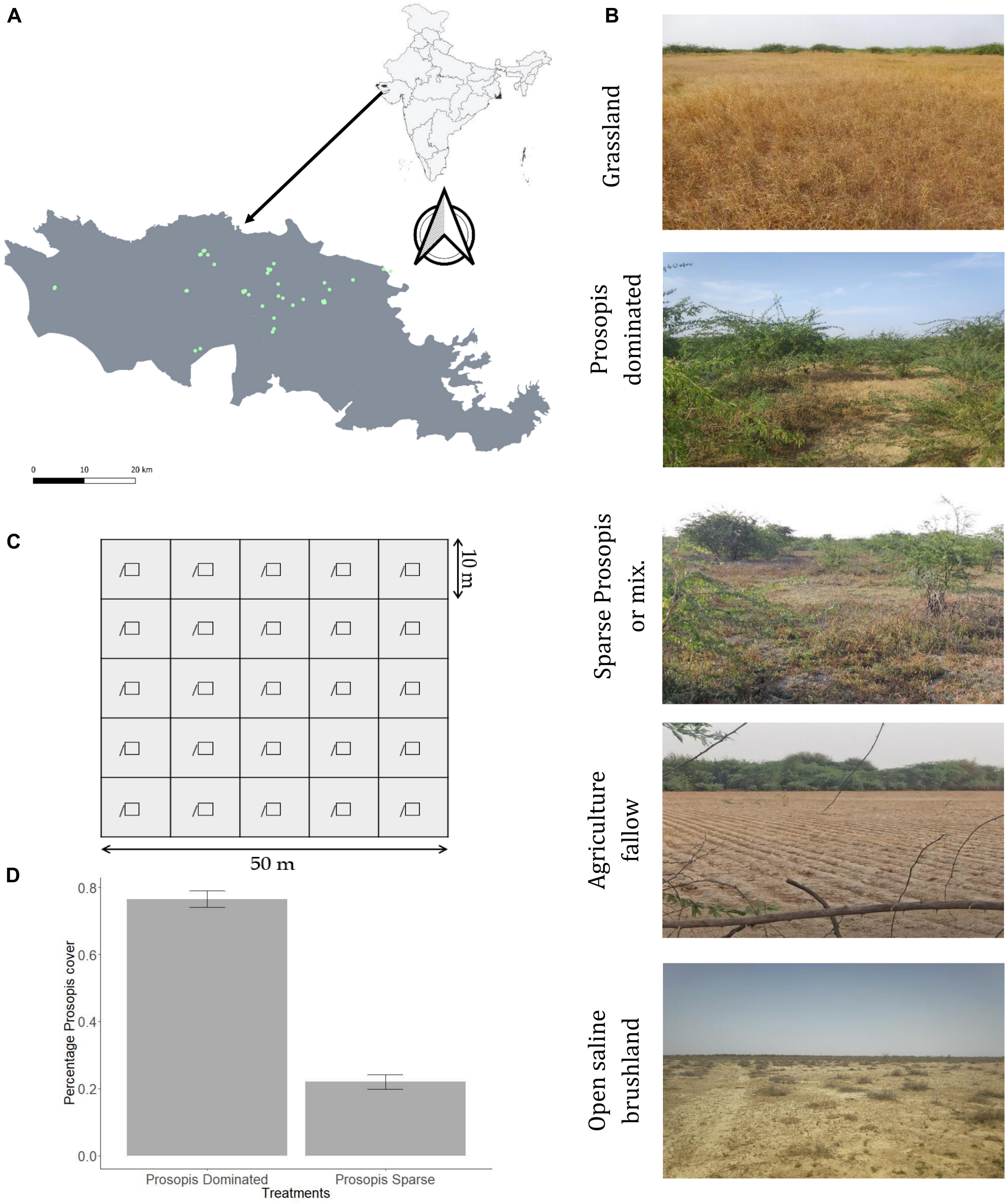

FIGURE 1 | Sampling schema. **(A)** Map of the study area (The Banni grassland) showing all the sampling sites as green points. **(B)** Representative photographs showing the physical structure of vegetation of each type of habitat. **(C)** Diagram depicting trap arrangements in each 50 × 50 m plot. **(D)** Difference in mean percentage Prosopis cover between Prosopis sparse (mean = 0.22, S.E. = 0.021) and Prosopis dominated (mean = 0.77, S.E. = 0.025) sampling plots.

was placed in the center of each sub-cell. We also counted the total number of burrows of the diurnal rodent species *Meriones hurrianae* as an index of abundance within the sampling grid because we were not able to trap during the daytime due to the risk of theft of our traps. The burrow counts in a colony have been found to correlate very well (r^2 = 0.96) with the abundance of *M. hurrianae* (Ramesh et al., 2013). Sampling was done for four consecutive nights at each site for each habitat type.

Traps were baited with a mix of peanut butter and pearl millet, and a piece of cotton was provided as bedding. Traps were set between 1700 to 1800 h and checked the next morning. Trapped individuals were captured and marked with numbered ear tags or non-toxic permanent markers. Information on sex, weight, body length, tail length, and length of hindlimb and forelimb were recorded for each trapped individual. Capture protocol was approved by ATREE's Animal Ethics Committee (No: AAEC/109/2019).

Analysis

The data analyses consisted of three steps. First, we estimated the rodent population for each sampled site using a suitable estimator as described in the "population estimation" section.

TABLE 1 | Summary of the total number of unique individuals of each species captured in the different habitat types. Also shown are the associated mean body mass, level of reproductivity, and diet type for each species (from Prakash and Singh, 2005).

Species	Total captured	Habitat type					Mean body mass (gm)	Reproductivity (young/female/year)	Diet
		Pros. (*N* = 10)	Grass. (*N* = 11)	Mix. (*N* = 9)	Agri. (*N* = 7)	Opn. (*N* = 6)			
T. indica	395	97	160	40	98	0	155.39	17.8	Granivore, Insectivore, Folivore, Carnivore
B. bengalensis	163	57	67	35	2	2	164.61	70	Granivore, Insectivore, Folivore, Carnivore
M. meltada	60	11	45	3	1	0	91	52.5	Granivore, Frugivore
M. gleadowi	1	0	0	0	1	0	–	–	Granivore, Frugivore
C. cutchicus	7	2	5	0	0	0	45	20	Granivore, Frugivore, Insectivore, Carnivore
M. booduga	6	2	3	2	0	0	–	21	Granivore
G. nanus	1	0	0	0	0	1	43	–	Granivore, Folivore, Insectivore
M. hurrianae	323*	0	0	0	0	323*	–	–	Granivore, Insectivore, Folivore, Carnivore

**Denotes total burrow count.*

Then, these population estimates were taken as response variable to run a linear mixed effect model to examine the relationship between rodent population and habitat category. Further, daily capture rates of three dominant species *T. indica*, *B. bengalensis,* and *M. meltada* were taken as an index of rodent activity and generalized linear models (GLM) were run to examine the effect of different habitat type, moonlight, and temperature on the activity of different rodent species. A GLM was also run to examine the relationship between species richness at each sampling occasion and habitat types. The results of the statistical analyses are shown in **Tables 2–5**.

Population Estimation

We used three different approaches to estimate rodent abundance at different sites to account for variation in capture and recapture rates. First we used Huggins' closed capture model with likelihood conditioned on the number of individuals detected or captured (Huggins, 1991). These models used "*p*" (probability of capture) and "*c*" (probability of individual getting recaptured after first capture occasion) to derive abundance parameter *N* for each sampling site in program Mark (Cooch and White, 2019). The best model was selected based on AIC values along

TABLE 2 | Result of a linear mixed-effect model comparing variation in log-transformed estimated rodent abundance across different habitat types. Shown are associated β estimates, standard error (S.E.), degrees of freedom (DF), t-statistics, and *p*-values. The habitat type "agricultural fallow" was the reference term (intercept) and individual site ID was included as a random effect.

Random effects: ∼1 | Site ID

	Intercept (Ψ)	Residual (σ)
Std. Dev:	0.8177522	0.3066571

Fixed effects: Pop. Est. ∼ Habitat

	Estimate	S.E.	DF	*t*-value	*P*-value
(Intercept)	3.270	0.330	33	0.907	<0.0001
Grasslands	0.539	0.422	33	1.276	0.211
Sparse prosopis	−0.737	0.440	33	−1.673	0.104
Prosopis dominated	0.050	0.430	33	0.116	0.908

TABLE 3 | Results of Tukey- pairwise comparisons for variation in log-transformed rodent abundance. The estimates are differences between means of two groups along with associated standard error (S.E.), Z statistic, and *p*-value.

Habitat pair	Estimate	S.E.	*z*-value	*P*-value
Grassland – Agricultural fallow	0.539	0.422	1.276	0.577
Sparse Prosopis. – Agricultural fallow	−0.737	0.440	−1.673	0.337
Prosopis dominated – Agricultural fallow	0.050	0.430	0.116	0.999
Sparse prosopis – Grassland	**−1.275**	**0.393**	**−3.249**	**0.006**
Prosopis dominated – Grassland	−0.489	0.382	−1.281	0.574
Prosopis dominated – Sparse prosopis	0.787	0.401	1.960	0.203

Bold values represent the variables with significant effect on the activity of modeled species.

TABLE 4 | Generalized linear model (GLM) ranked based on AICc values for each species.

Model Name	K	AICc	Delta_AICc
T. indica			
Habitat × Environment + Co-occurring species	13	868	0
Habitat + Environment + Co-occurring species	7	939.82	71.82
Habitat × Environment	12	1031.47	163.47
Habitat + Environment	6	1089.72	221.72
Habitat only model	4	1166.14	298.15
B. bengalensis			
Habitat × Environment	12	460.23	0
Habitat + Environment	6	492.32	32.09
Habitat only model	4	624.14	163.9
M. meltada			
Habitat + Environment	6	302.61	0
Habitat only model	4	338.49	35.88

TABLE 5 | Results of generalized linear models (GLM) for species richness, measured as the total number of species captured on each sampling occasion, as well as the activity (total individuals captured at each sampling occasion) of *T. indica*, *B. bengalensis,* and *M. meltada.* Predictors for the Environment models included habitat type (agricultural fallow was taken as the reference level), moonlight conditions, and minimum nighttime temperature.

	Variable	Estimate	SE	*Z*-value	*P*-value
Species richness	(Intercept)	0.298	0.401	0.743	0.457
	Grassland	**0.587**	**0.244**	**2.406**	**0.016**
	Sparse prosopis	0.113	0.271	0.418	0.676
	Prosopis dominated	**0.574**	**0.247**	**2.327**	**0.020**
	Moonlight	−0.003	0.002	−1.044	0.297
	Temp	−0.020	0.016	−1.208	0.227
T. indica	Intercept	−1.392	1.203	−1.157	0.247
	Grassland	0.943	1.267	0.744	0.457
	Sparse prosopis	0.071	1.395	0.051	0.960
	Prosopis dominated	3.973	1.249	3.182	**0.001**
	Moonlight	−0.002	0.003	−0.624	0.533
	Temperature	**0.152**	**0.055**	**2.769**	**0.006**
	B. bengalensis	−0.605	0.077	−7.902	**<0.001**
	Grassland × Moonlight	−0.015	0.004	−3.510	**<0.001**
	Sparse prosopis × Moonlight	0.026	0.006	4.238	**<0.001**
	Prosopis dominated **×** Moonlight	−0.005	0.005	−0.975	0.330
	Grassland **×** Temperature	−0.002	0.059	−0.029	0.977
	Sparse prosopis **×** Temperature	−0.081	0.062	−1.310	0.190
	Prosopis dominated × Temperature	−0.178	0.057	−3.132	**0.002**
B. bengalensis	Intercept	−1.231	15.709	−0.078	0.938
	Grassland	5.485	15.720	0.349	0.727
	Sparse prosopis	2.580	15.736	0.164	0.870
	Prosopis dominated	5.102	15.726	0.324	0.746
	Moonlight	−0.145	0.204	−0.712	0.476
	Temperature	−0.013	0.732	−0.017	0.986
	Grassland × Moonlight	0.140	0.204	0.685	0.493
	Sparse prosopis × Moonlight	0.178	0.204	0.870	0.384
	Prosopis dominated × Moonlight	0.166	0.204	0.812	0.417
	Grassland × Temperature	−0.183	0.733	−0.249	0.803
	Sparse prosopis × Temperature	−0.162	0.734	−0.220	0.826
	Prosopis dominated × Temperature	−0.233	0.734	−0.317	0.751
M. meltada	(Intercept)	−0.420	1.186	−0.354	0.723
	Grassland	**3.391**	**1.011**	**3.352**	**0.001**
	Sparse prospis	0.818	1.125	0.727	0.467
	Prosopis dominated	2.367	1.033	2.290	0.022
	Moonlight	**0.010**	**0.003**	**2.734**	**0.006**
	Temperature	**−0.181**	**0.034**	**−5.362**	**<0.0001**

Bold values represent the variables with significant effect on the activity of modeled species.

with site-specific observations during field data collection. We observed trap happy behavior of *T. indica* during sampling as the species was frequently captured within movements of trap placements, and recaptures were high. Based on these observations the effect of trap happy behavior on capture probability for the species cannot be rejected (Singh et al., 2010) therefore we selected model Mb to get abundance estimation at the sites where *T. indica* was the dominant species ($N = 4$, **Supplementary Table 1**).

Due to insufficient recaptures at a few sites ($n = 5$), Huggins' models failed to converge and provide estimates. Therefore, for these sites we used a second method in the package "Rcapture" to estimate the population (Baillargeon and Rivest, 2007). The package uses log-linear models to estimate closed population from capture history data. We compared models of abundance M0 (null model), Mh (heterogeneity model), Mb (behavior model), and Mt (time varying model) based on AIC values. The top selected model based on AIC was run through a bias correction described by Rivest and Lévesque (2001) using the function "*closedp.bc*" to get a robust estimate. It uses a correction factor for missed units along with total number of units caught at least once.

Finally, two sample sites (agricultural fallow) had an extremely low number (one individual captured only) of captures; thus, we couldn't estimate population size with any of the other methods. These low numbers of captures are also of biological significance, and therefore should not be truncated. We therefore used a canonical estimator to get the upper bound limit of rodent abundance for these sites. We calculated p^* (capture probability) using the formula $1-[(1-p)^4]$, where p is taken as the lowest value of capture probability at any occasion across all sampling sites and 4 is the number of sampling occasions. This novel approach of using three different methods to derive population estimates enables use of the most robust method where possible, thus reducing bias in estimates, but also allowed us to use the full dataset where captures or recaptures were low as this may reflect actual biological processes at these sites. The caveat here is that each method was not equally applied for each habitat type, and therefore may be a potential source of bias in the estimation of populations across habitats. However, we found a high correlation between the population abundance estimates from the Huggin's model and the Log-linear model ($r^2 = 0.91$, $p < 0.001$; **Supplementary Figure 1**). Furthermore, the canonical estimator was used only for two sites of agricultural fallow. Therefore, we are confident that the unequal application of various methods for estimating abundance is unlikely to have introduced any substantial bias in explaining the relationship between rodent abundance and habitat types. The estimated population of all sampling sites has been provided in **Supplementary Table 1**.

Linear Mixed Effect Models

Linear mixed-effect model was used to understand the relation between estimated rodent abundance and habitat types. We excluded saline open brushland from any further analysis as it was dominated by a single diurnal rodent species, the Indian desert jird *M. hurrianae,* as opposed to a nocturnal rodent-dominated community in all other habitats. As our sampling sites were distributed widely across the landscape, we used individual site ID as a random effect variable and habitat types as fixed effect variables. We used the "*lme*" function from package "nlme" in the R analysis environment (R Development Core Team, 2020) to run mixed effect models (Bates et al., 2015). We checked for data normality using the "*descdist*" function from the package "fitdistrplus". Our response variable (abundance) was log-transformed to meet the assumption of normality. We also performed *post hoc* Tukey tests using the package "*multcomp*" to identify significant pairwise interactions between the fixed effects of habitat type (Hothorn et al., 2008). To determine possible inter-annual variation in rodent densities between the sampling years, we ran a student *t*-test to compare the estimated rodent population in grasslands, Prosopis dominated habitat, and sparse Prosopis habitat. We did not find any significant difference in estimated rodent population between sampling years in grassland ($t = 0.002$, $p = 0.998$), Prosopis dominated habitat ($t = 0.191$, $p = 0.852$), and sparse Prosopis habitat ($t = 1.125$, $p = 0.298$) and therefore pooled the data across years for further analysis.

Generalized Linear Models

Daily capture rates of three dominant species *T. indica*, *B. bengalensis,* and *M. meltada* were taken as an index of rodent activity and were modeled with predictor variables using generalized linear models (glm). We determined the influence of different habitat types, percentage moon luminosity, minimum nighttime temperature (in °C), and co-occurring species on the activity of these rodent species. Data on percentage moon luminosity for each sampling occasion were collected from the lunar calendar from moongiant.com (accessed on 01/6/2020). Temperature data were collected from the weather station installed at BRC (Banni Research Center), which measures temperature at five-minute intervals. All our plots (except 1) were within 20 kms of this station, and given the flat topography of the landscape, we assumed that this station captured general weather patterns across the landscape. We used the minimum night time temperature for each sampling night as a predictor variable. Our response variable was count data with a non-normal distribution, hence we used Poisson distribution with log-link function during modeling (Bolker et al., 2009).

We first ran a model for the most commonly captured species, *T. indica,* with activity as a response variable and habitat type, environmental factors (temperature and moonlight), and the per night capture of co-occurring *B. bengalensis* as predictors. We modeled an interaction term between habitat type and each of the environment factors to determine the effect of moonlight and temperature under different habitat cover. We did not have sufficient sample size to model more complex interaction terms between *B. bengalensis* activity and habitat type. A similar model was run for *B. bengalesis* to understand the effect of habitat type, environment factors, and their interaction on their activity. We then constructed a series of sub-models based on the hypotheses tested (**Table 4**). We ran similar models for the activity of *M. meltada* but did not add co-occurring species as a predictor because we did not assume any potential competition for this species.

The best fit model was selected based on the AICc value, normal Q-Q plot were visualized and the effect size of each predictor was compared for the best fit model. All analyses were done in the program R v. 4.0.2 (R Development Core Team, 2020).

RESULTS

Abundance and Diversity

A total of 43 trapping sites were sampled during the winter of December 2017 to March 2018 ($N = 9$) and December 2019 to March 2020 ($N = 34$) (**Table 1**). We captured 633 unique individuals of 7 species in 4300 trap nights across sampling sites in five different habitat types. The relative abundances of species captured were *T. indica* (62.4%), *B. bengalensis* (25.75%), *M. meltada* (9.48%), *Cremnomys cutchicus* (1.11%), *M. booduga* (0.95%), *M. gleadowi* (0.16%), and *Gerbillus nanus* (0.16%). The diurnal species *M. hurrianae* was found only in open saline brushland (mean burrow count = 107.67, S.E. = 10.71). Generalized linear model predicted the highest per night species richness in both grasslands ($\beta = 0.59$, S.E. = 0.24, $p = 0.02$) and Prosopis dominated plots ($\beta = 0.57$, S.E. = 0.25, $p = 0.02$) compared to all other habitat types, though this result had limited ecological relevance with the difference in richness being <1 species. The species composition for both habitat types were similar and composed of four species; *T. indica*, *B. bengalensis*, *M. meltada*, *C. cutchicus*, and *M. booduga* (**Figure 2**). Agriculture habitats were dominated by *T. indica,* and sparse Prosopis sites had only three species; *T. indica*, *B. bengalensis*, *M. meltada*. The native brushlands had only open habitat specialist *G. nanus* and *M. hurrianae*.

Linear mixed effect models (**Table 2**) showed that 87% of residual variation ($\Psi = 0.82$, $\sigma = 0.31$) was explained by the random intercept term. Tukey's pairwise *post hoc* analysis (**Table 3**) shows rodent abundance in grasslands is significantly higher compared to sparse Prosopis plots ($\beta = -1.28$, SE = 0.39, $p = 0.006$). Total rodent abundance did not differ between grassland and Prosopis dominated habitat as well as between grassland and agricultural fallow significantly.

Rodent Activity

The models with interaction terms performed better than the main effects models for both *T. indica* and *B. bengalensis* (**Table 4**). Activity of *T. indica* was found to be higher under Prosopis dominated habitat ($\beta = 3.973$, S.E. = 1.249, $p = 0.001$), and no other habitats were significant predictors of activity. As moon phase progressed from new moon to full moon, the activity of *T. indica* in sparse Prosopis habitat increased from 1 to ∼13 individuals captured per night ($\beta = 0.026$, S.E. = 0.006, $p < 0.0001$), whereas it decreased in grassland habitat from ∼12 to ∼3 individuals captured per night ($\beta = -0.15$, S.E. = 0.004, $p < 0.0001$; **Figure 3**).

Overall minimum night temperature was positively correlated with the activity of *T. indica* ($\beta = 0.015$, S.E. = 0.06, $p = 0.006$). However, this pattern reversed in Prosopis dominated habitats ($\beta = -0.178$, S.E. = 0.06, $p = 0.002$); as the ambient temperature increased from 10°C to 30°C the activity of *T. indica* decreased from ∼9 to ∼5 individual captured per night.

The activity of *T. indica* was negatively associated with the presence of *B. bengalensis* ($\beta = -0.605$, S.E. = 0.08, $p < 0.001$), decreasing from ∼6 individuals captured per night

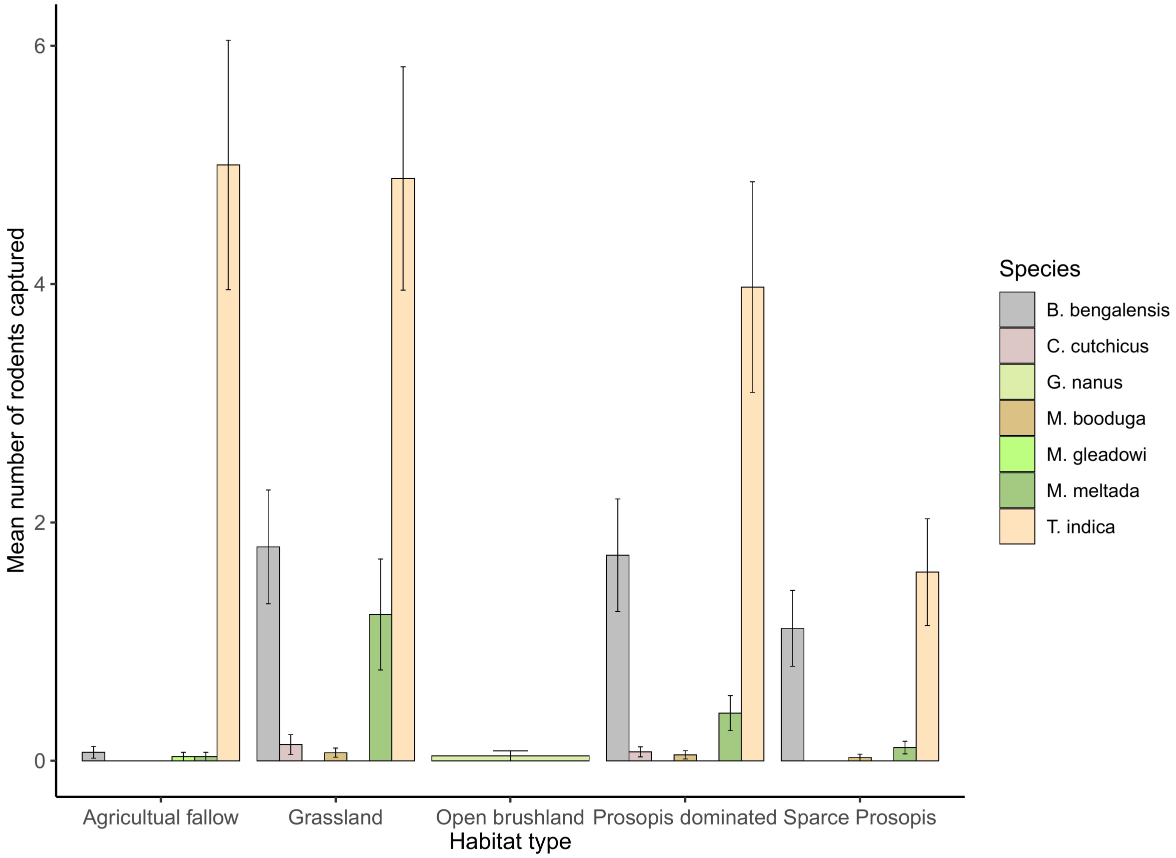

FIGURE 2 | Species composition of rodents in different habitat types based on per night captures. Note that grassland and Prosopis-dominated habitats show similar species composition.

to 0 individuals for every ∼5 unit increase in the activity of co-occurring *B. bengalensis*.

The activity of *B. bengalensis* did not show any significant relationship with any habitat type, moonlight or temperature. Models with habitat type, moonlight and temperature performed well for *Millardia meltada*. We found higher activity of *M. meltada* ($\beta = 3.39$, S.E. = 1.01, $p = 0.001$) in grassland and Prosopis dominated habitat ($\beta = 2.37$, S.E. = 1.03, $p = 0.02$). No other habitat type was found to be a significant predictor of activity. As moon phase progressed from new moon to full moon, the activity of *M. meltada* showed no ecologically meaningful change (∼0.6 to ∼1.4 individuals captured per night, $\beta = 0.01$, S.E. = 0.003, $p = 0.006$; **Figure 4**). As the minimum night time temperature rises from 10°C to 30°C the activity reduces from ∼4.8 individual to ∼0 individual ($\beta = -0.18$, S.E. = 0.03, $p < 0.0001$).

DISCUSSION

Bush encroachment has been known to have un-even effects on native vertebrate communities across biomes and continents (Stanton et al., 2018), and is mainly species and environment specific (Eldridge and Soliveres, 2014). In our study, as expected, we found highest abundance and diversity of rodents in native grassland habitats and lowest in the sparse Prosopis habitats compared to all other habitats. However, rodent abundance and diversity was not significantly different in invasive Prosopis-dominated habitats compared to grasslands. We found that habitat type mediated the effect of moonlight and temperature on the activity of the most common rodent species.

Bush Encroachment and Rodent Abundance and Diversity

Our results showed a high diversity and abundance of rodents in native grassland plots, potentially attributable to the high availability of food in the form of palatable grass and seeds (Nerlekar et al., 2021). Notably, these grassland plots in the Banni landscape are a result of habitat restoration, and that outside of the fenced restored grasslands, there are no large patches of native grasslands in Banni. The patch size of different habitats can influence rodent species richness and abundance across the landscape. Given how rapidly patches of Prosopis change (due to harvesting), we were unable determine patch size for these habitats. Previous studies have, however, shown that close to 50% of the landscape is now occupied by either dense or sparse

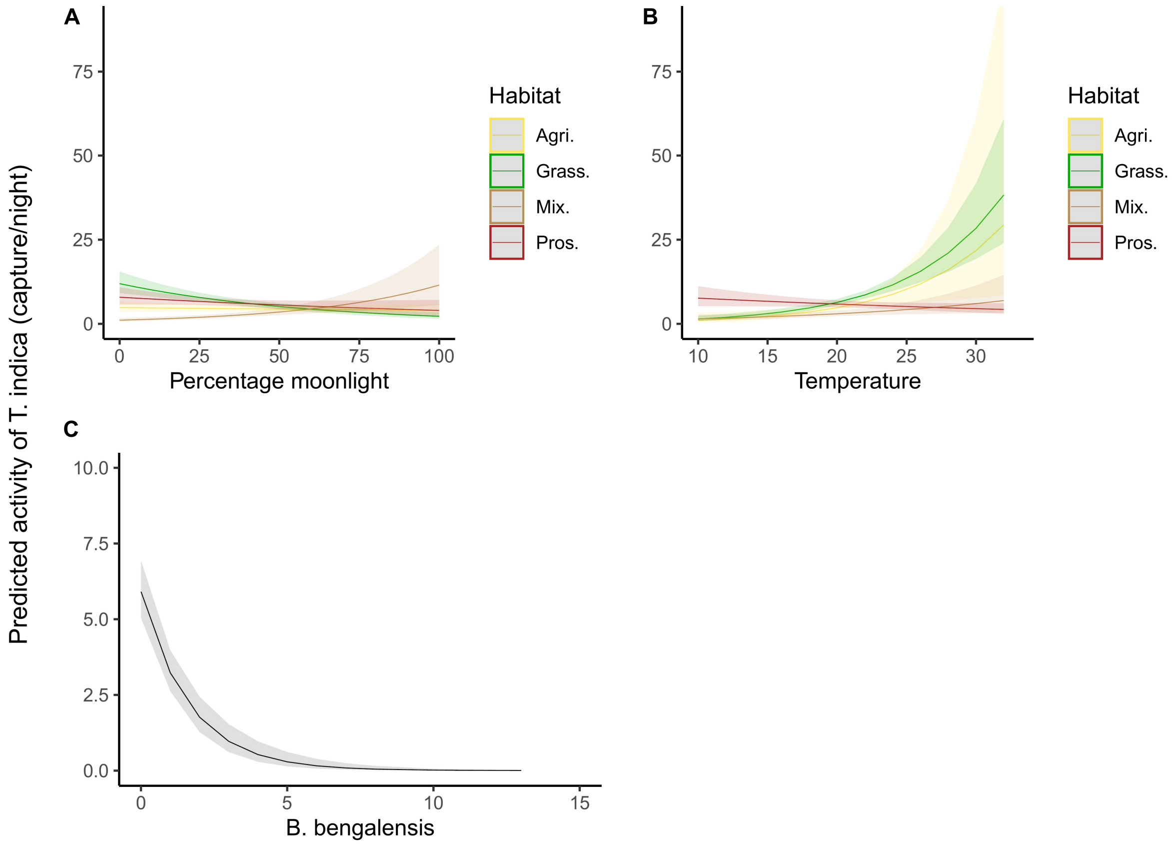

FIGURE 3 | Predicted response of the activity of *T. indica* to different predictor variables based on top model. **(A)** Effect of percentage moon luminosity on activity under different habitat cover. **(B)** Effect of minimum nighttime temperature on activity under different habitat cover. **(C)** Effect of co-occurring *B. bengalensis* on the activity of *T. indica*.

cover of Prosopis (Vaibhav et al., 2012). We found similar rodent richness and abundance in plots with high Prosopis cover as we did in the grassland habitats. A previous study in the same landscape has shown that dense Prosopis cover provides shelter from predators and supports a higher abundance of generalist rodent species compared to sparse Prosopis cover (Jayadevan et al., 2018). Our findings are consistent with this observation, and that the level of Prosopis cover may be altering species distribution at the landscape level.

Some species, such as *M. hurrianae* are highly adapted to xeric conditions and are restricted to those areas where Prosopis invasion is unlikely due to the saline nature of the soil. *M. hurrianae* along with co-existing nocturnal species *G. nanus* or pigmy gerbil were recorded only in the saline open brushland. Thus, rodents may show a non-linear "U" response to Prosopis invasion, occurring at their highest diversity and abundance in either native grasslands or in dense Prosopis, and at their lowest in sparse Prosopis. This could likely be linked to the relatively high productivity of these habitat types. A recent global meta-analysis shows that the negative effect of shrub-encroachment reduces in areas with higher net primary productivity (Stanton et al., 2018). Our Prosopis dominated plots were sampled close to the grassland dominated plots, and are likely to have similar levels of primary productivity and soil conditions. A similar response of the rodent community was also observed in Namibia where rodent species composition and abundance were similar in both bush-encroached and non-bush encroached habitats (Karuaera, 2011).

Our sampling sites were also widely distributed across the ∼2500 sq km landscape (**Figure 1**), and not surprisingly, random variation between individual sites explained a substantial amount of variation in rodent abundance. Expansion of agricultural land has become a major driver of land-use change beyond the Prosopis eradication efforts in recent years. Although agriculture here remains monsoon-dependent, it is expected to provide additional resource subsidies to generalist rodent species (Fraschina et al., 2014). For example, sugarcane monocultures in the African savannah support a high density of generalist species but have a lower diversity of species (Mamba et al., 2019). In the Banni we found a similar pattern as total rodent abundance did not significantly differ from restored grassland but was dominated by a single species *T. indica*. Given that agriculture here is often a single crop of non-grain produce, it is unlikely that these fields have sufficient resources to sustain multiple species of rodents beyond the harvest season.

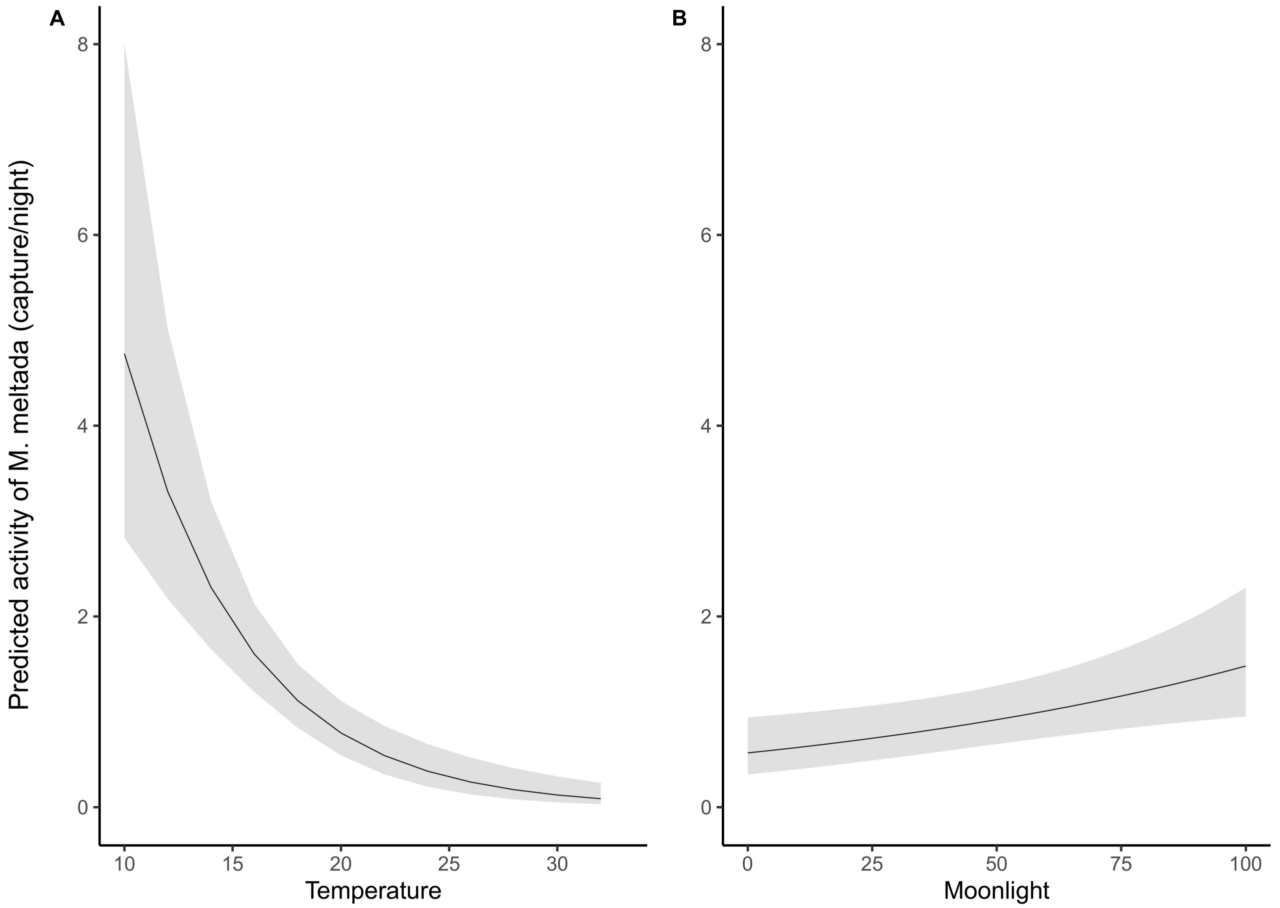

FIGURE 4 | Predicted response of the activity of *M. meltada* to different predictor variables based on top model; **(A)** effect of temperature **(B)** effect of moonlight.

Bush Encroachment and Rodent Activity

The most common species, *T. indica* was more active in Prosopis dominated habitat compared to any other habitats. The structural complexity of habitats can alter perceived predation risk (Ceradini and Chalfoun, 2017), and alter activity patterns of small vulnerable prey, especially on moonlit nights. As expected, in open grasslands, the activity of *T. indica* reduced with increased moon luminosity, whereas it increased under the cover of sparse Prosopis with higher moon luminosity, as observed in other systems (Kotler et al., 1993; Guiden and Orrock, 2019).

For small-bodied nocturnal rodents, the minimum nighttime temperature is an important predictor of activity (Kotler et al., 1993). Due to a lower surface-to-body mass ratio and reduced thermal conductance, the cost of foraging on colder nights is high and can result in rapid heat loss from the body (Ghosh et al., 1979). As the temperature increased, the activity of *T. indica* also increased across most habitat types, except under dense Prosopis. This could likely be due to rodents using more open areas adjoining Prosopis thickets on warmer nights. This provides additional evidence that vegetation structure mediates the effect of temperature on the activity of small mammals (Milling et al., 2017).

We found that *M. meltada* was active in both open grassland and Prosopis dominated habitat, but its activity showed an opposite response toward moonlight and temperature compared to those shown by *T. indica*. This response of *M. meltada* might also be driven by other variables such as habitat type or competition, but due to low number of captures we were not able to examine more complex models for this species.

The activity of *T. indica* was also negatively correlated with the presence of *B. bengalensis*. Both species are generalists with similar dietary habits (Prakash and Singh, 2005) and are comparable in size (body mass ratio < 1.5). However, *B. bengalensis,* due to its aggressive nature (Sridhara and Krishnamoorthy, 1983; Meehan, 1984) and higher reproductive capacity (70 young/female/annum) can have a competitive advantage over the more docile, and slower breeding (17.8 young/female/annum) *T. indica* (Prakash and Singh, 2005). It is likely that *T. indica* shows some form of spatial/temporal separation to potentially avoid interference competition from *B. bengalensis*. This response is likely independent of other factors such as year of sampling, since our plots were sampled under relatively similar conditions in consecutive years, and we found no difference in overall rodent abundance between years

(t = 1.125, p = 0.298; **Figure 5**). We were not able to model the interactive effect of habitat and *B. bengalensis* occurrence on activity due to sample size. Furthermore, *B. bengalensis* was absent in the first year of sampling, but was remarkably common across all habitat types in the second year. We speculate that this could be due to the increased rainfall in that year. Spatially, *B. bengalensis* was also found in areas that were inundated for longer periods, and thus had higher soil moisture (Sridhara and Tripathi, 2005). We also observed high consumption of Prosopis bark by *B. bengalensis* in all Prosopis habitats where the species was found, showing their potential dietary competitive advantage.

Overall, the effect of bush encroachment appeared to be highly species specific. Prosopis dominated habitats favor the abundance and activity of generalist rodent species *T. indica* and *B. bengalensis* while habitat specialists such as *M. hurrianae* and *G. nanus* were absent from bush encroached areas. These patterns of avoiding woody encroached habitat are also reflected in how other species, especially mammalian mesocarnivores such as desert fox *Vulpes vulpes pusilla* that are dependent on rodents, respond to changes in the habitat (Misher and Vanak, 2021). Though the Prosopis dominated habitat may represent similar diversity and abundance of rodents as do grasslands in Banni, their further expansion in native open brushlands can drastically change species composition at landscape level. These brushlands occupy a substantial proportion of the landscape and have escaped Prosopis encroachment due to annual water logging and high soil salinity, thus supporting highly specialized rodent community that is absent in Prosopis encroached areas.

The landscape has seen a higher mean annual rainfall consecutively for last 2 years. Such pulses of high precipitation can further influence the rodent community in the landscape. Although, we did not find any significant effect of sampling years on total rodent abundance, the species composition during our second sampling year was different due to the presence of *B. bengalensis*. Jayadevan et al. (2018) did not report presence of *B. bengalensis* during their sampling in 2016–2017, and we did not detect it either in our first sampling year. Long-term research is required to understand the effect of changing rainfall patterns on the small mammal community of the landscape. It is likely that a long dry spell of more than 2 years may again reduce the population of *B. bengalensis,* as the species is typically associated with more moist climatic conditions.

Although native, species such *T. indica* and *B. bengalensis* are also major agricultural pests in the dry-lands of India (Tripathi, 2014). They have been subjected to systematic long-term eradication programs due to the high economic cost they inflict by damaging crops (Sridhara and Tripathi, 2005). Further expansion of Prosopis along with high rainfall can also facilitate the expansion of generalist pests such as *T. indica* and *B. bengalensis* in these landscapes. Finally, our study provides a much-needed example of the impacts of shrub encroachment on vertebrate communities from the Asian continent (Stanton et al., 2018), and a starting point for further studies.

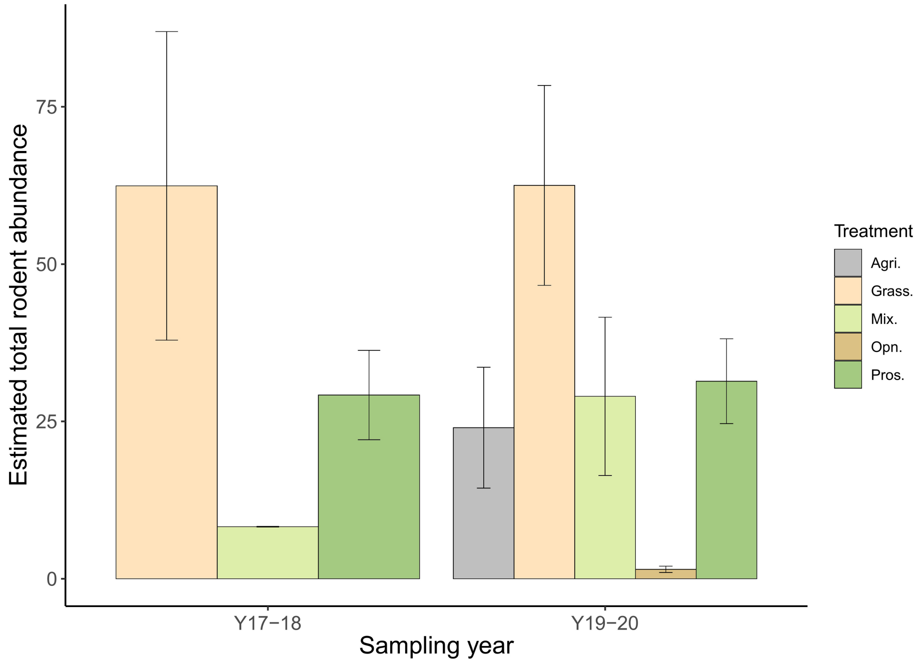

FIGURE 5 | Difference in estimated total rodent abundance between different habitat types and year. There was no significant difference observed (t = 1.125, p = 0.298) in estimated total rodent abundance between sampling years in grassland ($N_{2017-2018}$ = 3, $N_{2018-2019}$ = 8) (t = 0.002, p = 0.998), Prosopis dominated habitat ($N_{2017-2018}$ = 3, $N_{2018-2019}$ = 7) (t = 0.191, p = 0.852), and sparse Prosopis habitat ($N_{2017-2018}$ = 3, $N_{2018-2019}$ = 6).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors on request, without undue reservation.

ETHICS STATEMENT

The animal capturing protocol was reviewed and approved by ATREE's Animal Ethics Committee (Application No: AAEC/109/2019).

AUTHOR CONTRIBUTIONS

CM and AV conceived and designed the study. CM collected data, performed analyses, and wrote the manuscript. GV collected data. AV provided overall supervision. All authors edited and approved the final manuscript version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.755903/full#supplementary-material

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Ecological Drivers of Habitat Use by Meso Mammals in a Miombo Ecosystem in the Issa Valley, Tanzania

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Vast stretches of East and Southern Africa are characterized by a mosaic of deciduous woodlands and evergreen riparian forests, commonly referred to as "miombo," hosting a high diversity of plant and animal life. However, very little is known about the communities of small-sized mammals inhabiting this heterogeneous biome. We here document the diversity and abundance of 0.5–15 kg sized mammals ("meso-mammals") in a relatively undisturbed miombo mosaic in western Tanzania, using 42 camera traps deployed over a 3 year-period. Despite a relatively low diversity of meso-mammal species (n = 19), these comprised a mixture of savanna and forest species, with the latter by far the most abundant. Our results show that densely forested sites are more intensely utilized than deciduous woodlands, suggesting riparian forest within the miombo matrix might be of key importance to meso-mammal populations. Some species were captured significantly more often in proximity to (and sometimes feeding on) termite mounds (genus *Macrotermes*), as they are a crucial food resource. There was some evidence of temporal partitioning in activity patterns, suggesting hetero-specific avoidance to reduce foraging competition. We compare our findings to those of other miombo sites in south-central Africa.

Keywords: small mammals, miombo, habitat use, termite mounds, riparian forests, woodlands, meso-mammals

INTRODUCTION

Miombo woodlands cover a vast area of eastern and southern Africa, and typically consist of a mosaic of open to dense deciduous woodlands dominated by *Brachystegia* and *Julbernardia* trees, interspersed with patches of evergreen riparian forests and wetlands (Frost, 1996; Banda et al., 2008; Munishi et al., 2011; Gumbo et al., 2018). Despite sustaining a diverse plant life, mainly due to the high annual rainfall (up to 700 mm/year; Frost, 1996; Godlee et al., 2020; Muvengwi et al., 2020), these habitats are characterized by shallow, nutrient-poor soils, and by unpalatable grasses (Frost, 1996; Loveridge and Moe, 2004; Montfort et al., 2021). Coupled with the scarcity of surface water during the dry season, and with annual fires depleting standing vegetation biomass, these factors contribute to differences in diversity and abundance of large mammal species compared to other savanna-woodland ecosystems in Sub-Saharan Africa, especially in the dry season when abundance drops (Caro, 1999; Waltert et al., 2009; Kavanna et al., 2014; Amaya et al., 2021;

Davis et al., 2021). However, little is known about the effects of this environment on communities of small-sized mammals.

We know that some of miombo system characteristics could prove highly favorable for small (0.01–0.5 Kg) and "meso-mammals" (0.5–20 Kg; Frost, 1996; Timberlake et al., 2010). The availability of fruit, flowers, and seeds from a diverse woody plant flora, for example, might offer ample foraging opportunities for herbivorous rodents (and the small carnivores that prey on them), and allow for dietary niche differentiation and co-existence among multiple species (Frost, 1996). Furthermore, the low densities of ungulates and large carnivores (e.g., felids, canids) could attenuate the intensity of interspecific competition over food resources, and thus open up novel ecological niches for smaller species (Caro, 2001, 2002; Easter et al., 2019), especially if canopy cover prevents abundant grasses from sustaining large herbivore communities. Nonetheless, although such combined conditions (abundant food, reduced competition, and lower predation risk) are predicted to promote species-rich small and meso-mammal communities and large population sizes, available data point elsewhere.

Most studies reveal a general pattern of low rodent diversity and abundance in miombo systems characterized by vast expanses of uniform deciduous woodlands (Linzey and Kesner, 1997; Caro, 2001, 2002; Gaynor et al., 2021). By contrast, relatively larger numbers of small and meso-mammals (both at the species and population levels) are found in those miombo systems encompassing patches of well-watered, evergreen riparian forest or wetlands (e.g., Pettorelli et al., 2010; Rovero et al., 2017). This suggests that woodland resources might be of overall little value to small-sized mammals [possibly due to lower plant diversity, plant unpalatability, or water shortages, as proposed for larger mammals (Frost, 1996; Waltert et al., 2009)] with higher numbers found in more productive and botanically heterogeneous areas within the woodland matrix.

Rodent distribution in the miombo also appears to mirror that of widely dispersed biotic features, such as open grassland patches, human settlements, or termite mounds (Linzey and Kesner, 1997; Caro, 2001, 2002; Fleming and Loveridge, 2003). For example, in a test of the importance of termite mounds for small vertebrates in a Zimbabwe miombo system, results from live-trapping individuals revealed how several species were substantially more common on mounds, to the point that some would burrow only in proximity to termite colonies while avoiding the surrounding woodlands (Fleming and Loveridge, 2003). It is thus possible that the observed patterns of small-sized mammal diversity and abundance across a miombo system could also be heavily influenced by the availability of such "resource islands," likely representing an important food source in an otherwise low-diversity biome.

The association of small and meso-mammals with highly localized botanical communities and biotic features (e.g., riparian forests, termite mounds) could also promote high levels of interspecific competition. Rare or widely scattered food and water have been widely documented to increase the rate of encounter among competing mammalian species sharing the same resources, with substantial fitness costs in terms of direct interference competition (e.g., injuries, unsustainable energetic expenses; Dickman, 1991; Valeix et al., 2007). This is in turn is reflected by fine-scale strategies to avoid interference, among which temporal partitioning in activity patterns is the most common (Kronfeld-Schor and Dayan, 2003; Frey et al., 2017). One study of small carnivores reported activity patterns shifts among co-existing miombo-dwelling species with a similar diet (e.g., insects and rodents), therefore pointing to temporal partitioning as an important behavioral strategy to cope with limited resource availability (Easter et al., 2019).

So which habitat types and environmental features favor the presence of small-sized mammalian taxa within a miombo ecosystem? In the current study, we investigated the environmental factors underlying smaller mammal diversity and abundance in a relatively undisturbed miombo mosaic habitat, the Issa Valley of western Tanzania ("Issa" from now onward) using a network of motion-triggered camera traps (CTs) over a 3-year period (2016–2018). Since CTs are usually not triggered by animals < 0.5 kg in body mass (Rowcliffe and Carbone, 2008), we restricted our investigation to meso-mammals (rodents, elephant shrews, lagomorphs, pangolins, and small carnivores weighing more than 0.5 kg). This excluded a large proportion of small mammals which could not be detected by CTs, such as the entire guild of small rodents. We report also results for species smaller than 0.5 kg, with the caveat that the frequency of detection might be negatively biased by smaller body sizes. While there are published species lists of large mammals from the study area (Piel et al., 2019), little is known about the meso-mammal community. We first used the CT network to compute an inventory of the species found in the study area. Issa is characterized by a highly varied ecological landscape, with deciduous woodlands on high-lying plateaus, and an extensive system of river valleys hosting closed-canopy, evergreen riparian forests. We expected to find higher species diversity in river valleys characterized by riparian forests than in deciduous woodlands. Relative abundance was considered as an indicator of the intensity of habitat use rather than an estimate of local densities, given that individual identification was not possible and the same individuals could have been captured multiple times on CTs.

We then applied CT data to identify the ecological drivers of the intensity of site use by meso-mammals, using capture rates as indicators of relative abundance (Rovero and Marshall, 2009; Rovero et al., 2014). Specifically, we tested the hypothesis that the deciduous woodlands at Issa would represent a less suitable habitat for meso-mammals than the riparian forests, as proposed previously for larger species (Frost, 1996; Waltert et al., 2009). We further predicted that meso-mammals would be relatively more abundant at CT sites located in the riparian forests of river valleys (characterized by steep slopes and low elevations) rather than on plateau woodlands, given the supposedly greater availability of forage, cover, and water in the forests. We also predicted that all insectivorous species would be more frequently captured at CT sites located in proximity to termite mounds (of the genus *Macrotermes*), as the latter might provide important but highly localized food and shelter sources. Relative abundance was considered as an indicator of the intensity of habitat use rather than an estimate of local densities, given that individual identification was not possible and the same individuals could have been captured multiple times on CTs.

Finally, we explored whether the presumed scarcity and/or wide dispersion of miombo resources would translate into fine-scale temporal partitioning in activity patterns throughout the day and night among meso-mammal species. We thus predicted that species would exhibit little temporal overlap in primary time of activity between each species pair that shared similar diets. In particular, insectivorous, nocturnal species were expected to show a high degree of differentiation among them in night-time activity patterns, to avoid direct interference over shared food resources.

MATERIALS AND METHODS

Study Area

The Issa valley lies in the Tongwe West Forest Reserve, western Tanzania (**Figure 1**). Issa comprises steep river valleys (900 m asl) and high-lying plateaus (1,800 m asl; Piel et al., 2015, 2019; Mayengo et al., 2020). The entire region is dominated by deciduous miombo woodlands and closed-canopy, evergreen riparian forests, typically located in the valleys between steep slopes (Piel et al., 2019). Woodlands are dominated by *Brachystegia* and *Julbernardia* trees, while a variety of woody plant species typical of the central African lowland rainforests is found in the riparian forests (Piel, 2018; Piel et al., 2019). Mean annual temperatures range between 11 and 38°C, while mean annual rainfall ranges between 900 and 1,400 mm. Rainfall patterns denote distinctive wet (November–April) and dry seasons (May–October) (Piel et al., 2019; Mayengo et al., 2020). Common medium/large mammals include chimpanzee (*Pan troglodytes*), yellow baboon (*Papio cynocephalus*), roan antelope (*Hippotragus equinus*), Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), and bushpig (*Potamochoerus larvatus*), with larger predators such as lion (*Panthera leo*), leopard *(P. pardus*), wild dog (*Lycaon pictus*), and spotted hyena (*Crocuta crocuta)* also present but at low densities (Piel et al., 2019). Issa is surrounded by small (formerly refugee) settlements established in the 1970s. Humans sporadically visit the area for wildlife snaring, small-scale logging, honey collection, or livestock herding, but anthropogenic impacts on the landscape remain modest (Piel et al., 2015, 2019).

Camera Trapping

We deployed a total of 42 motion-triggered, infrared CTs (Bushnell Trophy Cam HD Aggressor; and Reconyx Hyperfire 2 HF2X) at Issa over a 3-year period (December 2015–December 2018). Due to mechanical camera failures, this was for a total of 21,517 camera days (**Supplementary Material**). Camera days were calculated as the number of calendar days in which a CT was deployed and active in the field. Distances between single CT sites were at least 150 m, covering an area of 14.45 km^2. We selected CT sites to sample different vegetation types, with half in deciduous woodlands (*n* = 21; camera days mean ± S.E. = 427.57 ± 68.82; range = 47–986), and the other half in riparian forests (*n* = 21; camera days mean ± S.E. = 597.05 ± 67.51; range = 49–940; **Supplementary Material**). We attached CTs to large trees, 30–90 cm above the ground, following recommendations for camera trapping of small- and medium-sized mammals (Rowcliffe and Carbone, 2008; Ortmann and Johnson, 2021). To maximize capture probability, we deployed CTs primarily along forest and woodland trails—commonly utilized by terrestrial vertebrates (Rovero et al., 2010; Cusack et al., 2015). Moreover, tall grass and woody plants growing in the CTs line of sight were artificially removed at regular intervals. Of the 42 CTs deployed, 15 were positioned in proximity of large termite mounds of the genus *Macrotermes* (the most common in the study area; Mayengo et al., 2020; **Table 1**). CTs faced the mounds, which were confirmed to be actively occupied by termite colonies in the course of a parallel study on primate feeding behavior. All CTs were set on video mode (video duration: day = 60 s; night = 15 s) with a 1 s delay between exposures, and visited once a month to retrieve SD cards and change batteries. For statistical analyses, CTs active for less than 30 calendar days ("camera days" from now onward) were removed from the dataset.

We identified all meso-mammals (rodents, hares, elephant-shrews, small carnivores, and pangolins) captured on CTs to species level (except when lighting conditions or poor video quality prevented an unequivocal identification). The giant and southern ground pangolins (*Smutsia gigantea* and *S. temmincki*, respectively) were considered together as "pangolins," since they could not be easily distinguished from each other based on the resolution of the available video material.

Environmental Covariates

In QGIS v. 3.14.1, we extracted the elevation (m) of each CT site from a Digital Elevation Model (DEM) at 90 m spatial resolution. We then then calculated slope as a percentage value (%), using the Terrain Analysis toolbox in QGIS. The vegetation type of all CT sites was derived from a vegetation map based on Landsat satellite imagery, at a spatial resolution of 30 m. Vegetation type was classified as either "deciduous woodland" or "riparian forest" and later confirmed on the ground. In a small number of cases (*n* = 4), there was disagreement between the available vegetation-class map and ground observations, probably reflecting a failure of remote-sensing imagery to capture small-scale variation in habitat structure. This was therefore rectified in our final dataset. Finally, we classified all CT sites as either located at termite mounds or not.

Statistical Analyses

We conducted all statistical analyses in R v. 3.5.2 (R Core Team, 2020). We calculated the Relative Abundance Index (RAIs) for all identified meso-mammals as the number of videos obtained for each species, divided by the overall number of camera days (Rovero et al., 2010; Palmer et al., 2018). We excluded multiple capture events of the same species on the same camera day from analyses. We did this to minimize the risk of pseudo-replication generated by double-counting the same individual on the same day, which was more conservative than the threshold adopted by other studies (Bowkett et al., 2008). Although not excluding the possibility of capturing the same individuals on different days and at different CT sites, this conservative

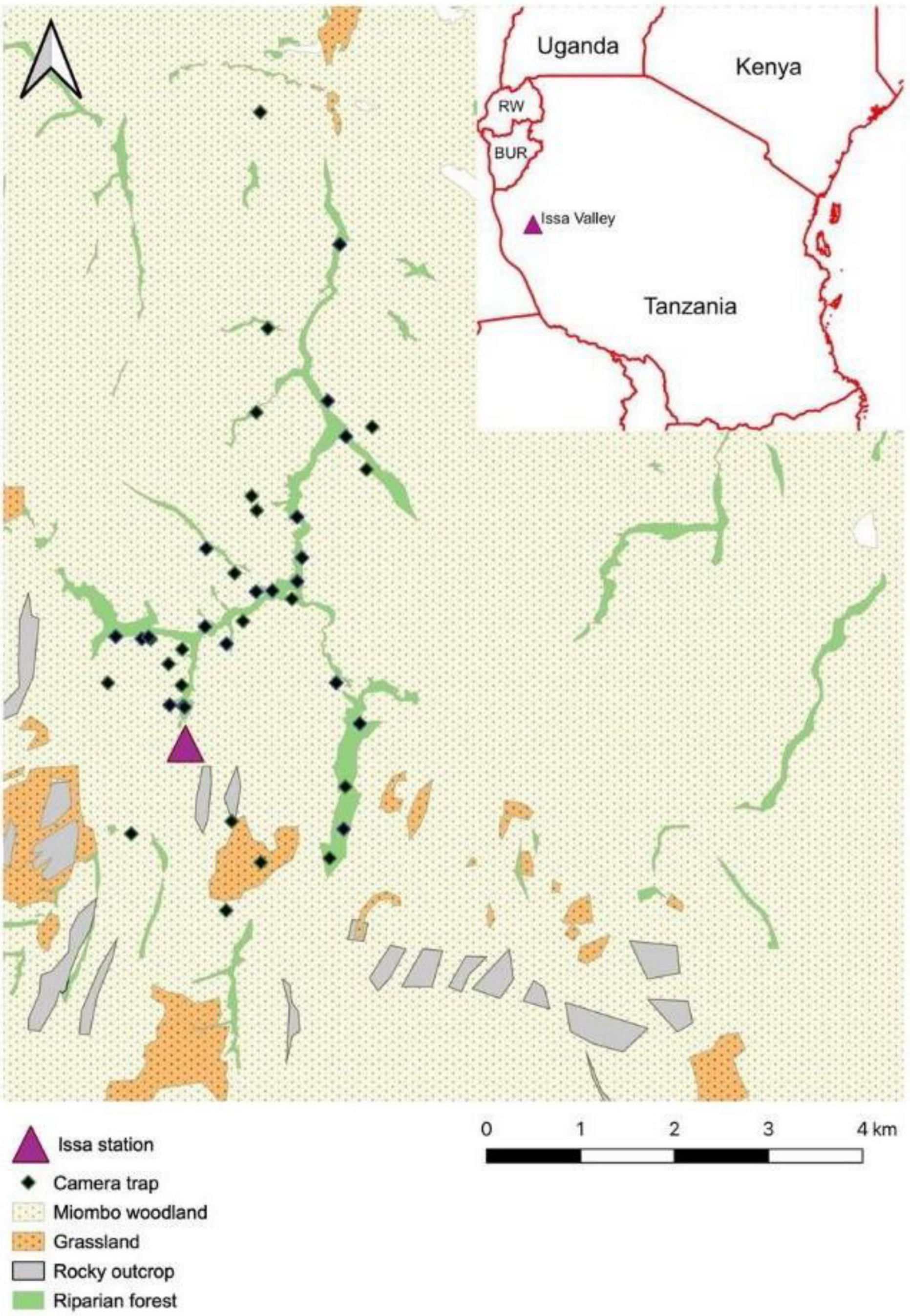

FIGURE 1 | Location of the camera traps (*n* = 42) deployed between January 2016 and December 2018 in the Issa Valley, in relation to the different vegetation types. The Issa station represented the main research base for the study. The camera trap site in "grassland/swamp" was instead located in a patch of deciduous woodland, and thus corrected upon field examination of the site.

approach was deemed necessary to exclude repeated sequences of videos from the same individuals of certain species remaining in proximity of CT sites with termite mounds for very long periods while feeding on termites or waiting for swarming events. RAIs also were calculated separately for woodland vs. forest vegetation types, to compare differences in meso-mammal relative abundance between the two main vegetation types found at Issa. We performed all computations in the package unmarked (Fiske et al., 2015).

To determine the drivers of meso-mammal relative abundance, we used the number of camera days on which different species were captured at each CT site as a proxy

TABLE 1 | Relative Abundance Indices (RAIs) for the meso-mammal species (*n* = 19) of Issa Valley, Tanzania.

Species	RAI total (camera days = 21,517)	RAI riparian forest (camera days = 12,538)	RAI deciduous woodland (camera days = 8,979)	Number of detections	Number of CT sites where the species was detected	Body mass range (Kg)	Typical diet
Giant Pouched Rat	5.010	7.324	1.904	1,078	30	1.0–1.4	Fruit, seeds insects
Bushy-tailed Mongoose	4.169	6.325	1.158	897	36	1.3–2.1	Insects
Large-spotted Genet	0.889	1.053	0.657	191	28	1.3–2.3	Insects, small vertebrates
Pangolins	0.730	0.781	0.657	157	23	30–35 (giant); 7–18 (ground)	Termites, ants
Crested Porcupine	0.428	0.375	0.501	92	21	12–27	Roots, tubers
Chequered Elephant shrew	0.363	0.471	0.212	78	14	0.5	Insects
African Civet	0.158	0.119	0.212	34	14	7–20	Small vertebrates insects, fruit
Dwarf Mongoose	0.079	0.056	0.111	17	9	0.2–0.4	Insects
Palm Civet	0.046	0.080	0	10	3	2.0–3.2	Small vertebrates insects, fruit
Banded Mongoose	0.028	0.048	0	6	4	1.5–2.25	Insects, small vertebrates
Marsh Mongoose	0.028	0.048	0	6	2	2.0–5.0	Crustaceans, molluscs, small vertebrates
Four-toed Elephant Shrew	0.023	0	0.056	5	1	0.2–0.3	Insects
Savanna Hare	0.019	0	0.045	4	2	1.5–4.5	Leaves, grass, roots
Serval	0.009	0	0.022	3	3	6.0–13.5	Small vertebrates
Honey Badger/Ratel	0.014	0.016	0.011	3	3	5.2–14.5	Small vertebrates, insects honey
Rock Hyrax	0.014	0.016	0.011	3	2	1.8–5.5	Leaves, grass
White-tailed Mongoose	0.005	0.008	0	1	1	2.0–5.2	Insects, small vertebrates
African Bush Squirrel	0.009	0.008	0.011	2	2	0.1–0.3	Fruit
African Clawless Otter	0.014	0.024	0	3	1	10–18	Small aquatic vertebrates

RAIs have been calculated for the overall study area, and separately for the two main habitat types (riparian forest and dry woodland). Information on body mass and diet were derived from Kingdon (2015).

for the intensity of site use (Bowkett et al., 2008; Rovero et al., 2010). We limited our analyses to five species that were captured by CTs on > 50 camera days (Mori et al., 2020), namely: Bushy-tailed Mongoose (*Bdeogale crassicauda*), Chequered Elephant-shrew (*Rhynchocyon cirnei*), Crested Porcupine (*Hystrix cristata*), Giant Pouched Rat (*Cricetomys gambianus*), and Large-spotted Genet (*Genetta maculata*). General characteristics of these species are presented in **Table 2**. We used Generalized Linear Models (GLMs) for count data to describe the relationship between relative abundance and the environmental covariates recorded at each CT site (elevation, slope, vegetation type, and presence of termite mounds; Bowkett et al., 2008). Models were fitted separately for each of the study species. Elevation was transformed from continuous to categorical (>1,450 m and < 1,450 m) following multiple convergence issues (Allison et al., 2004). The number of camera days also was entered in the models as an offset variable to control for variation in "effort" between CTs. Due to the small sample size for most species (≤150 captures over 3 years for three out of five species), and our GLM-based approach, it was not possible to account for seasonal variation in relative abundance, and this should be considered when interpreting our results. We selected a zero-inflated negative binomial distribution for all GLMs, given significant over-dispersion in the count data and the large number of non-captures (i.e., species absent at certain CT sites for the entire study period). All models were built in the glmmTMB package (Magnusson et al., 2017).

TABLE 2 | Averaged coefficient estimates and significance levels for predictors of relative abundance of five most common meso-mammal species in the Issa Valley, Western Tanzania.

A. Giant Pouched Rat

	B	*S.E.*	*z*	*P*
Habitat (Forest)	2.523	0.524	4.645	**<0.001**
Mound (Yes)	1.255	0.463	3.061	**0.008**
Altitude (Low)	1.198	0.435	2.658	**0.007**
Slope	0.141	0.038	3.544	**<0.001**

B. Bushy-tailed Mongoose

	B	*S.E.*	*z*	*P*
Habitat (Forest)	1.490	0.401	3.601	**<0.001**
Mound (Yes)	1.937	0.452	4.161	**<0.001**
Altitude (Low)	0.665	0.393	1.636	0.102
Slope	0.053	0.030	1.722	*0.085*

C. Chequered Elephant Shrew

	B	*S.E.*	*z*	*P*
Habitat (Forest)	1.708	0.834	1.987	**0.047**
Mound (Yes)	0.441	0.757	0.583	0.560
Altitude (Low)	3.812	1.044	3.570	**<0.001**
Slope	0.211	0.074	2.825	**0.004**

D. Large-spotted Genet

	B	*S.E.*	*z*	*P*
Habitat (Forest)	0.485	0.438	1.452	0.284
Mound (Yes)	2.703	0.421	6.218	**<0.001**
Altitude (Low)	0.657	0.401	1.585	*0.100*
Slope	0.044	0.032	1.333	0.182

E. Crested Porcupine

	B	*S.E.*	*z*	*P*
Habitat (Forest)	0.394	0.482	1.792	0.428
Mound (Yes)	0.591	0.690	0.834	0.404
Altitude (Low)	–0.393	0.561	0.681	0.404
Slope	0.055	0.039	1.378	0.168

Conditional averages were calculated for all models with $\Delta AIC \leq 2$. Significant p-values ($p < 0.05$) are in bold, and trends to significance in ($0.05 < p < 0.1$) in italics.

We tested model fit to a zero-inflated negative binomial distribution by using the dispersion test and the Kolmogorov-Smirnov test for fitted vs. simulated residual distribution in the DHARMa package (Hartig, 2017). All tests returned a *P*-value larger than 0.2, therefore confirming the goodness-of-fit of our models. Exact binomial tests did not detect any outliers. The potential for multicollinearity among environmental covariates was checked by computing Variance Inflation Factors (Kutner et al., 2005). Since all VIFs were < 2, and therefore well below the accepted threshold of concern (5–10; Kutner et al., 2005), we excluded that multicollinearity had a significant effect on model coefficient estimates.

We selected models with the lowest Akaike's Information Criterion (AIC, corrected for small sample size) and the largest Akaike's weights (*w*AIC) as those best explaining the relative abundance of each meso-mammal species (Burnham and Anderson, 2002; Wagenmakers and Farrell, 2004; Burnham et al., 2011). AIC values were compared among competing models containing all possible combinations of environmental covariates as main effects. For models differing by ≤ 4 in AIC, conditional averaged coefficients were calculated in the package MuMiN (Barton, 2015). To estimate the overall degree of temporal overlap in activity patterns among the five most common study species (see above), we reported the local time at which each species was captured on CT in our dataset. Capture events were again restricted to one per day (randomly selected) to minimize the risk of pseudo-replication; as the same individuals visited CT sites for prolonged periods while feeding on termite mounds, the choice of one event per day ensured that each observation corresponded to an independent activity bout, given the body size of the study species (a 1-day interval was taken as longer than the time required by meso-mammals to traverse a home range; Swihart et al., 1988). In the overlap package (Meredith and Ridout, 2014), we calculated the overlap coefficient of temporal activity pattern for each species pair (delta; Monterroso et al., 2014). We adopted the delta1 estimator when at least one of the study species was captured in ≤75 events, and the delta4 when both species were captured in ≥ 75 events (Monterroso et al., 2014). The 95% confidence interval for the delta obtained from each species pair was then computed using percentile intervals of 999 bootstrap samples (Monterroso et al., 2014). Overlap in activity patterns was considered low when < 0.05, moderate when between 0.05 and 0.75, and high when > 0.75 (Mori et al., 2021). We then tested for finer-scale differences in activity patterns between species pairs by using bootstrap tests (number of bootstrap repetitions = 999) with the function compareCKern in the package activity (Rowcliffe et al., 2014; Mori et al., 2021). Bootstrap tests compare two sets of circular observations (i.e., daily activity patterns of two study species over a 24-h period) and determine the statistical significance that the two observations belong to the same temporal distribution. Rejection of the null hypothesis ($P < 0.05$) was considered as indicative of significantly different activity distributions between species pairs. A limited sample size prohibited our estimating temporal activity overlap between woodlands and riparian forests. However, our study covered a small area, and thus spatial segregation between species is unlikely.

RESULTS

Species Inventory and Relative Abundance Indices

We detected 19 species of meso-mammals on CTs in Issa (**Table 1**). RAIs indicated that two species, namel the Bushy-tailed Mongoose and the Giant Pouched Rat, were substantially more common than the others and captured on a total of 897 and 1,078 camera days, respectively. Only three other species were captured on videos on more than 50 camera days.

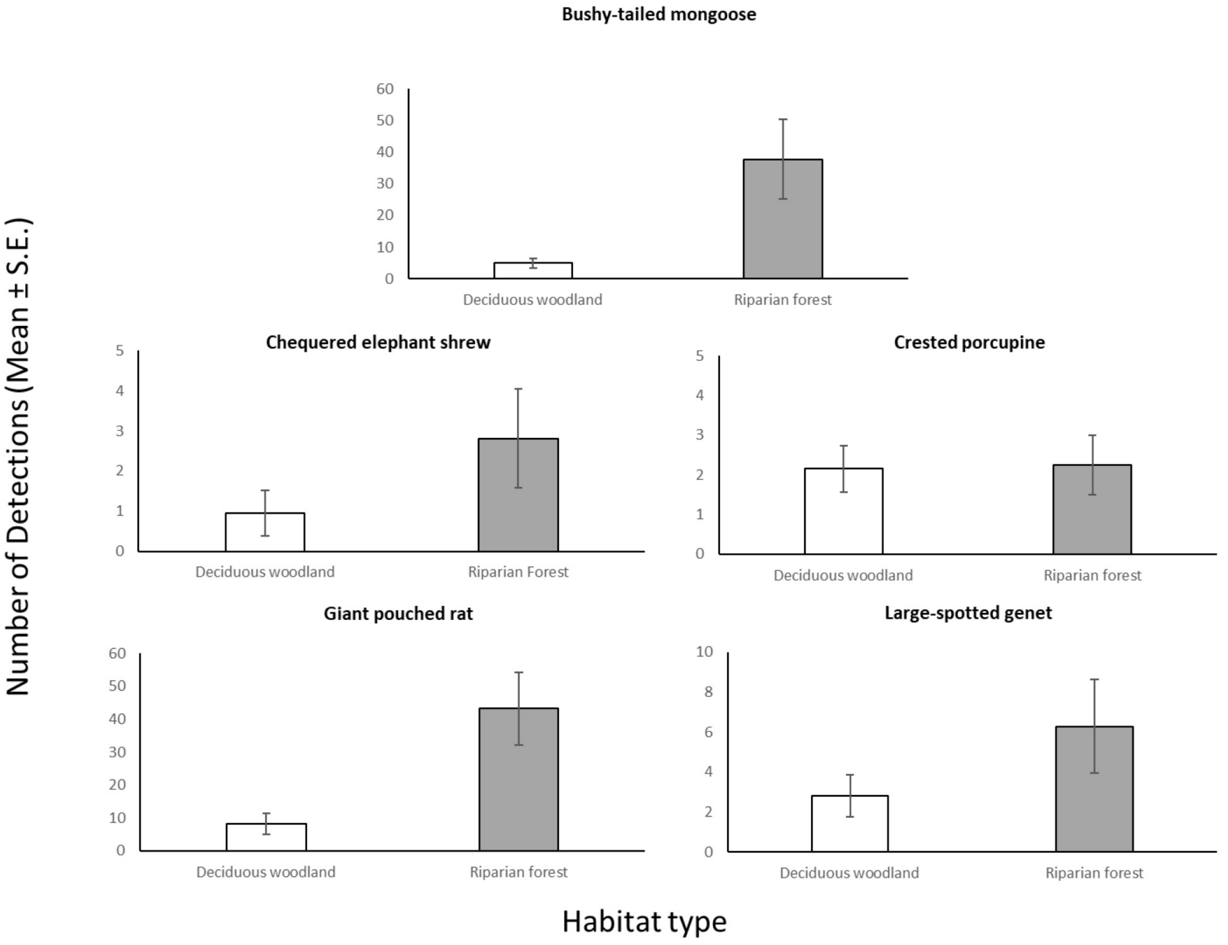

FIGURE 2 | Average number of camera days (Mean ± S.E.) in which each meso-mammal species in Issa Valley was detected, compared between CT sites in deciduous woodland (n = 20) and riparian forest (*n* = 22).

According to our expectations, most species (*n* = 10) exhibited a higher relative abundance at CT sites located in riparian forests rather than woodlands. Conversely, seven species were more often observed in the woodlands, while two (the Honey Badger *Mellivora capensis* and Rock Hyrax *Procavia capensis*) presented qualitatively similar RAIs between the two vegetation types. We also observed that some species completely avoided one vegetation type or the other (**Table 1**). For example, meso-mammals typical of open habitats, like the Serval (*Leptailurus serval*) and the Savanna Hare (*Lepus victoriae*) were never captured at riparian forest CT sites. On the other hand, species that are typical of dense habitats or are highly dependent on available surface water, such as the African Clawless Otter (*Aonyx capensis*), Marsh Mongoose (*Atilax paludinosus*), and White-tailed Mongoose (*Ichneumia albicauda*), were found only in the water-rich and well-vegetated riparian forests. These patterns suggest that species typical of different ecosystems coexist in Issa thanks to habitat heterogeneity. However, RAIs should be interpreted with caution, as most of them were computed for very small sample sizes and without taking into account the potential for spatial auto-correlation among CT sites. The use of RAIs also does not allow for estimating variation in the probability of detection among CT sites due to local micro-site conditions, and this should be taken into account for the interpretation of our results.

Ecological Drivers of Relative Abundance

Through our modeling approach, we found that three of the five most common meso-mammal species at Issa, namely the Bushy-tailed Mongoose, Giant Pouched Rat, and Chequered Elephant-shrew, were significantly more abundant at CT sites located in forests rather than woodlands (**Table 2** and **Figure 2**). Moreover, the relative abundance of the Giant Pouched Rat and of the Chequered Elephant-shrew was also higher at lower elevations (<1,450 m) and positively correlated with slope (**Table 2**), indicating that these two species utilized the Issa valley system more intensely than the plateaus. Similar trends, although non-significant, were also observed for the Bushy-tailed Mongoose (positive correlation with slope) and for the Large-spotted Genet (more abundant at lower elevations; **Table 2**). According to

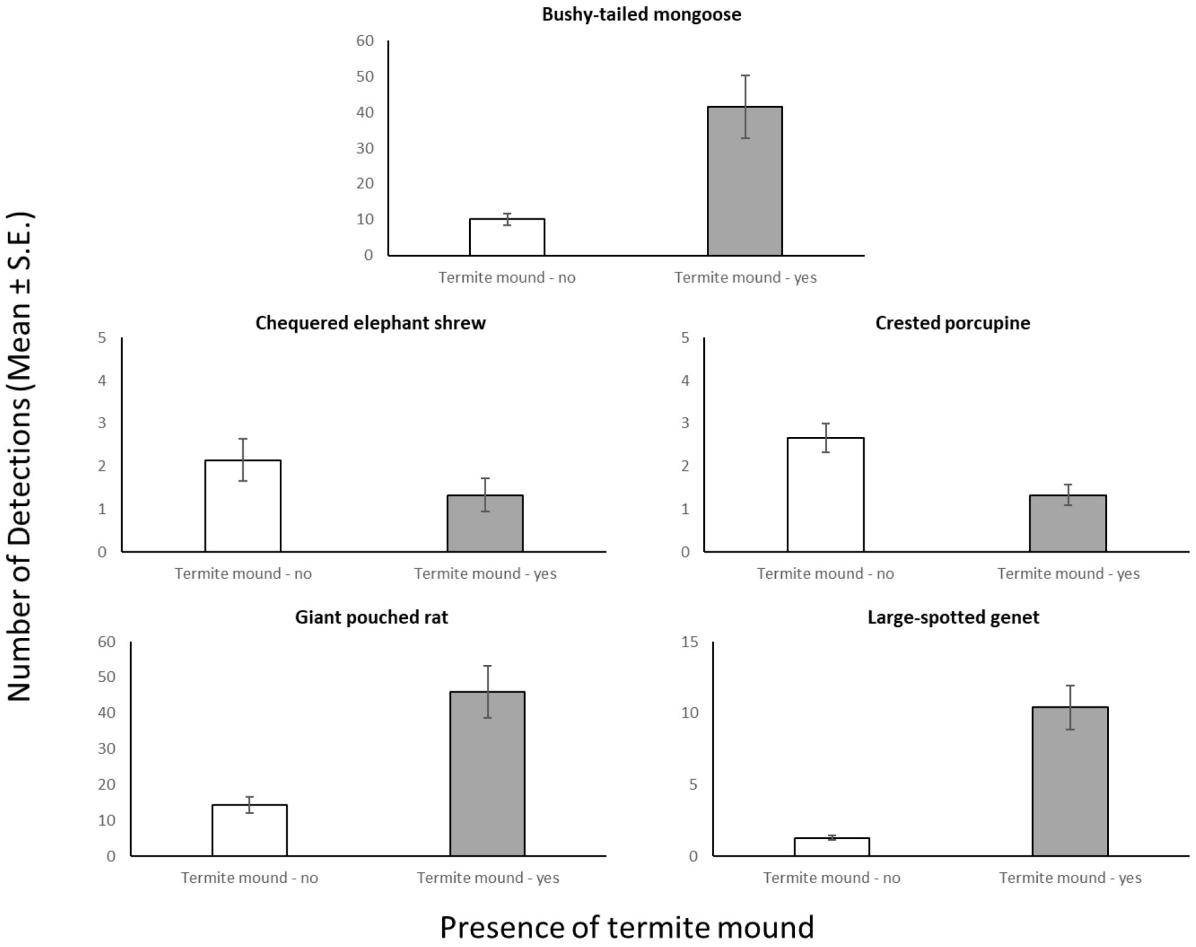

FIGURE 3 | Average number of camera days (Mean ± S.E.) in which each meso-mammal species was detected, compared between CT sites located at termite mounds (n = 15) and sites with no termite mounds in close proximity (n = 27).

our expectations, three of the four insectivorous-omnivorous species, the Bushy-tailed Mongoose, Giant Pouched Rat, and Large-spotted Genet, were also more frequently captured at CT sites located near termite mounds, rather than along game trails (**Table 2** and **Figure 3**). Only the Chequered Elephant-shrew, despite its insect-based diet, was not more common at CT sites with termite mounds than at sites without mounds (**Table 2** and **Figure 3**). No environmental covariates explained the variation in relative abundance among CT sites for the Crested Porcupine.

Temporal Overlap in Activity Patterns

We observed that four out of the five most common meso-mammals at Issa, excluding the Chequered Elephant Shrew, were largely nocturnal. Circadian overlap in overall activity patterns was thus high (>0.75) between all species (excluding the diurnal elephant shrew), irrespective of dietary similarities (**Table 3** and **Figure 3**). For example, the Large-spotted Genet, which is carnivorous but also consumes large quantities of insects at certain times of the year, exhibited substantial activity overlap ($\Delta > 0.75$; **Table 3**) with the Bushy-tailed Mongoose, and with the Giant Pouched Rat, which also often feed on insects. Nonetheless, some partitioning in activity patterns could be detected using bootstrap testing, as all species exhibited significant finer-scale differences in their temporal activity distributions between each other (**Table 3** and **Figure 4**). The Giant Pouched Rat was more active during earlier night hours compared to the Bushy-tailed Mongoose, in spite of substantial overlap in overall activity times ($\Delta > 0.75$; both species largely nocturnal; **Figure 4**). Similarly, the Large-spotted Genet was also active at night, but with more detections during early morning than the mongoose and the rat (**Table 3** and **Figure 4**). The Chequered Elephant-shrew, which is largely diurnal, appeared to almost completely segregate temporally from the larger Bushy-tailed Mongoose, Giant Pouched Rat, and Large-spotted Genet (**Table 3** and **Figure 4**) by concentrating its activity peaks in the late morning and early evening (09:00–12:00 a.m. and 08:00–09:00 p.m., respectively). Surprisingly, all primarily insectivorous species showed significantly different temporal distributions of activity from the herbivorous Crested Porcupine, which feeds mostly on roots and therefore does not represent a potential competitor over shared forage resources (**Table 3** and **Figure 4**).

TABLE 3 | Estimates of temporal overlap in activity patterns (Δ ± 95% C.I.) for pairs of the five most common meso-mammal species in the Issa Valley.

Species pairs and number of detections (in brackets)	Δ	Δ 95% C.I.	Bootstrap test *P*-values
Bushy-tailed mongoose (897)–Chequered elephant shrew (78)	0.326	0.249–0.410	*<0.001*
Bushy-tailed mongoose (897)–Crested porcupine (92)	0.833	0.748–0.909	*0.005*
Bushy-tailed mongoose (897)–Giant pouched rat (1078)	0.916	0.881–0.949	*<0.001*
Bushy-tailed mongoose (897)–Large-spotted genet (191)	0.832	0.769–0.899	*<0.001*
Chequered elephant shrew (78) – Crested porcupine (92)	0.473	0.368–0.584	*<0.001*
Chequered elephant shrew (78) – Giant pouched rat (1078)	0.366	0.297–0.438	*<0.001*
Chequered elephant shrew (78) – Large-spotted genet (191)	0.549	0.458–0.651	*<0.001*
Crested porcupine (92)–Giant pouched rat (1078)	0.821	0.731–0.900	*0.012*
Crested porcupine (92)–Large-spotted genet (191)	0.824	0.718–0.913	*0.031*
Giant pouched rat (1078)–Large-spotted genet (191)	0.781	0.715–0.742	*<0.001*

We considered Δ < 0.05 as small overlap, 0.05 < Δ < 0.75 as moderate overlap, and Δ > 0.75 as high overlap. The last column presents the statistical significance of bootstrap tests for fine-scale differences in temporal distribution of activity patterns between species pairs. Significant P-values (< 0.05) are highlighted in italics.

DISCUSSION

In this study, we used motion-triggered camera traps to investigate the ecology of a meso-mammal community in the miombo mosaic ecosystem of the Issa Valley, western Tanzania. We hypothesized that the vast deciduous woodlands characterizing the miombo would support a relatively low diversity of meso-mammal species due to the scarcity of resources for terrestrial vertebrates reported in other studies. We found that the meso-mammal community in the study area comprised a relatively small number of species (n = 19), most of them occurring at very low relative abundance. We also found that meso-mammals were more abundant in the riparian forests associated with river valleys than in the deciduous woodlands, likely due to the greater availability of forage, protective cover, and water in the wetter vegetation. Moreover, we observed that some insectivorous and omnivorous species were more abundant in immediate proximity to termite mounds, which could thus represent important resource islands for meso-mammals in the miombo. Finally, we investigated whether the presumed resource scarcity in the miombo could translate into temporal partitioning in activity patterns, so as to avoid interference competition among those species sharing similar diets, and we found evidence in support of this hypothesis.

Landscape heterogeneity may increase meso-mammal diversity through various mechanisms, from increasing food diversity (e.g., seeds, plants, invertebrates), to providing cover from predators, to increasing dispersal success through habitat connectivity (Price et al., 2010). At Issa, the species composition and relative abundance of meso-mammals mirrors that of other study sites characterized by high vegetative heterogeneity, such as Udzungwa and Mahale (Pettorelli et al., 2010; Rovero et al., 2017). Although forested areas are better represented in these sites, results from Udzungwa and Mahale also revealed that the most abundant meso-mammals were the Bushy-tailed Mongoose and the Giant Pouched Rat (Pettorelli et al., 2010; Rovero et al., 2017), similar to our findings. These were the only two species with RAIs > 1; only five other species occurred at RAIs between 0.1 and 0.5 (**Table 1**). All other species occurred at very low relative abundance, with RAI scores < 0.1. These patterns suggest that the Issa system might not represent a highly suitable environment for meso-mammals, given that only a handful of species thrive in it.

The greater relative abundance of several species in riparian forests suggests that these are important resources to meso-mammals in this mosaic system. Riparian forests usually have a very high diversity of plant species, offer nutrient-rich plant forage due to eutrophic soils, do not burn seasonally, and are located in proximity to permanent water sources (Naiman et al., 2010; Timberlake and Chidumayo, 2011). Moreover, the closed canopy cover of riparian forests provides a dark undergrowth environment, which might offer protection against larger diurnal predators (Prugh and Golden, 2014). Deciduous woodlands, on the other hand, grow on nutrient-depleted soils (resulting in low-quality plant forage), are seasonally depleted of plant forage, burn during the dry season, are well-lit due to sparser canopy cover, and generally have little to no surface water (Frost, 1996; Timberlake and Chidumayo, 2011). Riparian forests thus likely hold important year-round resources for meso-mammals, especially in terms of forage, moisture, and protective cover. The same patterns were found for rodents in the Ruvuma Landscape in southern Tanzania (Nkwabi et al., 2018). On the other hand, a study in the Katavi National Park (∼200 km South of Issa) reported a smaller number of meso-mammal species in the same size range examined here (14 species vs. 19 species at Issa; Table 1; Caro, 2003). Since Katavi is largely dominated by deciduous woodlands and grasslands, with little evergreen forest cover (Banda et al., 2008), our findings highlight the importance of riparian forests as key habitat for meso-mammals across different miombo systems.

Another possibility is that the greater relative abundance of meso-mammals observed in riparian forests at Issa could derive from a greater detectability at riparian forest CT sites, caused by differences in micro-habitat conditions between the two vegetation types. This seems unlikely, however, given that riparian forests present low-lighting conditions and more complex vegetation backdrops, which should make CT detections less likely compared to woodlands (i.e., the opposite of what we observed). Additionally, some species that are arboreal or climbers (e.g., the genet and, to a lesser extent, the Giant Pouched Rat), given similar local densities, should have been more easily detected at woodland sites, where they are forced to move for longer distances on the ground. Taken together, these

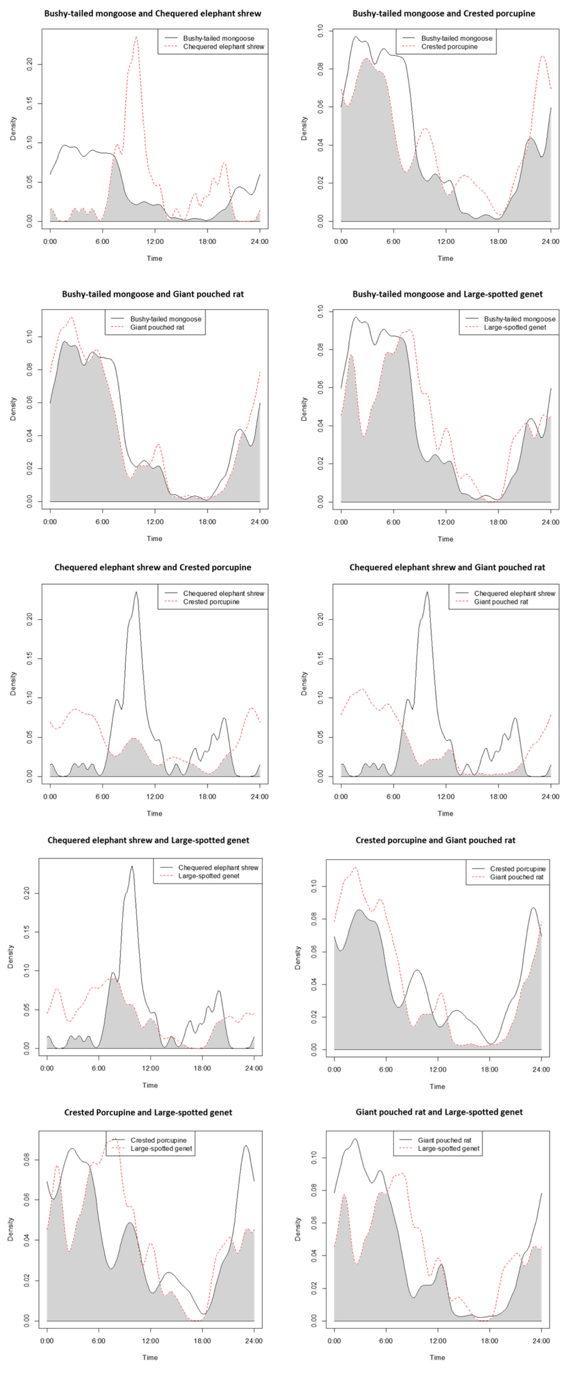

FIGURE 4 | Overlap in activity patterns between the five most common meso-mammal species in the Issa Valley, Tanzania. The plots show time over a 24-h period on the x-axis (note that at the latitude of Issa, sunrise is at about 06:00 h, and sunset at 18:00 h, throughout the year); and density of detection events, on the y-axis.

considerations indicate that the greater number of CT detections in riparian forests reflect a genuinely higher intensity of forest site use compared to woodland sites, and not an artifact of our sampling design.

Whereas some species exhibited clear preference for either open or closed vegetation, some generalist species (e.g., Crested Porcupine, Large-spotted Genet) were equally abundant in woodlands and forests. This could reflect their greater plasticity in habitat tolerance. Both the savanna/grassland species and the generalist species occurred at much lower relative abundances than the forest species; this may indicate an advantage for forest-dwelling species that lie in the miombo mosaic in the form of greater diversity of resources and greater availability of water and protective cover in riparian forests.

Termite mounds are known for their abundant supply of highly nutritious prey for mammals (Redford and Dorea, 1984) and role in increasing biodiversity (Fleming and Loveridge, 2003). Given increased RAI scores at termite mounds for 3/5 of the species we surveyed, these resources are clearly important predictors of meso-mammal habitat use in the miombo. The Bushy-tailed Mongoose is an ant and termite specialist (Kingdon, 2015), so we expected this relationship. On the contrary, the Large-spotted Genet usually feeds on beetles, grasshoppers, and small vertebrates where it has been studied previously (Roberts et al., 2007), but at Issa it may rely on termites in miombo areas between October-December when several swarming events are commonly observed (D'Ammando, pers. obs.). Similarly, the Giant Pouched Rat is reportedly granivorous, but we observed several instances of rats consuming termites from CT recordings. Termite mounds may offer protective cover to several mammal species, as nesting in mound burrows has been suggested to explain the greater abundance (both in terms of species and of individuals) of rodents in the vicinity of mounds in miombo ecosystems (Fleming and Loveridge, 2003). Future studies could resolve this issue by investigating whether the abundance of insectivorous mammals in miombo habitat increases in concomitance with alate swarming events (Dial and Vaughn, 1987), thereby indicating that the mounds may also act primarily as food sources.

The relatively low abundance of the Chequered Elephant-shrew on *Macrotermes* mounds is surprising, given that elephant shrews broadly (Woodall and Currie, 1989) and this species specifically (Redford, 1987) is known to feed on termites. It could be that the larger size of *M. subhyalinus* and *M. bellicosus* are chemically or anatomically prohibitive to consume (Longhurst et al., 1978; Phillips et al., 2021). Our interpretation is that this could reflect a behavioral strategy to avoid the other meso-mammals attracted to termite mounds. Chequered Elephant-shrews are much smaller than sympatric species at Issa and may thus incur substantial costs from competition with mongooses and genets. Moreover, the small carnivores commonly observed at termite mounds could also represent potential predators for the elephant shrew, thereby acting as a deterrent. These considerations were supported by the temporal segregation of the elephant shrew from other species.

High (temporal) overlap in activity patterns among three of four omnivorous and insectivorous species could be interpreted as evidence of little interference competition among meso-mammals in miombo ecosystems, implying that resources may not be limited. Most meso-mammal encounters were indeed in riparian forests and/or on termite mounds, which presumably offer plentiful resources (i.e., year-round green foliage, fruits, and termite swarms) when compared to deciduous woodlands. This interpretation is however, invalidated by the fact that significant differences in fine-scale temporal distributions of activity patterns were detected between all pairs of study species. These observations suggest that meso-mammals at Issa tend to actively avoid each other, thereby indicating a high potential for interference competition over limited resources. Indeed, although foraging opportunities might be abundant in riparian forests and on termite mounds, the small areal extent and patchy distribution of these habitat features likely constrains the amount of available food. Our findings thus corroborate the hypothesis that the miombo offers scarce and widely scattered resources to meso-mammals, reflected by the behavioral mechanisms of temporal avoidance observed within the omnivorous/insectivorous guild.

The unexpected differences in temporal activity distribution between the four insectivorous/omnivorous species and the root-eating Crested porcupine warrant further investigation. It is possible that the porcupine is avoided by other species due to its large size and quills, which could pose a serious danger to smaller mammals during direct encounters. Another possibility is that overlap in diet could be higher in miombo ecosystems, with species that are typically targeting insects or fruit also feeding on roots and other underground vegetal material favored by the porcupine. Detailed analyses of behavior and dietary preferences will be needed to clarify the ecological implications of this finding.

One of the distinguishing characteristics of miombo woodlands, especially in western Tanzania, is the extreme seasonality, with a 6-month wet season when most of the annual rain falls. Moreover, with anthropogenic fires burning the landscape a few months after the last rains, the physical environment is transformed in ways that are known to influence animal presence and behavior (Frost, 1996; Desanker et al., 1997; Mayengo et al., 2020). For example, rains stimulate termite activity, which can result in alate feasts for predators (Dial and Vaughn, 1987), and fires promote growth of new forage for herbivores (Green et al., 2015). Unfortunately, the effect of seasonality on the relative abundance of meso-mammals in the region remains unknown. For small mammals (<0.5 kg), which might share forage resources with meso-mammals (e.g., seeds, arthropods), reported seasonal effects on abundance are inconsistent. Using Sherman traps in Katavi National Park (~250 km SE of Issa), Caro (2001, 2002) reported a slight increase in overall captures of rodents in the dry season compared to the wet but later, Fitzherbert et al. (2007) reported no seasonal difference in captures using the same method and from the same area. In the Ruvuma area, in southern Tanzania, although data were collected across a single season, Nkwabi et al. (2018) found an interaction between vegetation and burned stage with more rodent diversity in riparian forests during sprouting, compared to freshly burned periods, whereas for miombo woodlands, they reported more diversity during recently burned periods. In the most comprehensive study, Taylor and Green (1976) used "breakback traps" to study reproduction in small mammals in Kenya. They reported a drop in abundance from early to late wet season and from mid to late dry season, similar to results from Malawi a decade later (Happold and Happold, 1991). Nonetheless, all these studies focused on smaller species than those considered for this study (therefore making comparisons difficult), and adopted different sampling methodologies.

We were not able to study the effect of seasonality and especially fire in the current study due to a limited sample size, constraints to our study design (i.e., sampling effort was biased toward the wet season, while most species had too few captures per season to estimate meaningful effect sizes), and lack of field data (on the effects of burning events at the scale of CT sites). Analyses of seasonal effects were also incompatible with our modeling approach, as duplicating camera trap sites for wet vs. dry season, while keeping all other variables constant (i.e., vegetation type, presence of termite mounds, slope, elevation) would have severely violated GLM assumptions of independence between data points and thus undermined our interpretation of the results, However, we hope that future studies incorporate these likely important influences on meso-mammal presence.

Moreover, while the number of cameras deployed for this study and the temporal coverage (36 months) are sufficient to address questions of relative abundance, there remain limitations. First, we made no attempt to quantify resource availability or evaluate habitat suitability for any of these species. Additional investigation into micro-habitat features that may promote some species over others would be very useful to discussion on inter-specific competitive dynamics. Second, comparative work from other miombo systems would allow us to better contextualize our findings. All studies to date have adopted live-trapping as a method to assess miombo small-sized mammal abundance (e.g., Caro, 2001, 2002) thus focusing on smaller species than those we considered for our CT approach. There is a dearth of published literature on meso-mammal assemblages across dry tropical woodland biomes, which means that we are unable to be confident in whether our results are typical or not for miombo mosaic systems. Finally, by identifying individual animals, we could further extrapolate population densities of each species and clarify the effects of differences in the probability of detection between CT sites on estimates of relative abundance and intensity of habitat use. Given the rise of machine learning applications to camera trap footage, future studies that integrate AI would allow even more robust analyses on resulting data (Ahumada et al., 2020).

While there are numerous, global studies on mammal declines in the Anthropocene, many focus on larger, especially charismatic species (Harris et al., 2009; Junker et al., 2012). Far fewer have focused on meso-mammals (but see Kennerley et al., 2021). This study, along with others in this Special Issue, represent an attempt not just to census meso-mammal assemblages, but also to begin to understand what drives their (relative) abundance, especially in a system that characterizes a large portion of eastern and southern Africa.

Small-sized mammal communities are reliable reflectors of biodiversity (Keller and Schradin, 2008) and anthropogenic activity (Griffiths et al., 2015) and thus can serve as important proxies through low-cost, low-maintenance remote monitoring like camera trapping. Compared to sympatric larger species, their smaller ranges and enhanced adaptability may make them more resilient to natural and anthropogenic pressures. As such, data that inform on their natural habitat preferences, strategies to minimize inter-specific competition, and overall ecology are critical when habitat change is imposed on their system. We hope to have shed light on a small (geographic) system here, but one that can serve as a model for other parts of eastern-southern Africa where miombo mosaic landscapes dominate.

DATA AVAILABILITY STATEMENT

The data have been deposited in a Dryad Repository (https://datadryad.org/stash/share/Ep6xSDSXQITHh-nfb6cviz1xSXF0VqeIG5nZ6c-VbYo).

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because data collection was based on camera traps, a non-invasive method which does not interfere with animal behavior, and does not involve contact with or manipulation of the study subjects-research was approved by Tanzania Commission for Science and Technology and by the Tanzania Wildlife Research Institute.

AUTHOR CONTRIBUTIONS

AP, FS, and GD'A conceived the study. GD'A, SP, and PS collected and cleaned the data. GD'A performed the statistical analyses. GD'A and AP wrote the manuscript to which TC, VO, FS, SP, and PS contributed. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.773568/full#supplementary-material

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The Role of Habitat Amount and Vegetation Density for Explaining Loss of Small-Mammal Diversity in a South American Woodland Savanna

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The focus of research and conservation in tropical regions is mainly devoted to forest ecosystems, usually neglecting the processes underlying widespread, more open biomes, like savannas. Here we test a wide range of sampled woodland sites across the South American savanna for the direct and indirect effects of habitat loss and vegetation density on the diversity of small-mammal species. We quantify the direction and magnitude of the effects of habitat amount (habitat loss), vegetation density (tree or foliage density), and patch size (species-area effect) on species composition and richness. We also test whether the relative effect sizes of landscape and patch-related metrics predict a persistence gradient from habitat specialist to generalist species across 54 sites. We used structural equation models (SEM) to test our predictions. After 22,032 trap-nights considering all sampled sites and 20 small-mammal species identified, the structural equation model explained 23.5% of the variance in the richness of small-mammal species. Overall, we found that landscape-level metrics were more important in explaining species richness, with a secondary role of patch-level metrics such as vegetation density. The direct effect of local landscape was significant for explaining species richness variation, but a strong positive association between regional and local landscapes was also present. Furthermore, considering the direct and indirect paths, SEM explained 46.2% of the species composition gradient. In contrast to species richness, we recorded that the combined landscape-level and patch-level metrics are crucial to determining small-mammal species composition at savanna patches. The small mammals from the South American woodland savanna exhibit clear ecological gradients on their species composition and richness, driven by habitat specialist (e.g., *Thrichomys fosteri*, *Monodelphis domestica*, and *Thylamys macrurus*) and generalist (e.g., *Didelphis albiventris*, *Rhipidomys macrurus*, and *Calomys callosus*) species' responses to habitat amount and/or vegetation density, as seen in dense-forest Neotropical biomes.

Keywords: indirect effect, patch size, regional landscape, small mammal composition, species loss, habitat quality, local scale, structural equation model (SEM)

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INTRODUCTION

In Conservation Biology, alternative hypotheses have been proposed to explain diversity loss such as the habitat amount and fragmentation *per se* hypotheses (Saura, 2020). The Habitat Amount Hypothesis (HAH) deals with the habitat amount that remains in a given landscape after disturbance and its effects on species diversity (Fahrig, 2013). On the other hand, fragmentation *per se* deals with habitat configuration, which is given by, e.g., the proportion of patches and edges (Haddad et al., 2015; Saura, 2020) or the landscape connectance (Horváth et al., 2019) present in a regional or local unit. Empirical supports for the effects of HAH and fragmentation *per se* have been found but they are difficult to disentangle (e.g., Melo et al., 2017; Gardiner et al., 2018), although there are tentative claims to put them in a more integrative framework (Horváth et al., 2019; Saura, 2020).

This debate is mainly fueled by the overall lack of standardization in such studies, such as the considered extension of landscape size (e.g., buffer of 1 km or 2 km radius), or configuration attribute (e.g., edges, patches, and isolation), leading to an at times biased conclusion in favor of one or the other (Chase et al., 2018; Horváth et al., 2019). Concerning landscape extension, some studies applied a "landscape scale effect" approach, which consists of a buffer around the sample site that varies in size according to species dispersal capacity (Melo et al., 2017; Viana and Chase, 2019). However, other studies claimed that such a local landscape view would be biased since the local landscape is inserted in a broader regional landscape context, which, in turn, will influence the local landscape dynamic (Hanski, 2015; Saura, 2020). Therefore, it's important to disentangle and understand the effect of habitat amount at different spatial scales and even in a nested landscape configuration (e.g., a local landscape nested in a regional one). Furthermore, habitat quality has been relatively successful in explaining biodiversity loss (Curran, 1982; Goward et al., 1985; Fischer and Lindenmayer, 2007). For example, habitat heterogeneity is one of the main drivers of mammalian richness and nestedness, overcoming habitat amount in a Neotropical savanna (Regolin et al., 2020). Specifically, Regolin et al. (2020) used a buffer extent of 8-km radius and concomitantly tested the effect of heterogeneity and habitat amount on mammals of different body sizes. Furthermore, patch size can affect (e.g., Lindenmayer et al., 2000) and explain local diversity (the so-called species-area relationship) by including edge effect, which decreases with patch size, and habitat diversity, which increases with patch size (Murcia, 1995; Chown et al., 1998). Therefore, there are different hypotheses for explaining the decay of biodiversity across disturbed sites, but we highlight the need of an overall standardization in studies dealing with these subjects. Combining them into an integrative framework can provide important insights (Horváth et al., 2019; Saura, 2020), particularly in poorly studied ecosystems like savannas.

The patterns and processes involved in the current biodiversity loss have been subjected to extensive studies (Dirzo and Raven, 2003). These studies have revealed important findings such as the biotic gradient in the occurrence of specialist and generalist species across landscapes or the extinction threshold in which species may or may not endure depending on the habitat amount in the landscape (Banks-Leite et al., 2014). However, research and conservation in tropical regions mainly focus on forest ecosystems, neglecting the processes underlying widespread open biomes like savannas (Olson et al., 2001; Pennington et al., 2018).

Small mammals from the South American savannas are a diversified mammalian group composed of a mix of marsupials and rodents weighing less than 1 kg on average. They exhibit different lifestyles, including arboreal, scansorial, terrestrial, and semifossorial species (Paglia et al., 2012). Essentially, marsupials tend to be more arboreal and scansorial, while rodents tend to be more terrestrial and semifossorial (Bubadué et al., 2019). In the forest biome, there are clues that they respond to the habitat fragmentation with local extinction of potentially habitat specialist species (Banks-Leite et al., 2014). On the other hand, it appears that there are common generalist species capable of occurring in different habitats of savanna, including disturbed landscapes of adjacent dense forest biomes (Melo et al., 2017; Palmeirim et al., 2020).

Studies in forest ecosystems have revealed that specialized species are more prone to local extinction in a disturbed landscape (Pardini et al., 2010). In fact, specialized species are more dependent on habitat particularities like proper microhabitats or food resources (Devictor et al., 2008; Gardiner et al., 2018). Yet, they can persist in landscapes with more habitat amounts or larger patches (Pardini et al., 2010; Melo et al., 2017; Gardiner et al., 2018). Interestingly, disturbed landscapes may be invaded by generalist species common in savannas (Maracahipes et al., 2018). This phenomenon has been observed in South America biomes such as the dense forests of Amazon and the Atlantic forest, which are invaded by species typically from the adjacent savanna (regionally named Cerrado) (Palmeirim et al., 2020). That suggests an ecological process of habitat specialization in the South American savanna biome, which is historically composed of a mosaic of grassland, woodland-savanna, and forest vegetation, but which is indeed dominated by woodlands rather than the African traditional open, grassland savanna (Eiten, 1982; De Vivo and Carmignotto, 2004). Such woodland savanna has a different characteristic regarding the forest biome, being essentially dry, highly seasonal, and less tall regarding tree or shrub height (Eiten, 1982). Therefore, one question here is to determine if there is a gradient from woodland habitat specialist to generalist species in such savannas as occurs in dense humid forests and if that species-composition gradient closely follows the habitat amount as a predictor or another habitat index such as vegetation density.

Here we test a wide range of sampled sites across the South American woodland savannas for the direct and indirect effects of habitat loss and vegetation density on the variation of small-mammal species diversity under the hypotheses of habitat amount (Fahrig, 2013) versus habitat complexity (August, 1983) as drivers of species diversity. Precisely, we quantify the direction and magnitude of the effects of habitat amount (habitat loss), patch size, and vegetation density (which are measures of habitat quality) on species composition and richness. We also test if the relative effect sizes of local, regional, and habitat-related metrics predict the species richness variation and a persistence gradient from habitat specialist to generalist species across savanna sampled sites. We predict that (1) overall habitat amount will be more critical than patch size (based on Melo et al., 2017, for small mammals using a 2-km radius buffer) in explaining the response variables. However, (2) vegetation density will be more important than habitat amount or patch size in driving the species-composition gradient (based on Regolin et al., 2020, for mammals). Overall (3) we expect to find negative effects of habitat loss and habitat quality on both species composition and richness, especially in savanna landscapes with low and intermediate levels of habitat amount (Pardini et al., 2010). That is, (4) we expect to find different community compositions according to habitat amount and vegetation density, (5) with more woodland-specialist species (disregarding taxonomic group, marsupial or rodent, but segregating those functionally more terrestrial species; Melo, 2023) occurring in landscapes with more woodland cover or in patches with high density of trees or foliage (Pardini et al., 2005).

MATERIALS AND METHODS

Study Area

Our studied samples are located in a woodland savanna region in the central portion of South America, regionally named Cerrado. The Cerrado occupies approximately 22% of Brazilian territory, extending to smaller parts of Paraguay and Bolivia. The vegetation is heterogeneous and contains different physiognomies, including grasslands, scrub-like savanna, woodland areas, and gallery forests (Eiten, 1982). We selected our samples from the southern part of this ecoregion (Cerrado) where the woodland savanna (regionally called as “cerradão”) is highly dominant (Silva et al., 2006). In this vegetation type, the occurrence of arboreal trees typical of savanna is common, giving an overall appearance of a dense forest (**Supplementary Figure 1**). Most open areas consist of highly modified grazing lands composed of exotic species.

The region has undergone intensive agricultural and pastoral expansion over recent years, being under a rapid conversion of natural areas to croplands and grazed lands. Some studies estimated the loss of around 50% of the Cerrado natural vegetation, replaced by anthropic land use, and that about 80% are under some form of human use (Mittermeier et al., 1999; Machado et al., 2004; Klink and Machado, 2005). Besides, only 6.5% of the Cerrado is legally protected (Françoso et al., 2015).

We sampled six regional square landscapes of 15 × 15 km (hence 22,500 ha each), between the coordinates 20°17′–21°15′S and 54°53′–56°31′W (**Figure 1**). These samples included different percentages of habitat amount (i.e., woodland savanna which occurs in more or less isolated patches): two with 10, two with 30, and two with 50% of natural habitat cover. The landscapes are similar in topography and climate but differ in the average distance between patches, which is higher in landscapes with less habitat amount. The maximum distance between the six regional landscapes was ∼ 160 km and the minimum distance between sampled areas was ∼ 1 km. All of them are inserted in the same river basin (left margin of the Paraguay River) to reduce the variation in species composition between sampled areas. Thus, differences in species composition between them should be primarily related to differences in the habitat amount and vegetation quality and not to differences in species distribution range between areas.

Small Mammal Sampling

In each regional landscape, we chose nine patches to sample small mammals. Each patch received 20 live traps distributed along two transect lines 300 m apart from each other and at 50 m from the patch edge. In each transect, ten live traps were placed alternately on the ground (wire: 33 cm × 12 cm × 12 cm) and in the understory (Sherman: 30 cm × 9 cm × 7 cm) at 1.5 m height. The transect lines were inserted only in woodland areas since the gallery or riparian forest can have a particular fauna and were not present in all patches.

Four field surveys of five or six consecutive nights were conducted, two in the rainy season (February/March 2012 and November/December 2012) and two in the dry season (July/August 2012 and June/July 2013). We believe that our effort (mean of 408 trap-night per patch) was enough to sample the local community structure of small mammals by sampling rather common species (and possibly some rare ones) living in each patch (see Regolin et al., 2020 for a similar approach).

We marked the small-mammal individuals captured with numbered ear-tags (Tag style 1005-1, National Band and Tag, Newport, KY, United States) and released them at the same point of capture. When identification in the field was not possible, we euthanized the individual for identification in the laboratory. The collected individuals were deposited in UFSM and UFMT mammal collections as vouchers. Sampling technique and specimen collection were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (protocol 30808-2) and comply with guidelines published by the American Society of Mammalogists for the use of wild mammals in research (Sikes and Gannon, 2011).

Measures of Species Composition and Richness

To infer ecological processes operating in fragmented landscapes, we quantified species composition and richness for each sampling site. Species richness was calculated by counting the number of small mammal species observed in each sampled site. Therefore, we considered the two transect lines of a patch together as a sampling unit (referred as “site” hereafter). To verify whether our results were biased by incomplete sampling, we extrapolated species richness in each sampled site with Chao (1984) non-parametric method, using the *estimateR* function in the vegan package (Chiu et al., 2014; Oksanen et al., 2020). Because the observed and extrapolated species richness models were highly associated (**Supplementary Figure 2**), we used the extrapolated results, placing the observed ones as supplementary. Based on species-accumulation curves from the *specaccum* function in the vegan package (Oksanen et al., 2020), we concluded that our sampling

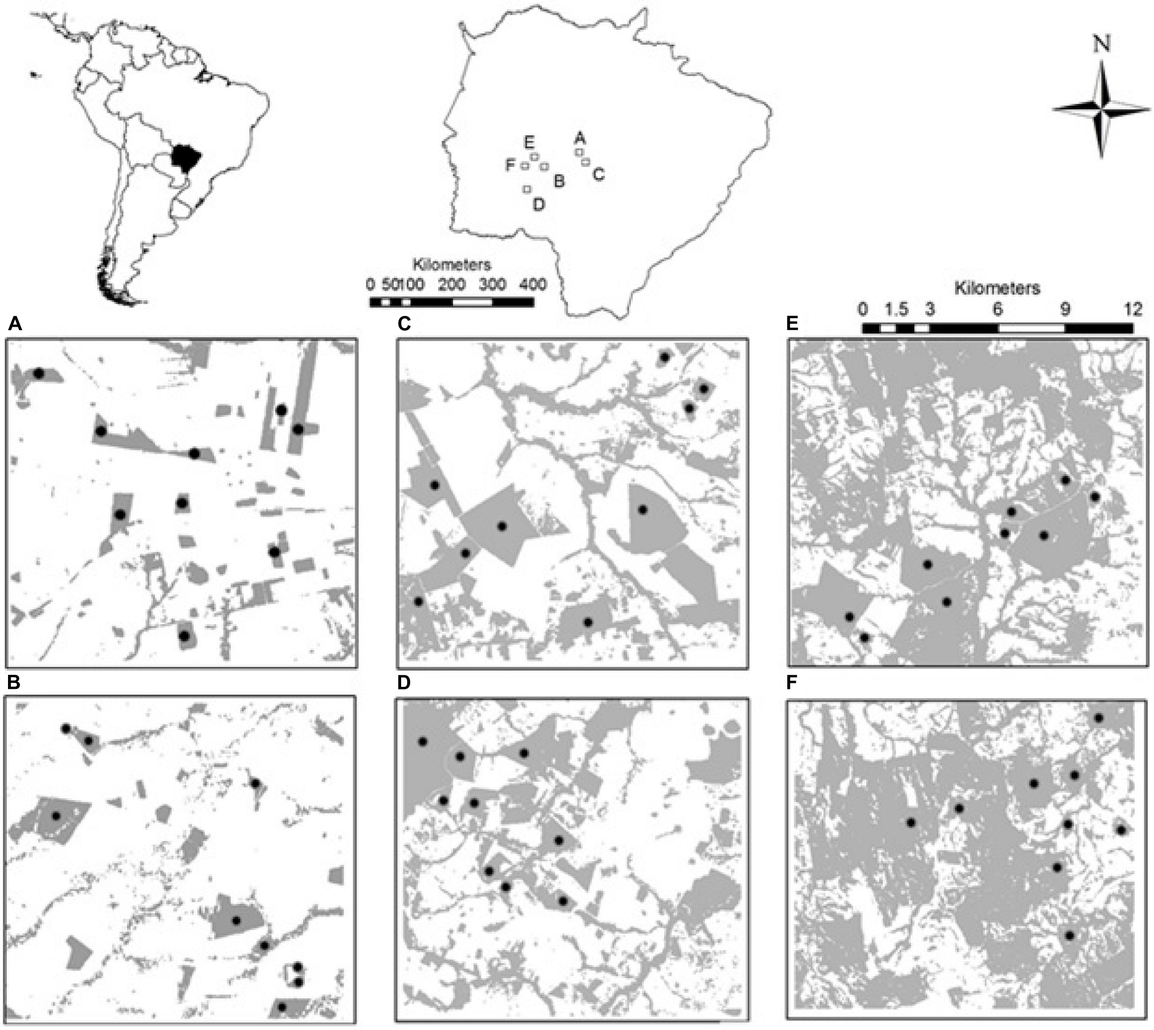

FIGURE 1 | Regional landscapes with 10% **(A,B)**, 30% **(C,D)** and 50% **(E,F)** of habitat amount indicating the distribution of sampled patches (dots). In gray, areas of natural remaining woodland savanna vegetation ("cerradão"). Empty white spaces indicate the matrix around woodland savanna patches which are mainly composed by pastures. The maps on the top situate the study area in South America (left) and the Mato Grosso do Sul state (right).

events were appropriate to detect most of the species present (**Supplementary Figure 3**).

The changes in species composition between all pairs of sites were detected using classical scaling (Principal Coordinates Analysis—PCoA) based on a Jaccard dissimilarity matrix. The Jaccard dissimilarity captures the degree to which communities differ in their observed composition (see Baselga, 2012, for further discussion on the topic). We used the scores of the first PCoA component to summarize the species composition among sampled sites. Jaccard dissimilarity was computed using the *vegdist* function from the vegan package (Oksanen et al., 2020) and the PCoA using the *pcoa* function from the ape package (Paradis and Schliep, 2019).

Specialist vs. Generalist Species

Determination of species habit regarding habitat selection was performed according to the classification in Melo et al. (2017). Small-mammal species were classified as specialist or generalist according to the following criteria: (1) publications indicating the species is sensitive to woodland savanna loss and/or (2) studies showing occurrence is restricted to woodland areas in the case of specialist species, i.e., generalist species are not sensitive to woodland loss and occur in different habitat types (e.g., grasslands and riparian forests). This *a priori* habitat-use classification was compared with a species gradient of woodland occurrence generated in this study, ordering species occurrence according to the degree of species affinity to sites with more habitat amount or vegetation density (see the PCoA analysis below).

Patch and Landscape Variables

We classified recent TM/Landsat-7 images of the south region of Cerrado using the GIS SPRING program (Camara et al., 1996). Using a supervised classification, we classified the study region following a two-step process. First, we classified the landscape as woodland/not woodland, and then we quantified the cover (habitat amount) by wooded habitat as a metric of "habitat" (**Table 1**).

Our study comprised three different hierarchical spatial scales: (i) six regional 225 km^2 square landscapes with 10, 30, or 50% of habitat amount; (ii) 54 local landscapes (nine local landscapes inserted in each regional landscape), which consists of a 1 km-radius buffer around the sampled patch; and (iii) the 54 sampled patches (one patch inside each local landscape), which received two transect lines that were grouped as a unique sampled site (**Figure 1** and **Table 1**). As the predictive power was very congruent when considering alternative buffers of 0.5, 0.75, 2, 3 km radius (**Supplementary Table 1**), we used the scale of 1 km-radius buffer to represent local landscape characteristics.

Our predictor variables in each scale were: (i) the regional habitat amount (corresponding to 10, 30, or 50% of habitat amount); (ii) local landscape habitat amount (continuous variable corresponding to the habitat amount at 1 km-radius local landscape); (iii) vegetation density, and (iv) patch size (both continuous) (**Table 1**). For vegetation density, we used the normalized difference vegetation index (NDVI) to quantify the average density of vegetation in each patch, whereby higher values indicate patches with denser, more complex vegetation. This index is based on the contrasting behavior of the spectral reflectance measurements acquired in the visible (red) and near-infrared regions. The NDVI provides an estimation of vegetation density in each patch because it is highly correlated with vegetation parameters such as green-leaf biomass, green-leaf area, and absorbed photosynthetically active radiation (Curran, 1982; Goward et al., 1985; Colombo et al., 2003; Wood et al., 2012). We quantified NDVI during the dry season of 2013 when the sky is free of clouds, which usually interferes in this estimation, by taking the images related to the time of field survey and processing them at the Instituto Nacional de Pesquisas Espaciais (INPE, Santa Maria).

Statistical Modeling

We implemented a Structural Equation Modeling (SEM) to assess the magnitude and direction of habitat loss and vegetation density on species diversity (i.e., species composition and richness). SEM is a powerful tool for exploring multivariate causal relationships and has been routinely used for several ecological applications (Grace et al., 2010; Fan et al., 2016). Our framework hypothesizes that differences in species composition and richness among sampled sites can be predicted by direct and indirect effects of variables measured at the patch (patch size and averaged patch NDVI = vegetation density, hereafter) and landscape levels (habitat amount at a local landscape within 1 km-radius, and habitat amount at a regional landscape within a ~7.5 km-radius). Specifically, the direct paths on the species composition and richness included the effects of patch size, vegetation density, habitat amount at 1 km-radius buffer (local landscape cover, hereafter), and habitat amount inside a 225 km^2 area (regional landscape cover, hereafter).

Additionally, we modeled three indirect paths in which the effects at the landscape level can be mediated through variables at the patch level. For example, the regional landscape cover was predicted to indirectly affect species richness through local landscape cover and vegetation density. Also, local landscape cover was predicted to affect species diversity (composition and richness) indirectly through vegetation density. Lastly, patch size was also adjusted to indirectly affect species diversity through vegetation density (*via* edge effect, for example). The total effect of a predictor on species composition and richness is defined as the sum of direct and indirect paths.

We considered linear fits for all paths in the SEM and ran separate models for extrapolated species composition and richness (PCoA axis 1). We used the standardized regression coefficients (β) to evaluate the relative contribution of each hypothesized effect. Unstandardized coefficients, which provide measures of the expected change in response variables in absolute units, are shown in the **Supplementary Material**. We also previously checked that the included variables in the SEM do not exhibit high collinearities (**Supplementary Figure 4**). SEM was conducted using the *sem* function from the R lavaan package (Rosseel, 2012). All procedures were performed in the R software (R Development Core Team, 2021).

RESULTS

Species Richness

Surveys resulted in 22,032 trap-nights considering all sampled woodland patches. We identified 20 small mammal species (eight marsupials and 12 rodent species) (**Supplementary Table 2**). The structural equation model (SEM) explained 23.5% of the variance in small mammal species richness (**Figure 2A**). Still, roughly similar results were recorded when using observed species richness instead of extrapolated richness (**Supplementary Figures 5**, **6**).

Overall, we found that landscape-level metrics appear to be more important in explaining species richness among sites (**Figure 2A**). The direct effect of local landscape cover was the main determinant of species richness ($\beta = 0.437$, $Z = 2.192$, $p = 0.028$), whereby local-landscape habitat amount is often translated into greater species richness (**Figure 3A**). We found strong positive associations between the regional and local landscape cover ($\beta = 0.592$, $Z = 7.253$, $p < 0.001$), which was translated into the effects of the regional landscape cover indirectly mediated by the local landscape cover as relevant for explaining species richness variation [$\beta = 0.259$ (0.592×0.437), $Z = 2.014$, $p = 0.007$]. We also found no direct association between the regional landscape cover and species richness ($\beta = -0.114$, $Z = -0.733$, $p = 0.464$).

Among patch-level variables, we only recorded significant direct effects of vegetation density on species richness ($\beta = 0.213$, $Z = 2.049$, $p = 0.040$), indicating that species richness and vegetation density are positively related (**Figure 3B**). We found no significant evidence for a direct effect of patch size ($\beta = -0.065$, $Z = -0.259$, $p = 0.796$) nor for remaining

TABLE 1 | The three level spatial extents measured in this study, which were used as predictors for small-mammal composition and richness.

Spatial predictor	Regional landscape	Local landscape	Vegetation density	Patch size
Hypothesis	Habitat amount	Habitat amount	Habitat quality	Habitat quality
Scale	Regional	Local	Local	Local
Extent	15 × 15 km (225 km^2) quadrat	1-km radio buffer	Patch area	Patch area
Sample design	9 patches or buffers	20 live traps	20 live traps	20 live traps
Sample units	6 landscapes (2 × 10%, 2 × 30%, 2 × 50%)	54 landscapes	54 patches	54 patches

All predictors have the woodland savanna ("cerradão") as focal habitat, measured on 54 sampled sites distributed across six regional landscapes.

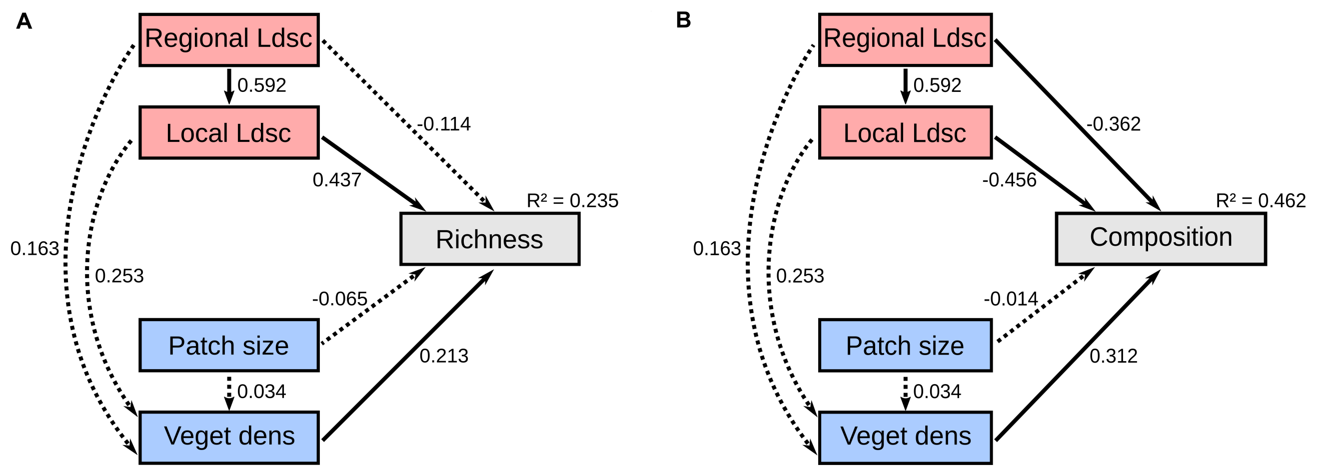

FIGURE 2 | Structural equation models examining the direct and indirect effects of landscape-level (red) and patch-level (blue) variables on small mammal diversity of a woodland savanna region of South America. **(A)** Extrapolated species richness and **(B)** species composition (PCoA axis 1). Species richness was extrapolated for each site using the Chao index. Significant paths ($p < 0.05$) are shown in solid black arrows and non-significant paths are shown in dashed arrows. The values underlying the lines indicate standardized path coefficients. extrapolated species richness (Richness), species composition (Composition), regional landscape cover (Regional Ldsc), local landscape cover (Local Ldsc), and vegetation density (Veget dens).

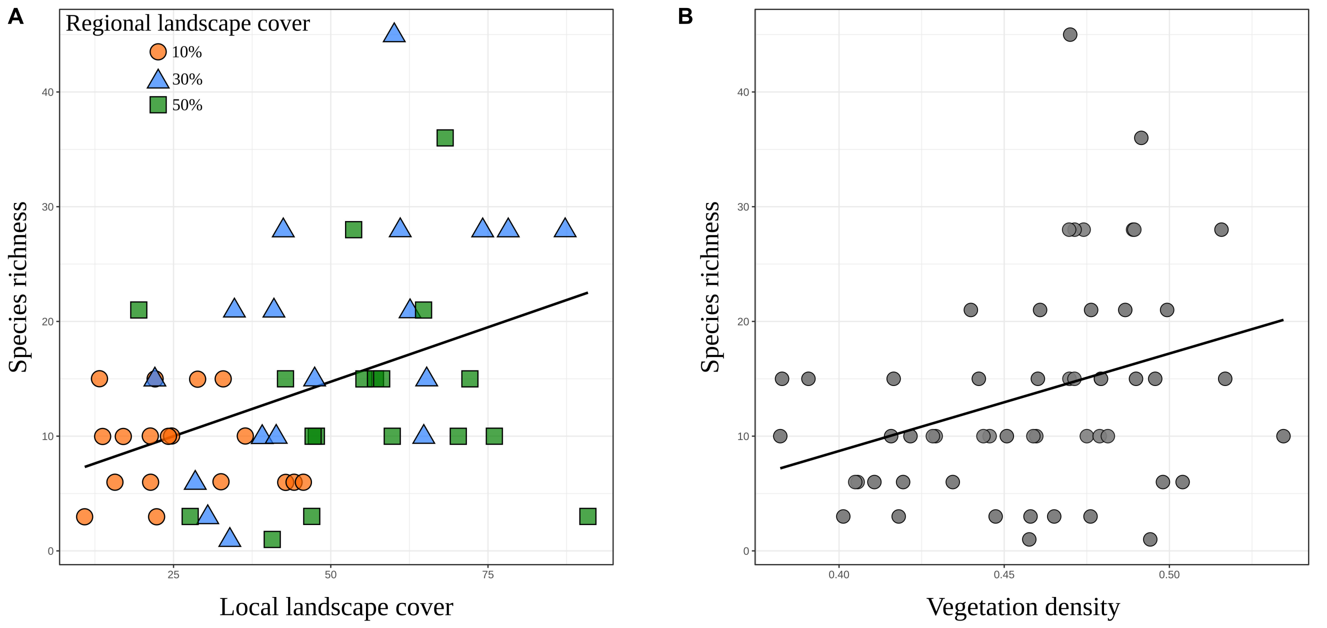

FIGURE 3 | Relationship between extrapolated species richness and **(A)** local landscape cover or **(B)** vegetation density in a woodland savanna region of South America. Points in panel **(A)** are color-coded according to regional landscape cover, which include 10% (orange), 30% (blue), and 50% (green) forest cover.

indirect paths influencing species richness, which included the effects of regional landscape cover on vegetation density [β = 0.035 (0.163 × 0.213), *Z* = 0.858, *p* = 0.391], local landscape cover on vegetation density [β = 0.054 (0.253 × 0.213), *Z* = 1.379, *p* = 0.168], and patch size on vegetation density [β = 0.007 (0.034 × 0.213), *Z* = 0.237, *p* = 0.813] (**Figure 2A**). Unstandardized (raw) parameter estimates, errors, and *p*-values are shown in **Supplementary Table 3**.

Species Composition

The SEM considering the hypothesized direct and indirect paths explained 46.2% of the changes in species composition (**Figure 2B**). In contrast to species richness, we recorded that both landscape-level and patch-level metrics are important to determine the species composition of small mammals (**Figure 2B**). On the species gradient measured by the PCoA analysis, the first two axes captured ∼44% of variation in the local communities, with the first axis responding for 24.1% (eigenvalue: 2.78) and the second one for 19.6% (eigenvalue: 2.26). The first five PCs summed 77% of explained variance, but having 54 axes generated (**Supplementary Figure 7**). The contribution of each species to the first two ordination axes can be found in **Supplementary Table 5**.

More specifically, local landscape cover was the main determinant of species composition (β = −0.456, *Z* = −3.271, *p* = 0.001), whereby some species were clearly associated with local landscapes with higher habitat amount (**Figure 4**). Similarly, the regional landscape cover had strong effects on species composition directly (β = −0.362, *Z* = −2.322, *p* = 0.020) and indirectly mediated through the local landscape cover [β = −0.269 (0.592 × −0.456), *Z* = −2.720, *p* = 0.007]. In fact, sites with low regional percentage of forest cover (10%) tended to harbor more similar sets of species that are remarkably different from those sites with higher regional percentage of forest cover (50%) (**Figure 5**). That reveals the existence of savanna-habitat specialist and generalist species of small mammals (see generalist-specialist species gradient in **Figure 4**). The *a priori* classification (Melo et al., 2017) mostly matches with our findings (70% for the 10 most specialist species) such as the woodland specialist species (e.g., *Hylaeamys megacepahlus*, *Marmosa rapposa*, *Thrichomys fosteri*, and *Monodelphis domestica*). However, despite the classification as generalist species, we have found *Thylamys macrurus* as a rather habitat specialist species and two species of *Cerradomys* (**Figure 4**).

At the patch level, we found significant and direct effects of vegetation density on species composition (β = 0.312, *Z* = 3.231, *p* = 0.001), implying that species composition is different according to places with more, or less, vegetation density (**Supplementary Figure 8**). These effects of vegetation density on species composition were even more evident when considering the second axis of the PCoA (**Supplementary Figures 9**, **10**). We also recorded that the effects of patch size were non-significant and weak (β = −0.014, *Z* = −0.106, *p* = 0.916). The remaining indirect paths were also not

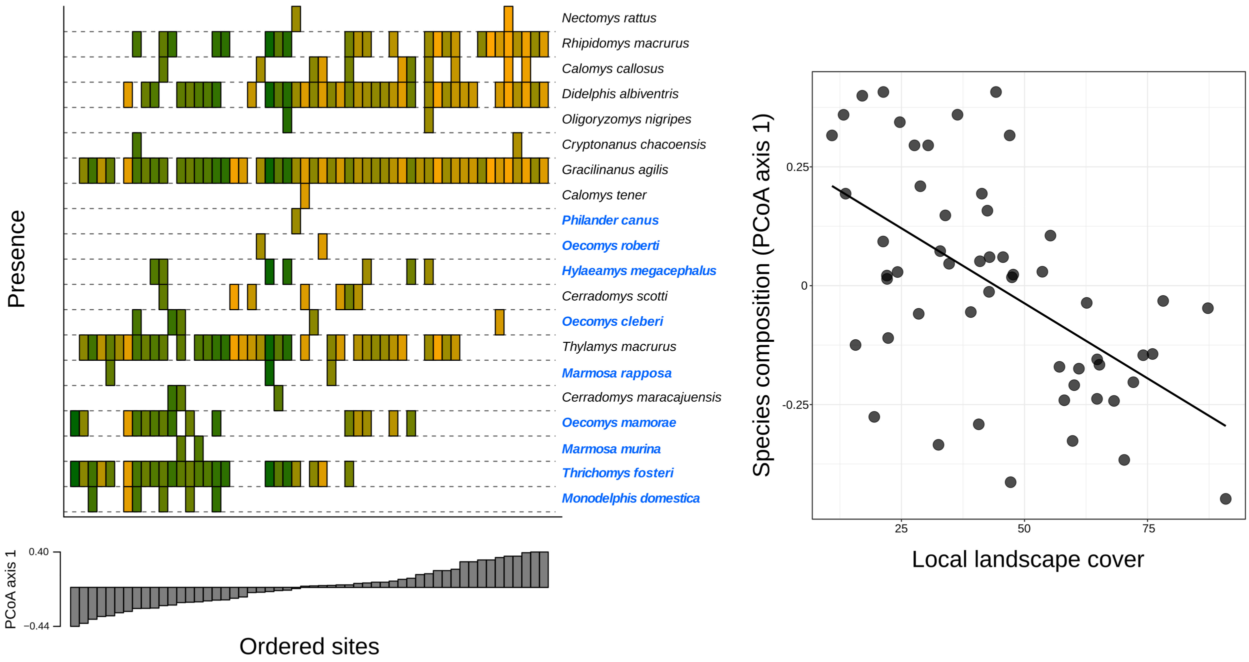

FIGURE 4 | Relationship of species composition and local landscape cover in a woodland savanna region of South America. Ordination histograms show species presence and composition among the sampled sites. Sites are ordered according to the first axis of a Principal Coordinates Analysis (PCoA axis 1) based on the Jaccard dissimilarity index. Adjacent columns (in gray; PCoA loadings) indicate sites with a more similar species composition. Colors represent the amount of local landscape cover, which ranged from least (orange) to most coverage in the local landscape (green). Note that sites located on the negative portion of axis 1 are more often associated with local landscapes that have greater vegetation cover and habitat-specialist species (species names colored in blue, according to Melo et al., 2017).

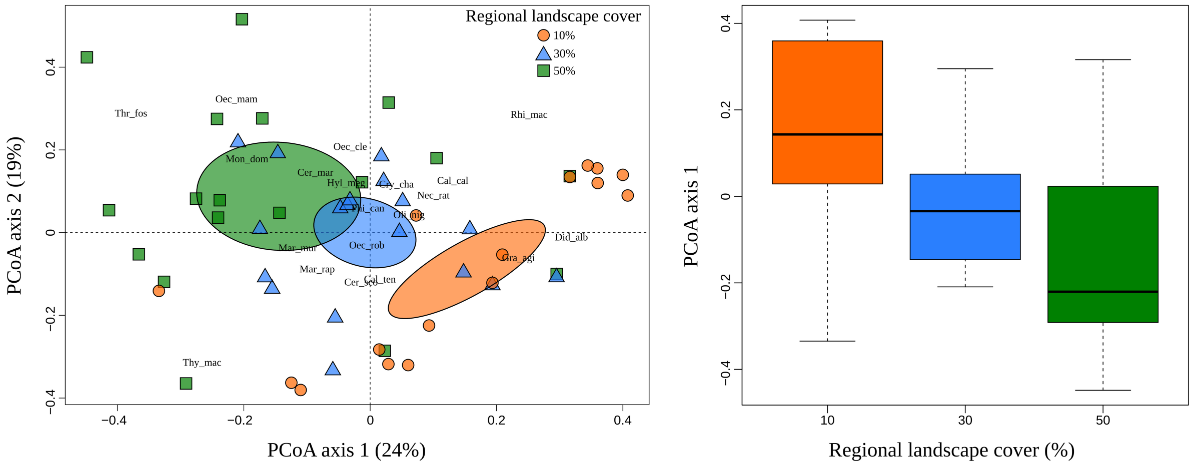

FIGURE 5 | First two ordination axes and boxplot showing the relationship of species composition and regional landscape cover in a woodland savanna region of South America. Principal Coordinates Analysis (PCoA) ordinations of sites within regional landscapes that have different amounts of the forest: 10% (orange circle), 30% (blue triangle), and 50% (green rectangle). Colored ellipses indicate the 95% confidence interval. For the sake of simplicity, we present abbreviated species names (see **Supplementary Table 2** for full names). The box-plot at right shows the median position and the inter-quartile range (lower and upper quartile) of species pool according to each regional scale.

significant (**Figure 2B**), which included the effects of regional landscape cover on vegetation density [β = 0.050 (0.163 × 0.312), Z = 0.958, p = 0.338], local landscape cover on vegetation density [β = 0.078 (0.253 × 0.312), Z = 1.339, p = 0.181], and patch size on vegetation density [β = 0.010 (0.034 × 0.312), Z = 0.232, p = 0.817]. Unstandardized (raw) parameter estimates, errors, and p-values are shown in **Supplementary Table 4**.

DISCUSSION

Our main findings suggest that mainly habitat amount but also vegetation density are important factors to determine the diversity of small mammal species (species richness and composition) across woodland patches of South American savannas. Furthermore, direct and indirect effects of the predictors analyzed are stronger on predicted species composition gradient (46%) than on species richness gradient (23%). However, all these results collectively also indicate the prominent effects of habitat amount over vegetation density in determining species diversity patterns (see Gardiner et al., 2018 for similar findings in Midlands region of Tasmania). Our predictions were partially anchored in Melo et al. (2017), who found habitat amount having a stronger effect on species richness than other predictors such as patch size and isolation. Another relevant result is the preponderance of vegetation density over patch size (but see Lindenmayer et al., 2000 for an important effect of patch size on Australasian mammals) in explaining small-mammal diversity, which we associate with the overall characteristic of the South American savanna, i.e., harboring a variety of different habitat types (forests, shrublands, and grasslands; Eiten, 1982) and favoring ecological filter, related to a somewhat variable small mammal composition. We discuss these findings in more detail in the following paragraphs.

The habitat amount was the best predictor for both compositional and richness variation, overcoming patch size and vegetation density. This finding has also been reported by Melo et al. (2017) based on a 2-km radius buffer. According to Melo et al. (2017) and Vieira et al. (2018), they demonstrate the extent of 2 km radius is the best buffer extant when considering the average small mammal dispersal capacity. However, our estimate using 1 km for buffer extent fit our expectations regarding habitat amount effect on small mammals. Studies on Landscape Ecology have shown that increasing spatial extent leads to the increasing importance of niche selection and the strength of these scaling effects depends on environment configuration, dispersal capacity, and niche breadth (Viana and Chase, 2019). Furthermore, a review study that included spatial scale studies in their estimates of biodiversity variation found frequent and strong scale-dependence in these estimates (Chase et al., 2018). The habitat amount theory to explain biodiversity variation is based on the quantity of remaining habitat in a standardized area (buffer), and the landscape connectance is key for maintaining biodiversity (Horváth et al., 2019) such as that of small mammals (Pardini et al., 2010). In fact, we found a strong effect of the habitat amount on species richness and identity of small mammals, reflecting that this fauna is significantly affected by the quantity of habitat within the landscape. Surely connectance between patches is fundamental to connect populations and avoid local extinction, maintaining higher species richness in landscapes with more preserved habitat. Species composition is also driven by habitat amount in which places with more habitat amount has different species composition, i.e., habitat-specialist species which have specific attributes (e.g., small body mass and more cursorial habit) important for their persistence in the landscape (Püttker et al., 2013; Melo, 2023).

An interesting finding is the indirect (but also the direct) effect of the regional landscape, through the local landscape, on small-mammal species composition and richness. This suggests that regional processes (at ~7.5 km radio extent in our study) more than local ones (at 1 km-radio extent) are driven the small-mammal species diversity, i.e., regional landscapes with more habitat amount will influence local landscapes (see Pardini et al., 2010) that also have more habitat amount to keep a higher species richness and population structure, maybe with a stronger effect as a whole (Henein et al., 1998). That is the same as saying certain local landscapes with less habitat amount will be compensated by surrounding local landscapes with more habitat amount within a given regional landscape. That is in accordance with the connectance hypothesis (Horváth et al., 2019), which helps connect semi-isolated populations, leading to the persistence of species over time (see e.g., Henein et al., 1998). However, when habitat loss extrapolates a species extinction threshold at a regional scale, a moderate local habitat amount is not enough to compensate and support viable populations in the long-term. This regime shift was already observed for the Atlantic forest (Pardini et al., 2010), the Amazon forest (Palmeirim et al., 2020), and elsewhere in temperate woodlands (e.g., Gardiner et al., 2018), and our results indicate a similar pattern for the savanna (see **Figure 3**). That is the same as saying that such ecosystems (composed by woodland savanna or dense forest) are similar in the case of having species that are capable of crossing the open matrix and others that cannot: the South American savanna has woodland specialist species that, when isolated in landscapes with low woodland cover will be extinct locally or regionally. However, in our study, the non-significant effects at the regional scale (e.g., *via* habitat quality variables) should be viewed with care due to our small number of replicates at this large scale.

Vegetation density was important to explain the variation in small-mammal species composition, as was habitat amount. It is noteworthy that vegetation density is independent of habitat amount while affecting species composition (**Figure 2**). Thus, places with more vegetation density harbor different species composition, such as the species *Monodelphis domestica*, *Thrichomys fosteri*, and *Marmosa murina* (**Figure 4**; see Cáceres et al., 2010), which are found in complex sites exhibiting, e.g., more foliage diversity (Wood et al., 2012). In the case mentioned above, these species are habitat specialists (Lacher and Alho, 2001; Melo et al., 2017), which we now confirm for the Neotropical savanna, as in forest biomes (Pardini et al., 2010; Palmeirim et al., 2020). According to our findings, three species previously classified as generalist species (based on Melo et al., 2017) could be woodland specialist species: *T. macrurus* and two *Cerradomys* species (*C. maracajuensis* and *C. scotti*). In the case of *C. scotti*, it is possible that adjacent, more open savanna habitats (e.g., "cerrado" stricto sensu; Melo et al., 2017) favor its occurrence in savanna woodlands, but in fact this species did not occur in areas with low habitat amount (**Figure 5**), indicating at least an intermediate sensitivity to habitat loss in the southern Cerrado. Thus, these species disappear from patches inserted within landscapes with severe habitat loss (such as those with only 10% forest cover; **Figure 5**; see simulations in Henein et al., 1998). As expected, these specialist species are mainly terrestrial (Paglia et al., 2012) as found in the Atlantic Forest ecosystem (Püttker et al., 2013; Melo, 2023). On the other hand, there are those habitat-generalist species of savanna that occur in less foliage-density patches (such as in grasslands, shrublands, and small and medium-sized patches with major edge effect and disturbance), such as *Didelphis albiventris*, *Gracilinanus agilis*, *Calomys callosus*, and *Rhipidomys macrurus* (Mares et al., 1986; Cáceres et al., 2010; Santos-Filho et al., 2012; but see Lacher and Alho, 2001, for *R. macrurus*).

In conclusion, the small mammals from South American savanna exhibit clear ecological gradients on their species composition and richness, driven by habitat specialist and generalist species responses, as seen in forested Neotropical biomes. We detected a clear pattern of species loss with decreasing habitat amount under both local and regional scales, besides an interaction between them. We also detected vegetation density as having a secondary role, but not less important, particularly on species-composition variation. Overall, patch size does not affect small-mammal diversity variation. Next, investigating how fragmentation *per se* acts within different regional landscapes (e.g., 10% or 30% habitat remaining) could be a path for new research in the savanna biome. It is also necessary to assess whether patch size is important in the context of a specific habitat-amount threshold for small mammals (or other taxa) of the savanna biome, as found for the forest biome (Pardini et al., 2010).

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

Sampling techniques were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (protocol number 30808-2). Ethics animal procedures followed ASM guidelines (Sikes and Gannon, 2011).

AUTHOR CONTRIBUTIONS

GM and NC conceived the study aim and hypotheses. GM and JS designed the data collection and carried out fieldwork. FC statistically analyzed the data with input of NC and GM. All authors reviewed the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.740371/full#supplementary-material

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Tropical savanna small mammals respond to loss of cover following disturbance: A global review of field studies

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Small-mammal faunas of tropical savannas consist of endemic assemblages of murid rodents, small marsupials, and insectivores on four continents. Small mammals in tropical savannas are understudied compared to other tropical habitats and other taxonomic groups (e.g., Afrotropical megafauna or Neotropical rainforest mammals). Their importance as prey, ecosystem engineers, disease reservoirs, and declining members of endemic biodiversity in tropical savannas compels us to understand the factors that regulate their abundance and diversity. We reviewed field studies published in the last 35 years that examined, mostly experimentally, the effects of varying three primary endogenous disturbances in tropical savanna ecosystems—fire, large mammalian herbivory (LMH), and drought—on abundance and diversity of non-volant small mammals. These disturbances are most likely to affect habitat structure (cover or concealment), food availability, or both, for ground-dwelling small mammalian herbivores, omnivores, and insectivores. Of 63 studies (included in 55 published papers) meeting these criteria from the Afrotropics, Neotropics, and northern Australia (none was found from southern Asia), 29 studies concluded that small mammals responded (mostly negatively) to a loss of cover (mostly from LMH and fire); four found evidence of increased predation on small mammals in lower-cover treatments (e.g., grazed or burned). Eighteen studies concluded a combination of food- and cover-limitation explained small-mammal responses to endogenous disturbances. Only two studies concluded small-mammal declines in response to habitat-altering disturbance were caused by food limitation and not related to cover reduction. Evidence to date indicates that abundance and richness of small savanna mammals, in general (with important exceptions), is enhanced by vegetative cover (especially tall grass, but sometimes shrub cover) as refugia for these prey species amid a "landscape of fear," particularly for diurnal, non-cursorial, and non-fossorial species. These species have been called "decreasers" in response to cover reduction, whereas a minority of small-mammal species have been shown to be "increasers" or disturbance-tolerant. Complex relationships between endogenous disturbances and small-mammal food resources are important secondary factors, but only six studies manipulated or measured food resources simultaneous to habitat manipulations. While more such studies are needed, designing effective ones for cryptic consumer communities of omnivorous dietary opportunists is a significant challenge.

KEYWORDS

climate change, endogenous disturbance, fire, grazing, landscape of fear, murid rodents, shrub encroachment, zoonotic reservoirs

Introduction

Tropical and subtropical savanna ecosystems (TSE) cover 20% of the land area of the Neotropics, sub-Saharan Africa, Southern Asia, and Northern Australia (Bond, 2016) and contribute around 30% of terrestrial primary productivity, globally (Grace et al., 2006). The pre-anthropocene structure of tropical savannas was dependent on the effects of endogenous disturbances, primarily fire and large-mammalian herbivory, which maintained the grassy understory and high native biodiversity (Buisson et al., 2019; Andersen, 2021). In general, fire is more frequent in TSE than in any other biome type (He et al., 2019). The native biodiversity of each region and type of TSE includes an assemblage of small mammals (< 1 kg), including rodents, small marsupials, and members of several insectivorous eutherian orders that primarily live on and just under the ground surface. The one small-mammal taxon in common to TSE on all four continents are native species and genera of the most diverse of mammalian families, Muridae (Mammal Diversity Database, 2022). Small mammals are important and potentially abundant components of tropical savannas and play ecologically important roles including ecosystem engineers (e.g., by digging burrows and tunnel systems that are used by many commensals and help to aerate savanna soils), insect and plant regulators, food sources for mammalian, reptilian, and avian predators, and reservoirs for realized and potential zoonotic diseases (e.g., Wurm, 1998; Hagenah and Bennett, 2013; Byrom et al., 2014; Limongi et al., 2016; Lamberto and Leiner, 2019; Teman et al., 2021). TSE small rodents are important reservoirs for diseases that are and may be zoonotic, including the bacterial diseases bubonic plague and Bartonellosis, hantaviruses (which cause various hemorrhagic fevers), and adenoviruses (one of which causes Lassa fever; Lecompte et al., 2006; Luis et al., 2013; Young et al., 2014).

Small mammals are highly influenced by habitat changes driven by common endogenous disturbances of TSE (mostly fire, grazing, and drought) and their effects on both vegetative cover and food availability (Seymour and Joseph, 2019). These factors may affect small-mammal species and communities differentially, however, in the distinct types of TSE around the world. Of the three major endogenous disturbances under which TSE evolved (Buisson et al., 2019), megafaunal extinctions culminating *ca.* 11,000 years ago have greatly reduced the native large-mammal herbivory disturbance component from savannas in Australia (although recent predator control has allowed kangaroos to increase to the point of overgrazing in temperate grasslands; Mills et al., 2020) and the Neotropics. In contrast, substantial populations of native large mammalian herbivores (LMH) remain in portions of the Afrotropics and Southern Asia. Domestic livestock on open range have arguably partially replaced the role of native LMH in many tropical savannas (but their interactive effects are complex; Riginos et al., 2012; Archibald and Hempson, 2016). Insect herbivory may have expanded particularly in Neotropical savannas after Pleistocene megafaunal extinctions (Costa et al., 2008), thereby limiting the extent of competitive release (i.e., primary production available, instead, to small-mammal herbivores). Exclusion of aboriginal fire regimes, in addition to LMH extirpation (as well as misguided afforestation efforts; Kumar et al., 2020), have allowed woody encroachment, non-native plant invasions, loss of biodiversity, and ironically, in some cases, greatly increased extent and intensity of wildfire.

The goals of restoring native biodiversity and stability or resilience to a tropical savanna require a determination of the deeper history of natural disturbance regimes in each of the TSE worldwide (Buisson et al., 2019), which may be difficult to determine in those areas depleted of native megafauna and in all areas because of the direct and indirect effects of global climate change and atmospheric CO_2 increases (Bond, 2016). The tremendous primary productivity of tropical C_4 grasses (Buisson et al., 2019) is largely what supports the massive native LMH community of savanna protected areas in East Africa, for example (as much as 75 kg/ha; Augustine, 2010), and this herbivore community both responds strongly to fire (Kimuyu et al., 2017) and can affect fire behavior in complex ways (Young et al., 2022). For millennia, mobile pastoralists have inserted domestic cattle into this fire-herbivory interaction and have enriched and diversified African savannas in unique ways (Charles et al., 2016; Martin et al., 2018). Where humans have reduced native LMH, productivity of otherwise intact savanna may be available for consumption by domestic LMH and/or by small consumers such as insects and small mammals—both of which can undergo irruptions—or it may be lost by catastrophic wildfires.

In the present review, we survey field studies from the past 35 years of how endogenous disturbances have affected small-mammal community structure (abundance, diversity, and species composition) *via* changes to their habitats in TSE globally, including Southern Asian, Afrotropical, Australian tropical, and Neotropical savannas. Here, we examine the results and conclusions of published field studies of ground-level habitat variation, mostly experimental, to determine whether the cover (=microhabitat selection) hypothesis or the food-competition (=resource availability) hypothesis is better supported when the major endogenous disturbances of tropical savannas (mostly grazing and fire, but also including shrub encroachment, soil enrichment, and drought) alter the ground-level environments of the native small mammals. This dichotomy largely aligns with a comparison of the strength of bottom-up vs. top-down limitation of small mammals, because loss of cover has often been linked to loss of concealment and consequent increased mortality from predation (Stobo-Wilson et al., 2020).

We expected fire to be a focus of such studies in all regions, because all tropical savannas are fire-prone and fire-adapted (Andersen et al., 2003; Figure 1). We expected herbivory by domestic LMH also to be a common factor, but we expected studies of native LMH to be based mostly in Africa. For example, it is known that when native and domestic LMH are experimentally excluded from savanna plots in East Africa, small-mammal abundance can increase as much as 20-fold for some species, and species richness can roughly double (Bergstrom et al., 2018). Control plots from such experiments have comparatively little above-ground biomass, resembling in that regard recently burned areas compared to unburned controls. These recently burned plots are often avoided by many (but not all) small mammals, just as heavily grazed plots are (Yarnell et al., 2007). It is possible that greater use by small mammals of savanna patches with greater above-ground biomass, particularly of grass, could reflect either increased forage availability or increased cover and concealment from predators. It follows that declines in small-mammal abundance or biomass in response to plant-biomass reduction by LMH could be explained by either the forage hypothesis, predicting a direct exploitative competitive effect; or the cover hypothesis, predicting an indirect interaction, in which LMH grazing and fire (the latter, in the short term) would both have similar indirect effects on small-mammal abundance or occupancy (Kutt and Woinarski, 2007; Hagenah et al., 2009). These effects would be mediated by the predation-risk perception behavior of the small mammals. Alternatively, fire can restore a flush of nutrients to the new grass growth and actually increase foraging by small folivorous mammals. We expect this positive

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Abbreviations: LMH, Large mammalian herbivores; TSE, Tropical savanna ecosystems.

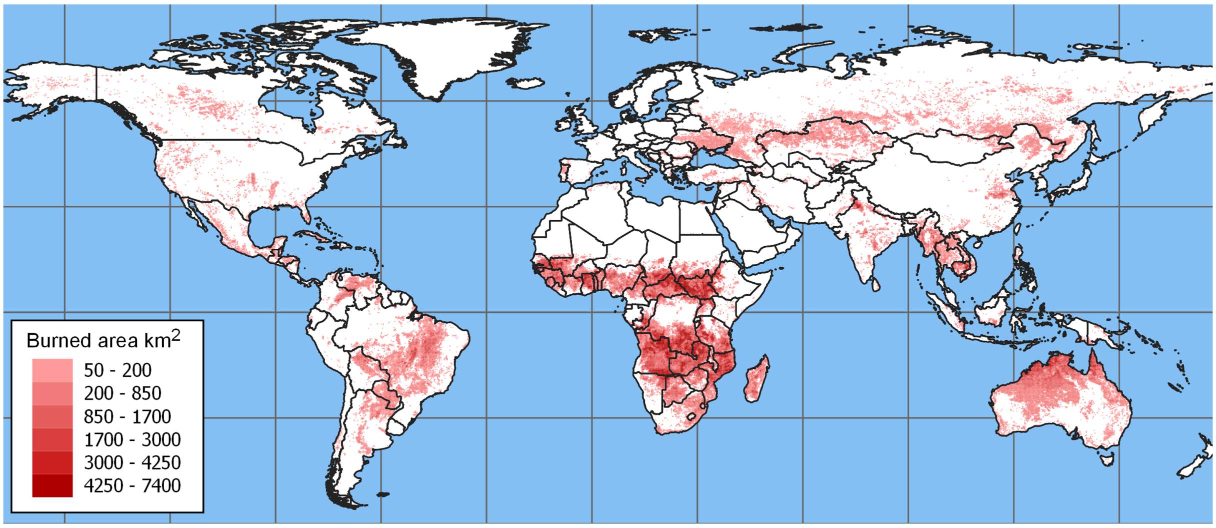

FIGURE 1
Satellite-derived data showing the annual total area burned in the world based on a time-series of rasters from 2008 to 2021. These data indicate that large fires are conspicuously concentrated in regions where tropical savannas occur, including Central Africa, Northern Australia, and the Cerrado of Brazil. The burned area is for all fire types and represents the total area (hectares) in each 0.25 degree x 0.25 degree grid cell. This figure was generated with MODIS/MCD64A1 data (Giglio et al. 2021).

impact of fire on small mammals to manifest in the medium or long term, even if not in the short term.

Methods

Our goal was a thorough if not exhaustive classical literature review, which had not previously been undertaken on this topic. We began by assembling published papers on field studies in TSE of potential habitat disturbance effects on non-volant small-mammal abundance, occupancy, vital rates, foraging behavior (excluding dietary shifts but including, e.g., time spent in disturbed vs. control habitat patch), and species diversity in tropical savannas already known to us. We added any additional relevant titles cited by these papers. We then conducted keyword searches on Web of Science, SCOPUS, Academic Search Complete (EbscoHost), JSTOR, Google Scholar, and Google to find additional peer-reviewed published field studies. We found titles from this set on Google Scholar and examined "cited by" papers, adding new titles that were relevant. After reading abstracts, we eliminated reviews, studies of primarily arboreal mammals or volant mammals or mammals >1 kg, or studies conducted primarily in forest or dense woodland (e.g., gallery forest). We also did not include studies that were primarily food supplementation experiments (rather than habitat manipulation experiments). We eliminated otherwise relevant studies (of small, non-volant, and terrestrial mammals in tropical savannas) where no habitat component was either explicitly varied or where no habitat variation could be inferred (as it might be, for example, in recently burned experimental plots vs. unburned controls in the same habitat). We also eliminated studies (mostly in the Neotropics) that examined differences in small-mammal community structure among different macrohabitats (e.g., grassland vs. thorn-scrub vs. woodland, which occur on sites with different edaphic factors and are not seral stages of each other), even when habitat components (e.g., grass, shrub, and tree cover) were quantified and random, replicated sampling was done. Finally, we excluded the few studies where the response variables were community nestedness or modularity, as these were not directly comparable to those studies included in the set.

The final set of potentially pertinent papers totaled 137: 67 African, 41 Australian, 28 Neotropical, zero Asian, and one multi-region (these are included in Supplementary Table S2 along with other studies providing background on the TSEs in which the studies were conducted). Upon more careful reading of each study's methods, we reduced the set of papers scorable by our criteria (examination of effects of ground-level habitat changes resulting from endogenous disturbances on abundance, occupancy, vital rates, activity, and/or richness of non-volant small mammals in TSE) to 55: 21 African, 19 Australian, and 15 Neotropical. A few of these 55 papers reported results for two or three of our target explanatory variables, so we summarized each such case as a substudy (hereafter "study"), and this brought our total to 63 studies (Supplementary Table S1). We included studies that presented original results on individual species as well as assemblages, and in the latter, response variables related to community structure (species composition, relative abundance, and diversity) were often included. In our analysis, we did not include reviews (or any data presented therein), republication of previously published results, or studies that were merely descriptive.

We tracked whether experiments were manipulative (ME; experimenter creates the variation in a replicated design with controls) or comparative mensurative (CM; nature creates the variation, and the experimenter imposes a replicated, randomized sampling design with *a priori* knowledge of that variation; see Hurlbert, 1984; McGarigal and Cushman, 2002). Regardless, we deemed both ME and CM studies experimental. If the range of variation in one or more explanatory variables (e.g., occurrence of fire and presence of LMH) was not known *a priori* but discovered only after data were collected, then such a study was deemed observational (Obs), or non-experimental. We noted where studies were otherwise of an experimental nature (i.e., an explanatory variable was manipulated) but did not meet, or barely met, the expected minimum of two replicates (randomized sampling units) per treatment and control, because such studies are not experiments (Krebs, 2014).

For each relevant study, we recorded whether an explanatory variable related to one or more of the following habitat treatments was manipulated or studied: fire, LMH removal, drought or precipitation, shrub removal or encroachment, soil enrichment, and soil type. Where applicable, we recorded effect sizes and significance levels of treatments on response variables including both per-species and overall small-mammal abundance, occupancy, residency time [e.g., at feeding trays for optimal giving-up density (GUD; *sensu* Brown, 1988) studies], and in a few cases population vital rates. Also where applicable, we recorded the same results for community indices of species diversity of small mammals. We used these summaries of results, usually in concurrence with the authors' conclusions as stated in their Discussion sections (except where we found errors in reporting or interpretation by authors of their own results), to score whether the authors concluded that the primary limiting factor of small mammals was herbaceous or woody cover (the microhabitat selection hypothesis, in which the small mammal seeks cover for concealment from predators and/or favorable microclimatic conditions) or food (the resource availability hypothesis), or some combination of the two (identified as "both," *cf.* Figure 2). The "both" categorization included studies whose authors concluded that both cover- and food-related limiting factors probably operated in conjunction as well as those studies in which one or more species were found to be food-limited and one or more other species were found to be cover-limited. In other cases, results either did not find significant changes in small-mammal metrics (see above) related to habitat treatments or did not control for confounding variables (e.g., by adequate replication); these studies were scored as no-effect or inconclusive. To avoid undue complexity, where habitat treatments showed significant effects on small mammals overall, and/or one small-mammal species but not others in the same study, we did not subdivide the study further and report separate results (e.g., Figure 2); rather, we here report the results and likely proximate cause(s) for the species found to respond significantly and include expanded, detailed conclusions regarding other species in Supplementary Table S1.

Overview of findings of field studies

Only six of the 63 studies (9.5%) of the effects of habitat manipulations on small mammals also simultaneously manipulated or otherwise tested changes in food quantity or quality or tested for dietary shifts related to the habitat variation (Supplementary Table S1). Of these six, three were inconclusive in that either the results were not significant or no direct linkage between habitat change and food availability or diet was established. The remaining three studies concluded that both cover (concealment from predators) and food resources were limiting factors of one or more small-mammal species that showed significant differences in abundance between/among habitat treatments (Supplementary Table S1). However, none of these studies of mostly omnivorous small mammals manipulated or measured changes in more than one food type, i.e., plant forage *and* insects, leaving alternative explanations for abundance changes a possibility in every case. Consequently, for all conclusive studies, we considered carefully the authors' logical arguments and citations of other studies within their systems and involving the same small-mammal species to characterize what was most likely the primary limiting factor or factors.

We found no relevant field studies from savannas of southern Asia. For Afrotropical, Australian tropical, and Neotropical savannas, we found 21, 19, and 15 peer-reviewed papers, respectively that met our criteria. Some papers in each of these three regions tested multiple explanatory variables, yielding 63 studies overall: 24 for the Afrotropics, 24 for tropical Australia, and 15 for the Neotropics (Supplementary Table S1). Of these, 14 studies were inconclusive, and 49 studies reached definitive conclusions as to which factor(s) primarily limited either small mammals as a group or at least one species, singly; overall, 29 of these (58%) concluded that factor was cover, two (4%) that it was food resources, and 18 (37%) that it was a combination of food or cover (i.e., either some species were food-limited and others cover-limited, or both limiting factors played a partial role in limiting one or more species; Figure 2; Supplementary Table S1 reports categorized results of each study). Conclusions of studies from the Afrotropics aligned with this percentage allocation of limiting factors fairly closely and had a more diverse representation of explanatory variables than studies from the other two regions. Studies from Australian tropical savannas were nearly evenly divided between cover and "both" as limiting factors and, with one exception, explored only fire and LMH as factors impacting small-mammal habitat. Factors evaluated in the Neotropical savanna studies included fire, shrub encroachment, prey availability, and drought and concluded overwhelmingly (eight of 10 conclusive studies) that small mammals were limited by cover (Figure 2).

Effect sizes (in terms of treatment means) were not reported in many of the studies we reviewed (including 22 studies of fire and six studies of LMH). We did not glean effect sizes from regression analyses, which pertains to most of the conclusive Neotropical studies; but seven of nine of those studying fire reported significant R^2. There were samples of >10 each of studies examining fire and LMH as explanatory variables that reported treatment effect sizes on small-mammal abundance (Supplementary Table S1). Significant effects of these two treatments on abundance ranged from 1.4 to 16 for individual studies, with the following mean effects ± S.E. from studies of fire (3.7 ± 0.6, $n = 11$) and LMH (5.0 ± 1.3, $n = 12$; multiple effect sizes from single studies were reported as a single arithmetic mean per study).

Summaries of findings and research gaps by region

Afrotropics

Studies from Afrotropical savannas were unique among the three regions in that diverse and abundant assemblages of native wild LMH were on the landscape in most cases, and their effects on terrestrial small-mammal habitat could potentially be distinguished from that of livestock. Ten experimental studies examined LMH-mediated habitat effects on small mammals and one directly manipulated grass height, as wild or domestic LMH would do. Of those 11 experimental studies, five concluded that small mammals responded positively to LMH removal primarily because of increased cover (or, in the one case, directly to experimentally increased cover as manifested by grass height; Bowland and Perrin, 1989; Saetnan and Skarpe, 2006; Young et al., 2015; Banasiak and Shrader, 2016; Bergstrom et al., 2018; Figure 3A; Supplementary Table S1). Of the four of these studies that experimentally reduced or removed LMH, three showed positive responses of small mammals to increased grass height and coverage, whereas one study failed to measure grass height but showed positive response to increased

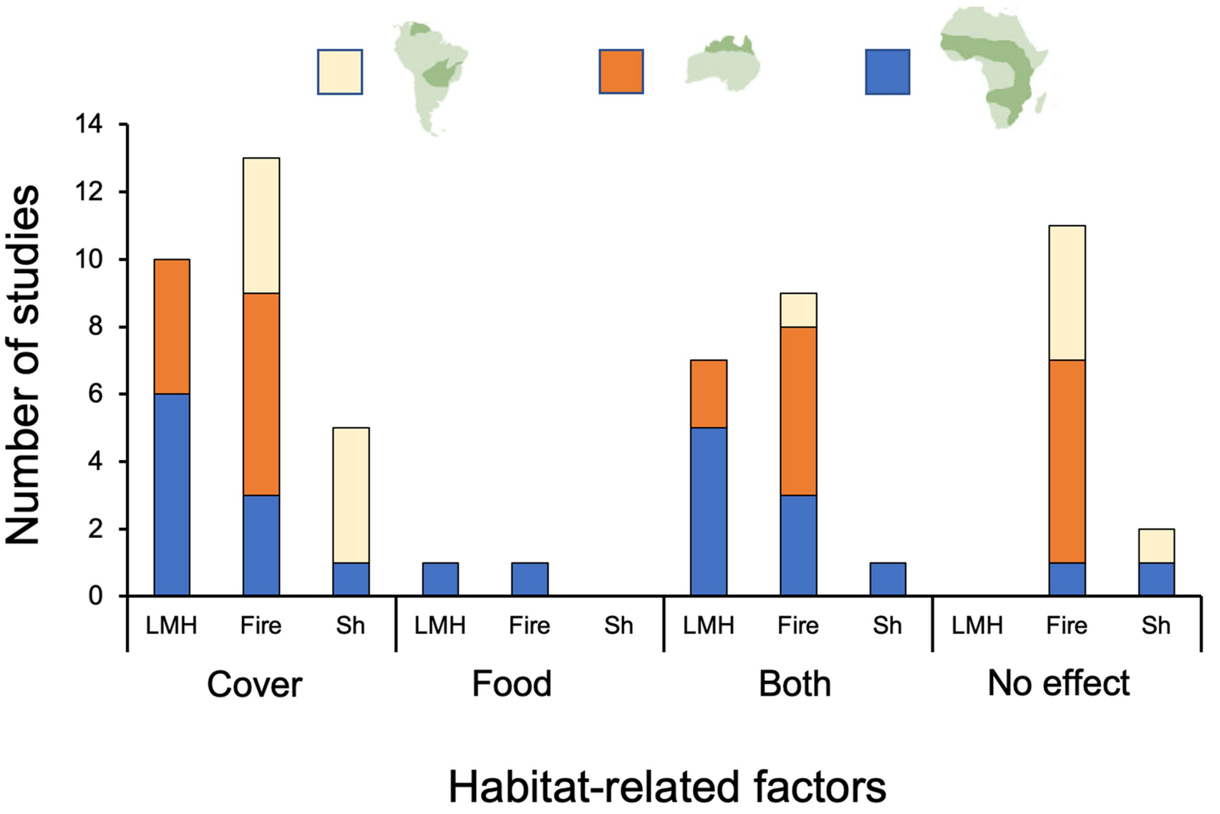

FIGURE 2
Number of published field studies from each region of tropical and subtropical savannas (beige: Neotropical; orange: northern Australian; blue: Afrotropical) in which either a conclusion was reached about which habitat-related factor—cover, food, or both—was the primary limiting factor for species or communities of non-volant small mammals or in which either no treatment effect was found or results were inconclusive ("No effect"). Studies scored "Both" included those in which some species were primarily limited by cover and others by food, as well as studies where there was evidence of both factors limiting small mammals (see Supplementary Table S1 for details). Manipulated or naturally varying factors affecting ground-level habitats and resources for small mammals were: (1) large mammalian herbivore reduction and/or removal (LMH; *n* = 18), (2) fire (Fi; *n* = 33), (3) shrub encroachment or reduction/removal (Sh; *n* = 8). This compilation includes substudies within individual papers for a total sample of 63. Additionally, two studies in Africa and one in South America assessed drought or rainfall seasonality effects (not included in the figure). The African studies indicated the role of "Cover" and "Both" while the South American study was inconclusive. Soil type (ST) and soil enrichment (SE)—which both concluded enhanced cover increased overall small-mammal abundance—were not included in the graph either, as only one study examined each of these treatment types (see "Summaries of Findings and Research Gaps by Region" and Supplementary Table S1).

grass cover. Five of the 11 studies (scored "both"; Figure 2; Supplementary Table S1) either concluded that both cover and food were likely to have played a role in the habitat-mediated limitation of small mammals or could not rule out either the food-competition or cover (concealment) mechanism as a factor (Yarnell et al., 2007; Hagenah et al., 2009; Kuiper and Parker, 2013; Okullo et al., 2013; Long et al., 2017). Hagenah et al. (2009) was the only one of the published studies in our set from Africa reporting on small-mammal abundance or occupancy as a response variable that explicitly tested for quantity and quality of food resources simultaneous to their habitat manipulations (Supplementary Table S1), yet even this study did not directly examine insect abundance, which could have been affected by LMH treatment and could in turn have affected omnivorous small mammals.

Additionally, Yarnell et al. (2007) showed that small-mammal abundance was positively related to grass coverage and grass height, which both fire and grazing reduce in the short term. Moreover, Long et al. (2017) found that small mammals responded negatively to increased bare-soil coverage and decreased tree cover, although they failed to measure grass height. In the only one of these 11 experimental LMH-removal studies that concluded food availability (i.e., resource competition with LMH) was the primary limiting factor (Keesing, 1998), again, the study failed to measure grass height and found no differences in vegetative cover variables among the LMH treatment plots (which later surveys of the same plots did find; Young et al., 2015). Although an observational study, Muck and Zeller (2006) offered evidence that small-mammal abundance was positively correlated with grass height and coverage and that grazing by cattle leaves a basal layer of vegetation through which small mammals can tunnel, whereas grazing by wild ungulates and domestic sheep removes that layer.

Overall small-mammal responses to manipulated LMH, fire, and other habitat perturbations were not necessarily uniform across species in multi-species studies in which species were analyzed separately. Some African savanna small mammals were shown to prefer open or bare-soil habitats and had different responses to vegetative variables in some LMH experiments, as compared to other species and to overall small-mammal abundance or occupancy (which generally favored increased cover). This includes gerbils of certain species (Blaum et al., 2006), as well as elephant shrews and the murid mouse *Steatomys pratensis* (Saetnan and Skarpe, 2006). Some common small mammals, including spiny mice (*Acomys* spp.), did not respond significantly to LMH removal and its attendant increase in grass height and vegetative

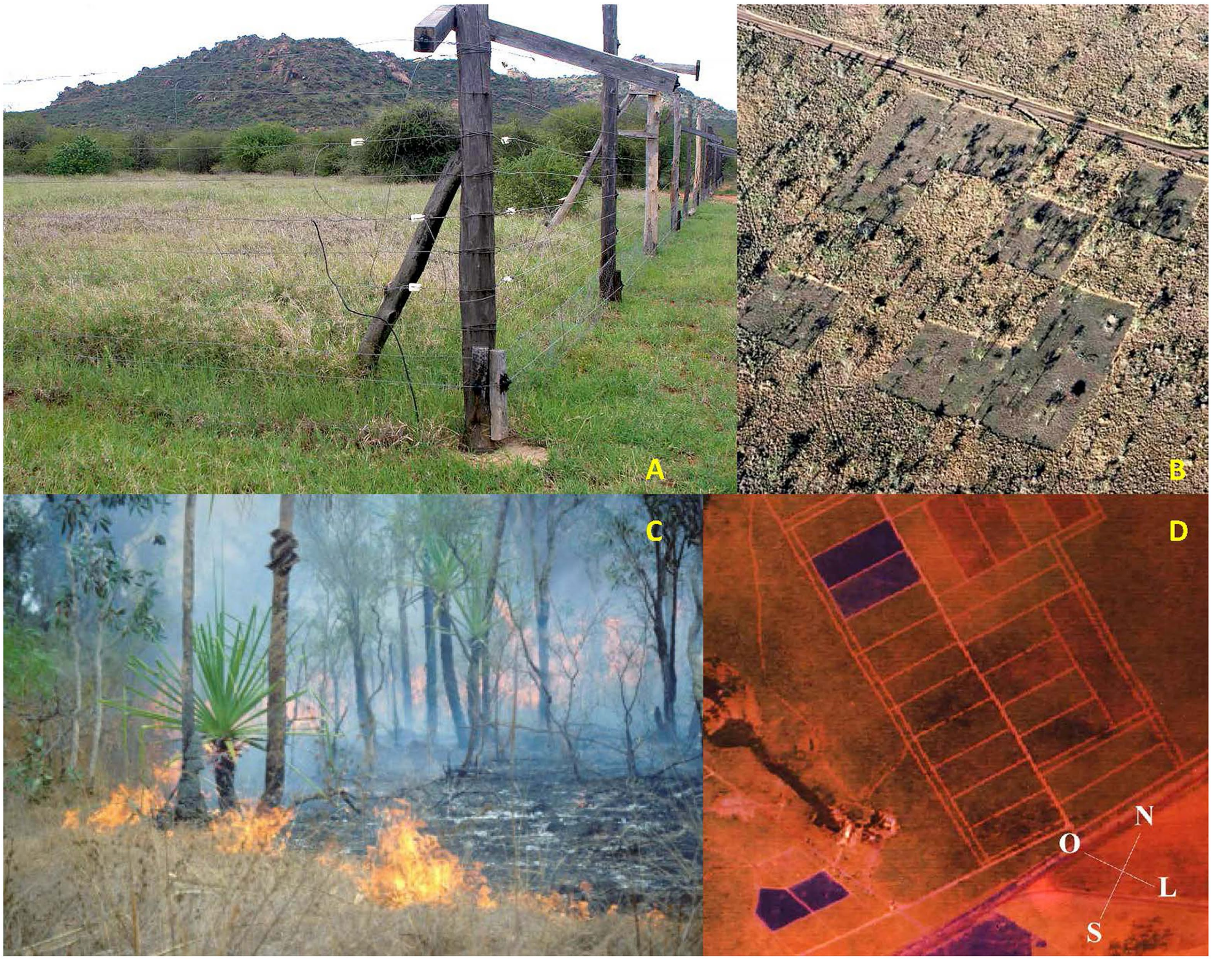

FIGURE 3
(A) Experimental LMH-exclusion plot on a glade (enriched soils of an abandoned cattle boma) on red sandy loam site at Mpala Research Center on the Laikipia Plateau of central Kenya. Electric fencing keeps LMH out but allows free passage of small rodents, shrews, and elephant shrews. Area outside the fence is an adjacent control plot. Overall abundance and diversity of small mammals was significantly greater inside exclosure than in the greener but shorter grazing lawn of the adjacent control (Bergstrom et al., 2018). Photo by BB. **(B)** Aerial photo of experimental "patchy" prescribed burn plot on whistling-thorn Acacia (*Acacia drepanolobium*) black cotton vertisol savanna habitat atop the escarpment at Mpala Research Center on the Laikipia Plateau of central Kenya. The 16-ha square area is divided into 1-ha pixels, nine of which have been burned, and seven unburned, and is surrounded by unburned matrix habitat. Small-mammal abundance was greater in unburned pixels, even 1–4 years after this photo was taken (Bergstrom et al., 2018). Photo courtesy of R. L. Sensenig. **(C)** Early-dry season wildfire on tropical savanna at Kapalga Research Station, Kakadu National Park, northern Australia (image taken by B. McKaige), which tends to be less severe and have less deleterious effects on small mammals than late-dry-season wildfire, from Griffiths and Brook (2015). **(D)** Aerial view of experimental plots of the "Fire Project" (Dias and Miranda, 2010), conducted between 1991 and 2011, in the Brazilian savanna (Cerrado). Rectangular areas in the image were 10-ha experimental plots covering typical Cerrado vegetation, burned with different fire frequencies (including every 2 years, every 4 years, and unburned control plots). Dark rectangles had just been burned when the image was taken (<1 month after burning). Two studies evaluated in the present review were conducted as part of the "Fire Project" (Vieira, 1999; Vieira and Briani, 2013).

cover, probably because these small murid rodents preferentially occurred in or near rock outcrops and relied on rock crevices for cover (Bergstrom et al., 2018).

Of six experimental studies on small mammal responses to fire in African savannas, one was inconclusive (MacFayden et al., 2012), three concluded both cover and food were, or could be, limiting, and two concluded primarily cover was limiting (Supplementary Table S1; Figure 2). These disparate conclusions probably were influenced by the fact that species-specific life histories, in part, determined responses to fire, making some small mammals fire-positive and others fire-negative (Plavsic, 2014). Moreover, amount of time since the fire affected mammals' responses (Yarnell et al., 2007), as did complex interactions with precipitation (Plavsic, 2014) and grazing (Yarnell et al., 2007; Bergstrom et al., 2018). The widespread, disturbance-tolerant, opportunistic feeding and often human-commensal multimammate mouse (*Mastomys natalensis*; see Avenant, 2000) showed no response to fire in a study where the cover-sensitive, diurnal grass rat (*Arvicanthis niloticus*; see Bergstrom et al., 2018) preferred unburned plots (Manyonyi et al., 2020; Supplementary Table S1 critiques authors' erroneous conclusion that *M. natalensis* showed a significant response). The aforementioned inconclusive study (MacFayden et al., 2012) discussed the complex and unpredictable relationship of *M. natalensis* to fire. In addition to the experimental studies, suggestive non-experimental evidence that increased nutritional value of burned savanna becomes an overriding advantage for cover-sensitive small mammals several months after a burn was provided for one southern African savanna mouse (*Steatomys pratensis*; Monadjem, 1999). Heavy grazing by abundant native LMH was found to delay positive post-fire responses by small mammals for years (Bergstrom et al., 2018; Figure 3B), whereas high rainfall was found to speed up that outcome (Yarnell et al., 2007). An observational study using radiotelemetry found that small elephant shrews increased their use of thickets after surrounding grass cover was removed by fire (Yarnell et al., 2008).

Three experimental studies varied shrub cover in southern African savannas and recorded effects on native murid rodents: Blaum et al. (2006) found that three open-country gerbil species (murid rodents of Tribe Gerbillurini) avoided shrub cover because of increased food availability in open microhabitats, whereas another gerbil and a striped mouse (*Rhabdomys pumilio*) preferred intermediate shrub cover, where grass height was also greatest; and Loggins et al. (2019) found that most rodents had greater foraging activity in proximity to shrub cover where, again, grass height was tallest, but that *Mastomys natalensis* was cover-neutral or even cover-averse. Lloyd and Vetter (2019) found that shrub encroachment caused a shift in food habits in the generalist rodent *Rhabdomys pumilio,* but the study was otherwise inconclusive regarding the response variables for which we screened (see the section Methods).

Northern Australia

Of five experimental studies examining livestock grazing effects on small mammals, three showed species-specific responses to increased herbaceous vegetative cover following destocking. In one, a smaller mouse (*Pseudomys delicatulus*) was grazing tolerant, whereas small-mammal abundance, generally, and abundance of two larger *Pseudomys* spp., *P. desertor* and *P. gracilicaudatus,* responded positively to increased cover (Kutt and Gordon, 2012). Two LMH studies were two-factor experiments including fire. In one, the endangered *Pseudomys desertor* declined due to cover loss, whether by grazing or fire. In contrast, *P. delicatulus*, an open-ground species, found enhanced forage after fire but responded negatively to grazing, and fire and grazing combined were synergistically deleterious (Kutt and Woinarski, 2007). Four smaller rodents and dasyurid marsupials showed stronger positive responses to destocking than larger species (one increasing about 10-fold 3 years after destocking). These positive responses could be explained by either increased cover mediated by feral cat predation or increased food resources, as allowed by the investigators (Legge et al., 2011). A large-sample observational study (n = 94) found that total small-mammal abundance and diversity increased, and mortality due to feral cats decreased, as three types of cover—rock, shrub, and perennial grass—increased, and as livestock grazing was reduced (Radford et al., 2021). A 13-year natural experiment with varying levels of livestock grazing and fire extent and intensity concluded that fire and domestic LMH each suppressed small mammals (murids and small dasyurid marsupials) and had a negative synergistic—but not additive—effect on overall small-mammal abundance and richness (but opposite effects on *P. delicatulus* compared to the four other commonly caught species; Legge et al., 2019). An observational study found that brush-tailed rabbit-rat occupancy was negatively associated with increased cattle stocking and concomitant decreased shrub cover and increased feral cat activity (Davies et al., 2017).

Of 17 studies of fire effects conducted in Northern Australia, 12 of which were experimental, six concluded that loss of cover explained significant small-mammal responses (Kutt and Woinarski, 2007; Legge et al., 2008; Kutt and Gordon, 2012; Leahy et al., 2015; Davies et al., 2017; Radford et al., 2021), five concluded that both cover and food resources were partly important as limiting factors (Lawes et al., 2015; McDonald et al., 2016; Ondei et al., 2020; Radford et al., 2020; Penton et al., 2021), and six studies were inconclusive (Pardon et al., 2003; Woinarski et al., 2004; Griffiths and Brook, 2014; Abom et al., 2016; Davies et al., 2018; Legge et al., 2019; Supplementary Table S1, Figure 2). One study found 90% direct mortality of small mammals from intense fires, with the individuals surviving being in unburned refuges (Legge et al., 2008). Two experimental studies were done at the Kapalga experimental site, where both fire frequency and fire intensity were manipulated, although none of them reported habitat (vegetation) variables; these collectively showed that severe declines in survival and recruitment of northern brown bandicoot (*Isoodon macrourus*) were exacerbated by more frequent fires and more intense fires (which occur later in the dry season; Pardon et al., 2003; Griffiths and Brook, 2015; Figure 3C). Varying fire intensity had no effect on grassland melomys (*Melomys burtoni*). Experimental studies on tropical savannas on Melville Island showed overall abundance of seven taxa of small mammals was greater with less frequent fire and a landscape consisting of mostly long-unburned patches (Davies et al., 2018); northern brown bandicoot and pale field mouse (*Rattus tunneyi*) had significantly greatest abundance in triennially burned patches (compared to annually burned and long-unburned), whereas grassland melomys had significantly greatest abundance in long-unburned patches, and other species' abundances did not vary among fire frequencies.

Most of the Australian fire studies found indirect mortality after fires (e.g., due to loss of cover and increased predation; Leahy et al., 2015). The rock rat, *Zyzomus pedunculatus*, preferred burned areas, because it sought cover in rock crevices but foraged on early-successional herbaceous plants; whereas *Pseudomys desertor* preferred unburned grass hummocks both for cover and for forage (McDonald et al., 2016; which was the only Australian study to simultaneously measure food resources). A unique study using radio-tracking confirmed: (1) increased mortality by predation in burned areas, and (2) that mammals were not food-limited in burned areas because they did not lose body mass over time (Leahy et al., 2015). Two studies concluded that fire, especially of large extent and high intensity, altered vegetative structure, and simplified habitats, which has led to widespread endangerment of tropical savanna small mammals and reduced community diversity; this was probably due both to loss of cover and concomitant increased predation and to loss of food resources such as fruits and seeds (Lawes et al., 2015; Ondei et al., 2020). In an aforementioned study, which varied both LMH and fire, richness of small-mammal species was most affected by large-scale (100 km^2) fire events and abundance by meso-scale fire (1 km^2); and, once again, *P. delicatulus* had opposite (i.e., positive) responses to fire compared to the other commonly caught small mammals (Legge et al., 2019).

Two non-climate-change related anthropogenic impacts have made fires more catastrophic and thus more deleterious to native Australian small mammals: (1) decline of patchy, aboriginal fires, and (2) culling of water buffalo (*Bubalus bubalis*, which kept grasses clipped) in wet savannas (Ondei et al., 2020). Although focusing on a different set of mammals than most studies we reviewed, Penton et al. (2021) found that two larger, semi-arboreal rodents (brush-tailed rabbit-rat, *Conilurus penicillatus*, and black-footed tree-rat, *Mesembriomys gouldii*), which den in tree cavities (borne by larger, older trees, which are negatively affected by frequent, intense fires and other disturbances), were not limited by abundance of those trees or their cavities but rather by shrub cover (which is reduced by fire and livestock grazing) as protection against predators while they forage and move on the ground.

Neotropics

The 15 Neotropical studies meeting our criteria included only one manipulative experiment (Durigan et al., 2020; which had the bare minimum of two replicates), but 11 others were CM and three were Obs. Most of these studies investigated the effects of plant cover (mainly altered by fire events) on rodent populations. Two studies evaluated fire's effects on food availability and thereby on rodent populations, but without measuring vegetative variables (Layme et al., 2004; Vieira and Briani, 2013). Using regression designs to investigate the same population of the murid *Necromys lasiurus* in an Amazonian savanna, two studies concluded that densities and population growth of this omnivorous rodent were strongly correlated with availability of invertebrate prey (Layme et al., 2004; which, however, was not related to vegetation structure in a study that examined both food and cover variables; Ghizoni et al., 2005).

Neotropical vegetative cover studies evaluated small-mammal responses at distinct habitat scales. At microhabitat scale (capture stations or sampling points spread over trapping areas ranging from 1.8 to 7.7 ha), there were mixed responses from murid rodents. *Necromys lasiurus* and *Cerradomys scotti* from open areas (shrubby grasslands and savannas with 10–60% of tree cover) responded positively to grass height, and *Oxymcyterus roberti* responded positively to forb ground cover, tree cover, and shrub cover, whereas *Calomys tener* responded negatively to grass height (Henriques and Alho, 1991; Vieira et al., 2005; Rocha et al., 2011). At a larger scale (40 plots spread over 200 km^2), *N. lasiurus* densities and population growth rates in Amazonian savannas were significantly associated with principal component analysis (PCA) axes representing increasing tree, shrub, and small-grass cover (PC1) and increasing tall-grass cover (PC2) (Ghizoni et al., 2005). For community responses, the effects of habitat structure variables on community structure were evaluated in seven sites of Cerrado rocky fields by Santos and Henriques (2010), who reported a significant relationship between plant complexity (a PCA axis representing a gradient with an increase in plant height and in number of plants) and community composition (first Multidimensional Scaling—MDS axis) but no clear relation between habitat structure and small mammal richness.

Nine of our 15 Neotropical studies evaluated effects of fire on small savanna mammals. These studies varied in terms of temporal and spatial scale analyzed and in relation to the analytical approach used, which precluded unambiguous summaries of fire effects on small mammals. Some common patterns, however, were highlighted. Direct mortality caused by fire was not commonly found, probably because small mammals found refuge in burrows (mainly made by armadillos; Vieira and Marinho-Filho, 1998; Vieira, 1999). Short-term responses to fire were reported for some species, including the murid rodents *Oxymycterus roberti* and *Necromys lasiurus* in grasslands, which showed abrupt reductions in abundance after fire (fire caused a drastic reduction of grass cover). Abundance of both murid species increased as grass recovered after fire (Vieira and Marinho-Filho, 1998). In typical Neotropical savanna habitats, at local scales (burned areas of 10 ha), population size of *N. lasiurus* reduced drastically up to 4–6 months after fire, generally recovering to pre-fire numbers after this period (Vieira, 1999; Owen, 2013; Vieira and Briani, 2013; Figure 3D). This post-fire reduction in abundance was not caused solely by food limitation, as invertebrates were still available in burned areas (Vieira and Briani, 2013). *Necromys lasiurus*, at much larger spatial scales (distinct 4-ha plots covering about 100 km^2), did not show significant changes in population densities related to fire-induced abrupt reduction in plant cover (Layme et al., 2004).

Responses of small-mammal communities to fire changed depending on the time elapsed since fire when they were evaluated. Briani et al. (2004) evaluated six sites with distinct fire histories and reported a strong negative correlation ($r = -0.81$) between community abundance and time since the last fire (1–26 years) in typical Neotropical savanna (i.e., cerrado *sensu stricto*). Studies conducted at small temporal scales (up to 1 year after fire), however, failed to show reduction in overall abundance or richness of small mammals (Vieira, 1999; Durigan et al., 2020). On the whole, fire in the Cerrado affected small-mammal communities mainly by temporary changes in dominance patterns within communities occurring in habitat types with sparse to moderate tree cover (Vieira, 1999). In areas of Cerrado dry woodlands, however, fire tended to increase species homogenization. The occurrence of fire in Cerrado dry woodlands (locally known as "cerradão") reduced tree cover and increased patchiness of these formations, allowing open-area terrestrial rodents to invade such habitats (Camargo et al., 2018).

While not directly examining fire, Furtado et al. (2021) found that shrub encroachment resulting from years of fire suppression in the southeastern Cerrado is changing the small-mammal community composition from open-country or grassland specialists (e.g., *Necromys lasiurus* and *Cryptonanus* spp.) to closed-canopy forest specialists (e.g., *Didelphis albiventris* and *Oligoryzomys nigripes*).

Conclusion

Unlike the Afrotropics, Neotropical and Australian tropical savannas have not had a significant native LMH presence for roughly the past 10,000 and 45,000 years, respectively (Malhi et al., 2016). The role of extinct megaherbivores may have been replaced, at least partially, by domestic herbivores, and although this issue has been investigated somewhat in Australian tropical savanna small-mammal studies, it has not been adequately investigated with respect to small-mammal habitat in Neotropical savannas. Another future research need for Neotropical savanna small-mammal habitat responses is manipulative field experiments on the effects of endogenous disturbances on small-mammal community structure, of which we found only one (and that with only two replicates; Supplementary Table S1). In African savannas, there is some evidence of additive negative effects of cattle and native LMH on vegetative cover and small-mammal abundance (Bergstrom et al., 2018), and cattle grazing in the absence of native LMH can be more conducive to cover-sensitive small mammals than native LMH grazing in the absence of cattle (Muck and Zeller, 2006). We recognize, however, that stocking rates and grazing strategies can vary widely between regions and cultures and interact differently with different habitats, vegetation, climates, and native fauna. Very few studies exist that examine effects of differential stocking rates on any native fauna, much less on small mammals (Wells et al., 2021). A recent global review found that domestic LMH grazing suppresses a wide variety of native bird and mammal populations but found very few studies focused on small mammals (Schieltz and Rubenstein, 2016).

In different ways, LMH grazing and browsing, fire, and drought can all be considered disturbances that reduce above-ground plant biomass and alter structure, nutrition, and species composition of tropical savanna plant communities, and this in turn affects the small-mammal community. Partial to complete shrub removal (which can mirror effects of fire or heavy browsing in Africa) was found indirectly to cause grass-cover reduction, which caused most small rodents to decrease their foraging time (Loggins et al., 2019). Although some species of small mammals respond positively to these disturbances [e.g., some gerbils and the generally disturbance-tolerant *Mastomys* spp. in Africa, *Calomys expulsus* (= *callosus*) in the Cerrado, *Pseudomys delicatulis* in Australian tropical savannas, and other open-ground inhabitants, which, importantly, are nocturnal and have cursorial and/or burrowing adaptations that aid their escape from predators], our review found that most species, and small-mammal abundance, overall, responded negatively, at least in the short term, to these disturbances (see also Andersen et al., 2005; Griffiths and Brook, 2015; Stobo-Wilson et al., 2020; Andersen, 2021). Thus, a "landscape of fear" (Laundré et al., 2010) on heavily grazed and recently burned areas may cause many less-cursorial small mammals to avoid them or reduce their time spent there due to a perception of increased predation risk, and from some evidence an actual increase in predation risk (Leahy et al., 2015). Supporting this conclusion is that, across three tropical continents, the commonality of negative response by most non-volant savanna small mammals to these disparate types of disturbances was most often concluded to be primarily or at least partially related to loss of cover. The best direct evidence of increased predation (especially by feral cats) being the mechanism by which reduced cover from fire and/or LMH increases mortality rates and extirpations of small mammals comes from Australian TSE studies (Frank et al., 2014; McGregor et al., 2014, 2015; Hohnen et al., 2016; Tuft et al., 2021). But in the other two TSE regions, this same conclusion can be inferred from two frequent observations: (1) most small mammals avoid recently burned areas and heavily grazed areas even though forage palatability and nutrient content is usually higher in these areas (Monadjem, 1999; Yarnell et al., 2007), and (2) in small murid rodents, the affinity to high-cover sites is particularly strong among the few diurnal species (e.g., *Arvicanthis niloticus*; Bergstrom et al., 2018; Manyonyi et al., 2020 and *Necromys lasiurus*; Ghizoni et al., 2005; Vieira et al., 2005). These diurnal rodents are most susceptible to predation by visual hunters such as birds of prey, and their fine-scale foraging and home ranges are often limited precisely by the boundaries of these "overgrown" refuges (Vieira et al., 2005; Whittington-Jones et al., 2008; Bergstrom et al., 2018).

Most studies concluding that loss of cover was the predominant reason for small-mammal declines due to LMH grazing or recent fire (as did the majority of those we reviewed) did not rule out shortage of food resources as a contributing or simultaneous factor, especially for omnivorous small mammals for which fruit, seeds, and insects are important in the diet (see Bergstrom, 2013; Vieira and Briani, 2013). Taller grass protected from grazing in Kenyan (Pringle et al., 2007) and South African (Jonsson et al., 2010), savannas has been found to have greater arthropod diversity and abundance. Somewhat contrastingly, in Neotropical savannas, the temporary post-fire replacement of the diurnal *N. lasiurus* by nocturnal rodents of the genus *Calomys* as dominant species was related to both a reduction in plant cover and a relatively higher availability of invertebrates (compared with plant resources) in just-burned areas (Vieira, 1999; Owen, 2013; Vieira and Briani, 2013). The diurnal *Necromys lasiurus* is probably more affected by the fire-induced reduction in plant cover and consequent increase in risk of predation by visually oriented raptors. In contrast, the nocturnal *Calomys tener* and especially C. *expulsus* are probably less affected by the reduction in plant cover and able to take advantage of the invertebrate increase, consuming more invertebrates and becoming more abundant after burning than before burning (Vieira and Briani, 2013).

Reduction of conifer seeds as a food source in burned Australian savannas was mentioned as a possible explanation for reduced small-mammal abundance in addition to loss of cover (Lawes et al., 2015). The grass hummock specialist in Australian tropical savannas, *Pseudomys desertor*, was found to prefer unburned grass hummocks within a fire matrix for both food and protection from feral cat predation (McDonald et al., 2016), the latter because it was thought cats would have reduced hunting efficacy in this habitat structure.

Very few studies in our sample concluded that food reduction, alone, and not cover loss, or a combination of the two, was the primary limiting factor for small mammals when habitats underwent fire, drought, or heavy grazing (recall that only six studies measured or manipulated food resources simultaneous to habitat manipulations or measurements). Only one African study that experimentally reduced LMH grazing concluded, inferentially, that food availability was the primary limiting factor for small mammals when LMH were present (Keesing, 1998). In part, this inference was based on the lack of difference in percent vegetative cover between recently established experimental and control plots, but the study did not measure a variable that many others have found critical—grass height. Consider that a close-cropped lawn may have 100% coverage of herbaceous vegetation but 0% visual cover to reduce perception of (or, indeed, actual) vulnerability to predation (see Figure 3A). In fact, grazing lawns are a feature of African savannas with a history of nomadic pastoralism (Veldhuis et al., 2014) and are also a feature of recently burned Australian tropical savannas where livestock are grazed (Bond and Keeley, 2005). In the only African experimental LMH study that explicitly tested both food quantity and quality and vegetative cover and structure, Hagenah et al. (2009) showed how meso-herbivores remove the higher food-value lawn grasses, whereas larger LMH reduce the height of taller, less nutritious grasses that are more useful for visual cover; therefore, a full complement of native African LMH can reduce both food and cover resources for small mammals.

Nine separate studies from African savannas, some of them experimentally manipulating multiple habitat-altering factors, concluded that those manipulations (grazing, fire, and drought) did significantly reduce grass (or vegetation) height, and that grass-height differences between treatments did significantly affect small-mammal species and/or communities (Blaum et al., 2006; Muck and Zeller, 2006; Saetnan and Skarpe, 2006; Plavsic, 2014; Yarnell et al., 2007; Kuiper and Parker, 2013; Banasiak and Shrader, 2016; Bergstrom et al., 2018; Loggins et al., 2019). All of these studies concluded that cover was either the primary, or an important contributing factor explaining the response of the small-mammal assemblage and of the individual species, but especially of those species whose responses to grass height were positive (and thus were grazing-negative and short-term fire-negative). It is important to note that some studies in our review (e.g., Durigan et al., 2020; Supplementary Table S1) found no effect of fire on small-mammal species richness or abundance.

Conservation implications and future research needs

In studies reviewed herein, as a rule, endogenous disturbances in TSEs—especially fire, LMH, and drought—reduced small-mammal abundance or occupancy at least in the short term, due to loss of cover, which led either to loss of concealment from predators and/or unfavorable microclimates. Increased predation in burned and heavily grazed areas in Australian tropical savannas has been established by several studies detailed in this review, including direct confirmation of that predation by radiotelemetry. Under anthropogenically exacerbated disturbance regimes that Australia is currently experiencing, with attendant loss of vegetative cover, feral cat populations are increasing in its tropical savannas (Davies et al., 2020), and increased predation on declining small mammals has been linked to intensively burned areas (Leahy et al., 2015). To a much greater degree (as currently known) than in African or Neotropical TSE, endemic TSE small mammals in Australia are declining, and many of them are endangered (Woinarski et al., 2011). So it is particularly important to understand what landscape factors combine to offer them the best chance of recovery. One prescription is to preserve unburned and ungrazed refuges of vegetative cover for at least 4 years (Radford et al., 2015, 2021). This will be critical as long as climate change-driven drought and wildfire, and uncontrolled feral cat predation, continue unabated (Woolley et al., 2019; Hale et al., 2021).

Twenty of the studies we reviewed reported effect sizes, overall, on small mammals averaging 4–5-fold in response to LMH and fire in tropical savannas. Small mammals' generally negative responses (as noted previously, certain species are "increasers" in response to disturbance) to both disturbances point to both positive and negative consequences: positive in the prevention of irruptions of some small-mammal species that are important reservoirs of zoonotic disease; and negative in that some once-common species of TSE small mammals are now threatened by loss of understory habitat (cover); that community diversity is being suppressed; and that threats to already rare, cryptic, or understudied small mammal species will emerge. Native small mammals have coevolved with large mammalian herbivory and natural (often aboriginal) fire in all geographic regions of TSE, but increased intensity and frequency of fire under current and forecast conditions of anthropogenic climate change—in the face of negative synergistic effects of overgrazing by domestic LMH, and of drought—pose a challenge for us to monitor, much less predict how small mammals will fare under this new reality.

In all regions, managers should increase use of prescribed fire to forestall catastrophic wildfires, and researchers should establish refuges against domestic LMH (and more experimental exclosures against native LMH) to begin to understand the potential diversity of small mammals that exists in TSE. For example, more than 60 new species of rodents were described from the Afro-Malagasy region between 1989 and 2018 (Taylor et al., 2019). The most speciose genus of mammal is the shrew genus *Crocidura* (Family Soricidae, Order Eulipotyphla), of which an unknown number (though more than 100) of species occur in Africa, many of which are not identifiable morphologically and are little known ecologically, because they are difficult even to census. But they are important secondary consumers and prey species of TSE; some are also known reservoirs for hantavirus and other zoonotic disease, and one is critically endangered (Igbokwe et al., 2019). As much as additional study of the effects of endogenous disturbances on murid rodents of TSE is needed, the need for similar studies of these cryptic shrews—of which almost no ecological studies exist—is even greater. Similarly, 118 species of small mammals occur across the Cerrado savanna region of Brazil, with local richness as high as 26, yet *N. lasiurus* represented >20% of individuals captured in the aggregate of 96 field studies (Mendonça et al., 2018); this, and only a handful of other small-mammal species are the focus of habitat-related studies we found for the current review, meaning that responses to habitat perturbations by most native Cerrado small-mammal species are unknown. Importantly, Furtado et al. (2021) fills some of this knowledge gap for seven species of small mammals of the Cerrado. Finally, as we mentioned earlier, we found no studies of habitat effects on small mammals from South Asian TSE at all.

We recognize the limitations of this narrative, first-ever global review of field studies on this topic. Only 14 of the 63 studies we reviewed were manipulative experiments. Experimental designs, spatial and temporal scales of the study, field methodologies, analytical techniques, and degree of replication varied widely among those experiments. For all studies, whether experimental or not, the nature of herbivory varies by species of large mammal, and the behavior of fire varies across vegetative biomes and with temporally varying environmental conditions in any given biome. The above disparities make direct comparisons among studies challenging. Finally, there is every possibility that one or more forms of publication bias (Lortie et al., 2007) constrains the sample of field datasets that is published and, if published, is discoverable *via* our search methods. This may mean that studies that found no treatment effect are especially underrepresented. It is our hope that this initial review will inspire further studies, especially experimental ones that fill the abovementioned gaps and that, in future, a more systematic review and meta-analysis of experimental findings may be possible, enabling clearer conclusions of how endogenous disturbances affect small-mammal community structure in all TSE regions.

Author contributions

BB conceived the review and wrote much of the first draft, with the contribution of EV. BB and EV conferred on and contributed to several revised drafts. BB, EV, and SS compiled potential studies, and BB and EV decided on which to include and proofed the manuscript. SS compiled the initial spreadsheet and bibliography. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1017361/full#supplementary-material

SUPPLEMENTARY TABLE S1

Spreadsheet summarizing methods and findings of 63 published field studies of effects of endogenous disturbances on small-mammal communities in tropical savanna ecosystems. Details of explanatory and response variables, study type, disturbance type, effects and effect sizes, and authors' conclusions about mechanism(s) for significant responses.

SUPPLEMENTARY TABLE S2

Bibliography on habitat responses of tropical savanna small-mammal communities, and related studies and sources, including other reviews.

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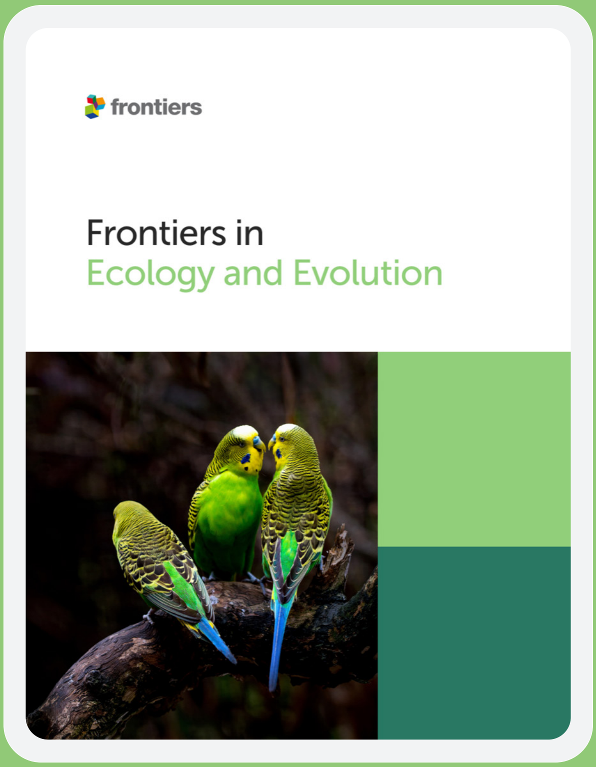

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