The pivotal role of land cover around forest fragments for small-mammal communities in a Neotropical savanna

Clément Harmange, Cyntia Cavalcante Santos, Fabio de Oliveira Roque, Franco Leandro Souza, Damien Arvor, Manon Bonnet, Emerson M Vieira, Olivier Pays

Received: 25 January 2023 | Revised: 5 July 2023 | Accepted: 1 August 2023

DOI: 10.1111/csp2.13005

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

WILEY

The pivotal role of land cover around forest fragments for small-mammal communities in a Neotropical savanna

Clément Harmange[1,2] | **Cyntia Cavalcante Santos**[3] | **Fabio de Oliveira Roque**[3] | **Franco Leandro Souza**[3] | **Damien Arvor**[4] | **Manon Bonnet**[1,2] | **Emerson M. Vieira**[5] | **Olivier Pays**[1,2]

[1]Univ Angers, BiodivAG, Angers, France

[2]REHABS International Research Laboratory, CNRS—Université Lyon 1—Nelson Mandela University, George, South Africa

[3]Bioscience Institute, Federal University of Mato Grosso Do Sul, Cidade Universitária, Campo Grande, Brazil

[4]LETG-Rennes, UMR 6554 CNRS, Université de Rennes 2, Rennes, France

[5]Laboratório de Ecologia de Vertebrados, Departamento de Ecologia/IB, Universidade de Brasília, Brasília, Brazil

Correspondence
Clément Harmange, Univ Angers, BiodivAG, 2 Bd Lavoisier, 49000 Angers, France.
Email: c.harmange.pro@gmail.com

Funding information
Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Grant/Award Numbers: 23038.001818/2020-70, Capes-PrInt41/2017, 88881.311897/2018-01; COFECUB, Grant/Award Number: Sv 875-17; Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Grant/Award Numbers: 302755/2018-7, 307599/2021-3

Abstract

While harboring the bulk of the planet's biodiversity, tropical ecosystems have experienced intense land conversion for agriculture. Studies examining the impacts of land-use change on tropical biodiversity have primarily focused on forest cover loss but have overlooked the ecological potential of habitats surrounding forest fragments to modulate biodiversity loss. We examined whether small-mammal communities changed with the land cover surrounding forest fragments, and how functional traits affected responses to land cover. Small mammals were sampled in the Brazilian Cerrado using live-trap transects. Three landscape types were identified according to the surroundings of the transects (within 750-m-radius buffers): forest- (≥50% forest cover), pasture-, and crop-dominated landscapes (<50% forest cover, with predominance of pastures or crops, respectively). We examined the composition of functional traits across landscape types and used abundance models to analyze the response of small-mammal communities to land cover. From forest-dominated to pasture- and crop-dominated landscapes, the abundances and/or species richness of the largest, forest-specialist, frugivorous/granivorous, and terrestrial species decreased. In forest-dominated landscapes, abundances and species richness were slightly affected by land cover surrounding forest fragments. In pasture- and crop-dominated landscapes which represent the less-preserved landscapes, increased proportions of native forests, open formations, and, to some extent, pastures, supported the increased abundance of small mammals. Land cover surrounding forest fragments is critical for maintaining the diversity of species and functional traits within small-mammal communities. Our results emphasize the need to maintain native vegetation in human-modified landscapes to maintain biodiversity and ecological functions.

KEYWORDS

Cerrado hotspot, farming landscape, functional traits, land cover, small-mammal communities, tropical biodiversity

1 | INTRODUCTION

Tropics harbor the bulk of the planet's biodiversity, with 16 out of 25 biodiversity hotspots located in the tropics, 15 of which are mainly characterized by tropical forests (Myers et al., 2000). Newbold, Oppenheimer, et al. (2020) reported that tropical forests, savannas, and grasslands are the biomes that experienced the greatest reduction in species richness (by 30%) in response to intense land-use change. Nevertheless, cultivated areas have more than doubled from 1961 to 2019 in tropical countries (Oakley & Bicknell, 2022), with agriculture responsible for 90%–99% of tropical deforestation recorded between 2011 and 2015 (Pendrill et al., 2022). Strategies to conciliate agriculture and long-term maintenance of biodiversity, ecological functions, and services have thus become increasingly challenging (Ellis, 2021; Foley et al., 2011), and rely on a fine understanding of the response of biodiversity to land use. Studies examining the effects of land-use change on terrestrial biodiversity have often focused on the loss of native forest cover using global measures of biodiversity (e.g., total abundance and species richness; Davison et al., 2021). However, the response of functional groups to a detailed description of the agricultural matrix surrounding remnants of native vegetation has been largely overlooked (de Souza Leite et al., 2022).

The effects of land use on biodiversity may vary across landscapes, depending on agricultural practices and land-use intensity (Beckmann et al., 2019), or on the habitat types available in the agricultural matrix (Carvalho et al., 2009). For instance, the species richness and abundance of small mammals are affected when the amount of native vegetation cover falls below a certain threshold (e.g., 30% in the Atlantic Forest; Pardini et al., 2010). In farming landscapes with limited native vegetation cover (e.g., in parts of the Brazilian Cerrado), forest remnants are the most speciose habitat for small mammals followed by native open formations (i.e., cerrado and grasslands; Ribeiro et al., 2020; but see Carmignotto et al., 2022). Both contribute positively to the diversity of small mammals due to habitat-specific species composition (Furtado et al., 2021; Mattos et al., 2021). However, the remaining habitats may also modulate the effects of land-use change on biodiversity. Small forest patches surrounded by pastures may reduce or reverse the effects of forest cover loss on the species richness and abundance of small mammals compared with those surrounded by a mixed matrix of pastures and crops (Palmeirim et al., 2020). Fragments of native vegetation surrounded by pastures would be less disruptive to insect communities than those surrounded by intensive crop farming (e.g., sugarcane or coffee fields treated with pesticides; Dias et al., 2013; Martello et al., 2016). Similar results have also been reported for plant species richness, which decreased less in fodder than in crop production systems in response to land-use intensification (including pesticide input, monoculture, and harvest intensity, Beckmann et al., 2019). Compared with crops, pastures may mitigate the expected negative effects of forest cover loss on biodiversity in farming landscapes.

The effects of land use on species vary with their functional traits (Newbold, Bentley, et al., 2020) including body size (Magioli et al., 2021; Rocha et al., 2018), specialization in resource use (including habitat: Mattos et al., 2021; and food: Magioli et al., 2019; Ribeiro et al., 2019), and locomotion modes (Cassano et al., 2014). First, although the high movement capacity of large-bodied mammals may allow them to cope with sparse habitat patches, they would be more vulnerable to the loss of native forest cover than smaller species because they require larger home ranges to fulfill their biological requirements (Fritz et al., 2009; Galetti & Dirzo, 2013). Consequently, small-mammal species are often considered less sensitive (Magioli et al., 2021; Rocha et al., 2018). Second, greater flexibility in habitat selection makes generalist species less sensitive to forest cover loss than forest specialists (Mattos et al., 2021). Because of their greater dietary plasticity, omnivorous and insectivorous species are less sensitive to forest cover loss than frugivores. Magioli et al. (2019) and Godoi et al. (2017) found that frugivorous mammals and birds are the most dependent guilds on forest remnants for resources in Brazilian agricultural landscapes (see also Ribeiro et al., 2019). Third, arboreal species are highly dependent on canopy connectivity (Galán-Acedo et al., 2021). They would be particularly more affected than terrestrial and scansorial species (Cassano et al., 2014), more inclined to use less-forested landscapes (e.g., native open formations and pastures) to fulfill their biological requirements, and disperse and colonize neighboring habitat patches (Pires et al., 2002).

The current study aimed to examine whether small-mammal communities changed (in terms of species richness and abundance of individuals) with native forest cover loss, particularly with the type of landscape surrounding forest fragments, and how the functional traits of species affected their responses to land use in a Neotropical savanna (Brazilian Cerrado). This study specifically focused on habitat amount, identified as the most important predictor (compared with configuration metrics) of small-mammal species richness and composition in a previous study (Melo et al., 2017; but see Vieira et al., 2018). Three types of landscapes depicting different land-use intensities (forest-, pasture-, or crop-dominated landscapes) were examined in the Bodoquena Plateau. The Cerrado biome has experienced strong land

conversion for agricultural use (Song et al., 2021; Strassburg et al., 2017) despite its importance for biodiversity conservation and ecosystem service provisioning (Myers et al., 2000). We focused on small-mammal communities for several reasons: among mammals, these communities host one of the greatest species richness in Brazil (rodents represent one third of mammal species of the Brazilian Cerrado, Paglia et al., 2012; see also Mendonça et al., 2018) including endemic and threatened species (Carmignotto et al., 2012); they offer a wide diversity of functional traits whose influence on response to land use can be tested (Carmignotto et al., 2022); and they are important contributors to ecosystem services (e.g., pest control: Camargo et al., 2022) and disservices (e.g., vectors of zoonotic diseases: Gonçalves et al., 2016).

We expect small-mammal communities (abundance and species richness) to be negatively affected by the loss of native vegetation cover, particularly when remnants are predominantly surrounded by crops compared with pastures. Indeed, pastures would be less disruptive in terms of abundance and diversity of resources (e.g., plant and insect communities: Beckmann et al., 2019; Dias et al., 2013). Frugivores/granivores are expected to be negatively affected by forest cover loss to a greater extent in crop-dominated landscapes than in pasture-dominated landscapes, since the latter can offer maintenance of plant diversity and thus feeding opportunities (Beckmann et al., 2019). Large-bodied (body mass >50 g), forest-specialist, and arboreal small mammals are expected to be negatively affected by the loss of forest cover regardless of land use in the surrounding landscape. Regarding the locomotion mode, terrestrial and scansorial mammals are expected to be unaffected by the amount of pastures, as they allow the maintenance of movement and dispersion (Pires et al., 2002). Finally, we predict that in crop-dominated landscapes, remnant forest cover, native open formation (ranging from <75% tree cover to natural grassland), and pastures may affect positively the abundance and species richness of functional groups.

2 | METHODS

2.1 | Study area

The study was conducted from February 2016 to November 2017, on the Bodoquena Plateau region (from 20°25′29.28″ to 21°44′19.72″ S and from 56°52′24.46″ to 56°17′23.36″ W), Mato Grosso do Sul, Brazil (Data S1, Figure A.1). The Bodoquena Plateau which is mostly preserved inside the Serra da Bodoquena National Park (SBNP), is covered by deciduous and semi-deciduous seasonal forests considered part of the Atlantic Forest sensu *lato*. In the study area, which covers 9000 km^2, these seasonal forests consist of patches inside the Cerrado biome. The Cerrado and Atlantic Forest biomes are considered biodiversity hotspots (Myers et al., 2000). Land cover—the biophysical attributes of the land—is closely related to and can be used to characterize land use, that is, human activity applied to the land (Brown et al., 2000). In the study area, land cover is mainly characterized by native forests; native open formations, including savanna formation and natural grasslands; and agriculture, including anthropogenic pastures and crops (mainly soybean; Klink & Machado, 2005). In recent decades, native vegetation cover has undergone a drastic decline (Strassburg et al., 2017) expected to continue in the coming years because of rapid agricultural expansion in the Cerrado (Song et al., 2021).

2.2 | Small-mammal sampling and functional traits

The small-mammal communities of the study area were sampled using live traps set along transects ($n = 106$) distributed across a gradient ranging from 0 to 100% forest cover, with a large variety in the surrounding agricultural matrix to test for its effect on mammal communities. Transects were mostly set in forest. However, some of them may have been set in the surrounding matrix in less forested landscapes, dominated by pastures or crops. A live-trap transect consisted of 26 sampling stations separated by approximately 30 m, each of which combined a Tomahawk trap (70 × 35 × 40 cm, 45 × 20 × 20 cm, or 30 × 17.5 × 15.5 cm) set on the ground and a Sherman trap (30 × 8 × 9 cm) at 1.5 m high in the vegetation. Traps were baited with fruit slices and a mixture of oats, peanut butter, and banana (see Palmeirim et al., 2020 for similar experimental design). Each transect was surveyed over three consecutive nights. This resulted in a total of 8268 trap-nights across all the sampling stations. Each morning, the field operator (Cyntia Cavalcante Santos) collected individuals trapped at night. Most captured individuals were identified in the field using Neotropical mammal identification guides (Bonvicino et al., 2002, 2008; Emmons et al., 1997), marked on their backs with a non-toxic color spray, and released at the capture site. Individuals with uncertain identification were collected as vouchers, identified by small-mammal specialists, and deposited in the zoological collection of the Federal University of Mato Grosso do Sul, Campo Grande, Brazil (Data S2).

We categorized the captured species into functional groups: *body size* (small: mean adult body mass ≤50 g;

large: >50 g), *habitat* (forest specialist; generalist), *diet* (frugivore/granivore vs. insectivore/omnivore), and *locomotion mode* (terrestrial, arboreal, or scansorial) (see Data S1, Table A.1 for details).

2.3 | Landscape characterization

Two annual land-cover maps were prepared to characterize the landscape from 2016 to 2017, following a multi-step process based on forest maps derived from the Global Forest Change project and Mapbiomas annual land-cover maps for those years (see Data S3). This resulted in five land-cover classes: "*Forest*" represented 31.8% (mean for the years 2016–2017) of the study area's land cover, "*Native open formation*" represented 21.1%, "*Pasture*" (exclusively anthropogenic and mainly represented by exotic *Brachiaria* spp.) accounted for 43.4% of the study area and 97.6% of the total grassland cover, "*Crops*" (3.5% of the study area, 90% of which represented by soybean), and "*Other*" (0.2% of the study area) referring to non-vegetated land cover that represents non-habitat (Data S3, Tables C.1 and C.2).

2.4 | Calculation of landscape metrics

To characterize the landscape in the surroundings of the live-trap transects, we calculated landscape metrics from the previously prepared annual land-cover maps. Our ability to detect the effects of land cover on small-mammal communities may depend on the spatial extent over which the metrics are calculated (Jackson & Fahrig, 2012). Therefore, we calculated the proportion of *forest*, *native open formation*, *pasture*, and *crops* classes at four different spatial extents, defined as buffers of 750, 1000, 1500, and 2000 m radius from the centroid of live-trap transects. We used a minimum radius of 750 m to ensure that all transects lay within the buffers (mean transect length = 907 m; min = 386 m; max = 1438 m). We used 2000 m as the maximal radius to limit the overlap between neighboring buffers (Data S4, Table D.1). Metrics were calculated for each buffer using the *ClassStat* function from the R package *SDMTools* (van der Wal et al., 2014). The proportions of each land-cover class within the buffers are presented in Data S3, Table C.2. These proportions were used as covariates in the analyses of the effect of forest cover on the small-mammal communities (Section 2.6.2) and the response of functional groups to land cover (Section 2.6.4).

2.5 | Defining landscape types

To examine how landscapes affect the composition of functional traits within small-mammal communities (see Section 2.6.3 of statistical analyses) and their response to land cover (see Section 2.6.2), we defined three landscape types that reflect the context of landscapes mainly represented in the Cerrado: landscapes dominated by native forests (preserved), pastures, or crops (the two most represented anthropogenic land use). First, from the 106 live-trap transects, we selected those in which the land cover within the 750 m radius buffer (see statistical analyses for the selection of spatial extent) was dominated by forest cover, with ≥50% forest cover in their surroundings. 50% is a critical threshold below which the forest landscape connectivity may change (see Michalski et al., 2008). Above this, forests should not be limiting so that small mammals, including forest specialists, were not expected to respond to forest habitat amount (Pardini et al., 2010). Finally, this threshold represented approximately the 3rd quartile of percent forest cover (45.7%) within 750 m radius buffers. Using this conservative threshold resulted in a total of 24 forest-dominated landscapes. 16 live-trap transects in which *forest* area was higher than the areas covered by *native open formation*, *pasture*, or *crops*, but below the threshold of 50% forest cover, were not considered in forest-dominated landscapes. This guarantees a more accurate portrayal and distinction among typical landscape contexts to be compared. Because the area covered by the remaining non-forested land covers was highly variable, and several transects did not have a land cover >50% of the 750 m radius buffer, we categorized the remaining landscapes according to their dominant land-cover type. The second landscape type, hereafter "pasture-dominated" ($n = 50$), consisted of live-trap transects wherein the area of *pasture* within 750 m radius buffers was higher than the areas covered by *forest*, *native open formation*, or *crops* (minimum, mean, and maximum values of pasture cover: 35.2%, 67.7%, and 100%, respectively). Finally, the third landscape type, hereafter "crop-dominated" ($n = 9$), designated live-trap transects for which the area of *crops* within 750 m radius buffers was greater than the areas covered by *forest*, *native open formation*, or *pasture* (min, mean, and max values of crop cover: 37.6%, 63.6%, and 98.9%, respectively). In pasture- and crop-dominated landscapes, pastures, and crops accounted for at least 35% of the land cover in the transect surroundings. The few remaining transects ($n = 7$) located in landscapes dominated by native open formations were not considered in the analyses, as the models failed to work because of this small sample size.

2.6 | Statistical analyses

First, we selected a suitable spatial extent to examine the response of small mammals to land cover. Buffers of 750 m radius from the centroid of live-trap transects (hereafter called "Buffers of 750 m") provided the best statistical support in modeling the response of the small-mammal communities (total abundance and species richness) to land cover (Data S4, Figure D.1 and Table D.2). Buffers of 750 m further reduced the overlap between nearest-neighbor buffers (mean overlap = 3.91% ± 8.79 SD, Data S4, Table D.1) to prevent spatial autocorrelation in model residuals (Amiot et al., 2021; Zuckerberg et al., 2012). This does not mean that species do not respond to land cover at buffer extents below 750 m. However, we were unable to test this aspect because of the mean transect length.

2.6.1 | Modeling process

This section describes the general modeling process applied in the analyses presented in Sections 2.6.2 and 2.6.4. In these sections, the effects of land cover on small-mammal communities were analyzed through abundance modeling using the function "pcount" (N-mixture models) of the R package *unmarked* (Fiske & Chandler, 2011). Abundance λ (i.e., the total abundance of mammal individuals, the total species richness, and the abundance of individual or species richness within functional groups) at each transect location and the detection probability p_d were modeled as a function of covariates x_i and z_i using log link and logit link functions, respectively (see Fiske & Chandler, 2011 for details).

First, we estimated the detection probability p_d. We used a stepwise process starting with model $\lambda(.)p_d(.)$ where the abundance and detection probabilities were constant. The probability of an individual being captured at the sampling site may be influenced by several factors, including the length of the transect, sampling date, and predominant type of vegetation along the transect. Thus, three covariates z_i were computed: log (transect length), sampling date (Julian day), and predominant cover type (open vs. dense vegetation; Data S5). We then tested their effects on the models $\lambda(.)p_d(z_i)$ where the abundance λ was constant using likelihood-ratio tests (LRT). When a significant effect of z_i was detected ($p < 0.05$), the given covariate z_i was conserved in the following procedure.

Then, we ran the model $\lambda(x_i)p_d(z_i)$ including one landscape metric in the model (x_i, which is the proportion of *forest* [Section 2.6.2], or the proportion of *forest*, *native open formation*, *pasture*, or *crops* [Section 2.6.4]) and tested their effects on the abundance λ using LRT. When a significant landscape metric effect was detected, p values and abundance estimates (±SE) were extracted from the model. Predicted abundances (±95% CI) were represented as a function of landscape metric x_i using the *predict* function for the *unmarked* package objects.

2.6.2 | Effect of forest cover on the small-mammal communities

We examined the response of small-mammal communities to forest cover, considering all the live-trap transects sampled in the current study ($n = 106$). We applied the modeling process described above to each of the following dependent variables: total abundance of small-mammal individuals, total species richness, abundance of individuals within functional groups (*body size*: small, large; *habitat*: forest specialist, generalist; *diet*: frugivore/granivore, insectivore/omnivore; *locomotion mode*: terrestrial, arboreal, scansorial), and species richness within the functional groups. The proportion of *forest* was used as a single independent variable. This analysis was repeated excluding the most abundant species (*Thrichomys fosteri*) to investigate its influence on the significant patterns.

2.6.3 | Composition of functional traits according to landscape type

Chi-squared tests were performed on the number of small-mammal individuals to test for homogeneity in the composition of functional traits related to *body size*, *habitat*, *diet*, and *locomotion mode* across three landscape types: forest-dominated ($n = 24$), pasture-dominated ($n = 50$), and crop-dominated landscapes ($n = 9$).

2.6.4 | Response of functional groups to land cover

Our dataset did not allow us to consider forest, pasture, and crop cover as continuous variables all together in a single model for two reasons: (i) including them with their two-way interactions to test for threshold responses of small mammals requires a large sample size and thus led our models to fail; and (ii) increasing pasture or crops was related to a decrease in forest cover and led to multicollinearity between predictors. Therefore, we first ensured that no threshold response of small mammals to land cover was detected (Data S1, Table A.2 and Figure A.2). Then, we opted to analyze the response of small mammals separately in forest-, pasture-, and crop-dominated landscapes. This allowed us to (i) fix the

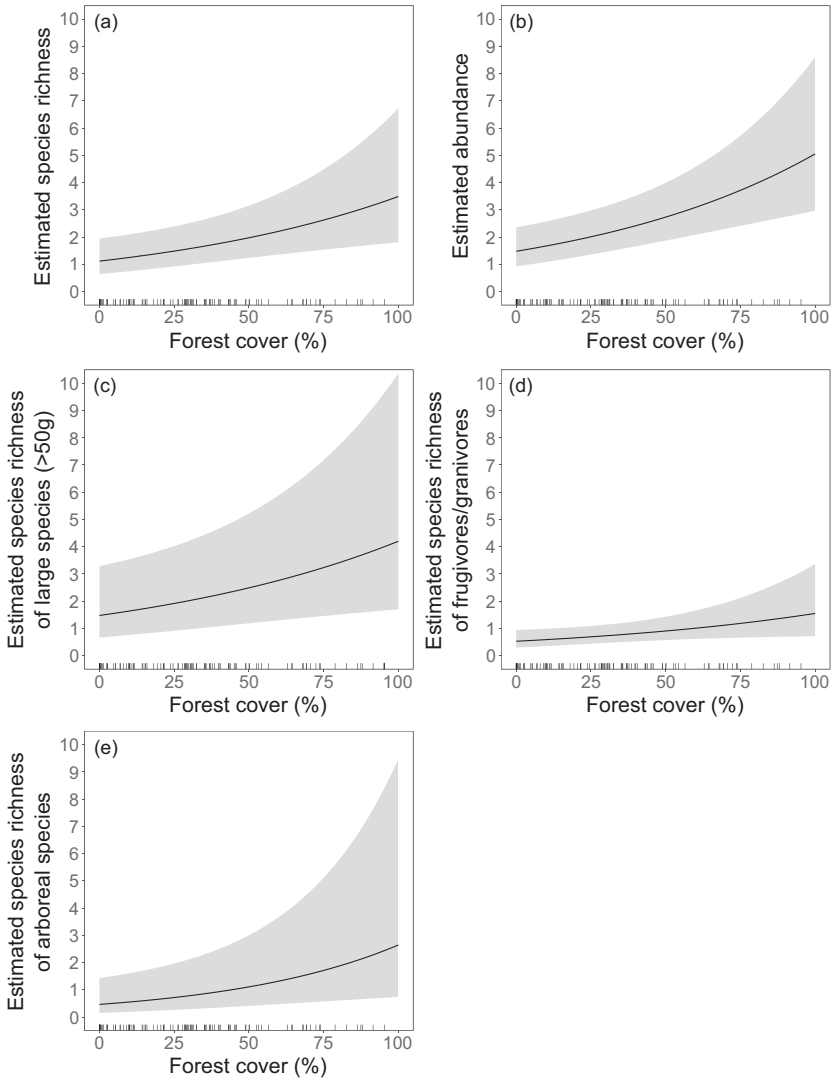

FIGURE 1 Predicted relationships (solid lines) with 95% confidence interval (gray envelope) between forest cover within buffers of 750 m from the centroid of live-trap transects and the (a) total species richness of small mammals, (b) total abundance, and (c–e) species richness within functional groups. Forest cover values of buffers are shown as vertical lines on the x-axes.

dominant land-cover type, and (ii) examine how the communities responded to variations in the percentages of the remaining non-dominant land cover types (e.g., *native open formation*, *crops*, and *pasture* for forest-dominated landscapes), used as continuous covariates (z_i). The above-mentioned modeling process was used for each of the three landscape types, and the dependent variables used were the total abundance of small-mammal individuals, total species richness, and abundance of individuals and species richness within functional groups. When a significant response of the small-mammal communities to land cover was detected, the analyses were repeated, excluding *T. fosteri* for the functional groups in which this species was involved (i.e., large, forest-specialist, frugivore/granivore, or terrestrial). This allowed us to test whether the variation of a given trait in the landscape could result from the variation of the most abundant species. When no response of the small-mammal communities to land cover was detected, this suggested that the given trait and ecological function remained available in the landscape regardless of land cover variation.

All statistical analyses were conducted using R (R Core Team, 2021).

3 | RESULTS

A total of 179 individuals belonging to 15 species were trapped during the study (Data S1, Table A.1), corresponding to an overall capture success rate of 6.5% per sampling station. The mean number of individuals and species captured per transect was 1.7 ± 2.7 SD and 0.9 ± 1.1 SD, respectively (see Data S5 for detailed capture information per transect, and Data S1, Figure A.3 for accumulation curves). The most abundant species were *Thrichomys fosteri* (42% of captures), *Gracilinanus agilis* (12%), and *Didelphis albiventris* (10%) (Data S1, Table A.1; see also Data S5 for details for each functional group). Because *T. fosteri* was highly predominant in the

TABLE 1 Effects of forest cover within buffers of 750 m from the centroid of live-trap transects on measures of the small-mammal communities including the total species richness, total abundance of individuals, and species richness and abundance within functional groups of small mammals, using likelihood-ratio test (i.e., χ^2)

		All species				Excluding *Thrichomys fosteri*		
Dependent variable	**Functional group**	χ^2	**Df**	***p* value**	**β ± SE**	χ^2	**Df**	***p* value**
Species richness	Small species (≤50 g)	2.247	1	0.134				
	Large species (>50 g)	5.572	1	0.018	1.047 ± 0.433	0.126	1	0.723
	Forest specialists	3.627	1	0.057	(1.091 ± 0.559)	0.079	1	0.779
	Generalists	2.333	1	0.127				
	Frugivores/granivores	4.098	1	0.043	1.079 ± 0.520	0.002	1	0.964
	Insectivores/omnivores	2.168	1	0.141				
	Terrestrial	1.678	1	0.195				
	Arboreal	6.084	1	0.014	1.74 ± 0.688			
	Scansorial	0.080	1	0.777				
	Total	7.937	1	0.005	1.14 ± 0.396	1.634	1	0.201
Abundance	Small species (≤50 g)	0.027	1	0.870				
	Large species (>50 g)	10.709	1	0.001	1.227 ± 0.367	0.003	1	0.958
	Forest specialists	10.786	1	0.001	1.470 ± 0.436	0.218	1	0.641
	Generalists	1.532	1	0.216				
	Frugivores/granivores	10.247	1	0.001	1.33 ± 0.405	0.028	1	0.867
	Insectivores/omnivores	1.481	1	0.224				
	Terrestrial	8.224	1	0.004	1.33 ± 0.451	2.544	1	0.110
	Arboreal	5.511	1	0.019	1.499 ± 0.624			
	Scansorial	0.015	1	0.902				
	Total	12.755	1	<0.001	1.23 ± 0.334	0.864	1	0.353

Note: Analyses were conducted considering all the data, and excluding the most abundant species, *Thrichomys fosteri* (see Section 2.6).

communities, analyses were performed, including and excluding this species.

3.1 | Effect of forest cover on the small-mammal communities

The total species richness (Figure 1a) and abundance of small mammals (Figure 1b) increased with forest cover in buffers of 750 m (Table 1). The observed patterns strongly depended on the functional traits of the species. The richness of the largest (>50 g; Figure 1c), frugivorous/granivorous (to a lesser extent; Figure 1d), and arboreal species (Figure 1e) in the communities increased with forest cover, whereas no effect was detected on the richness of the smallest, forest-specialist (marginal effect), habitat generalist, insectivorous/omnivorous, terrestrial, or scansorial species (Table 1). All these results remained consistent for the abundance of individuals within each functional group. Additionally, the abundance of forest-specialist and terrestrial mammals increased with forest cover (Table 1 and Data S1, Figure A.4) namely due to the increased abundance of *T. fosteri* (Data S1, Figure A.5). Except for arboreal mammals, all significant results were no longer significant when *T. fosteri* was excluded from the analyses (Table 1).

3.2 | Composition of functional traits according to landscape type

The composition of functional traits within the small-mammal communities changed with the landscape type (Figure 2). The relative abundances of individuals of large (>50 g) ($\chi^2 = 6.35$; df = 2; $p = 0.042$), forest-specialist ($\chi^2 = 10.61$; df = 2; $p = 0.005$), frugivorous/granivorous ($\chi^2 = 6.50$; df = 2; $p = 0.039$), and terrestrial species ($\chi^2 = 17.43$; df = 2; $p = 0.001$) decreased from forest-dominated to pasture- and crop-dominated landscapes, whereas those of small (≤50 g), habitat generalist, insectivorous/omnivorous, and scansorial species increased, respectively. The relative abundance of arboreal mammals was

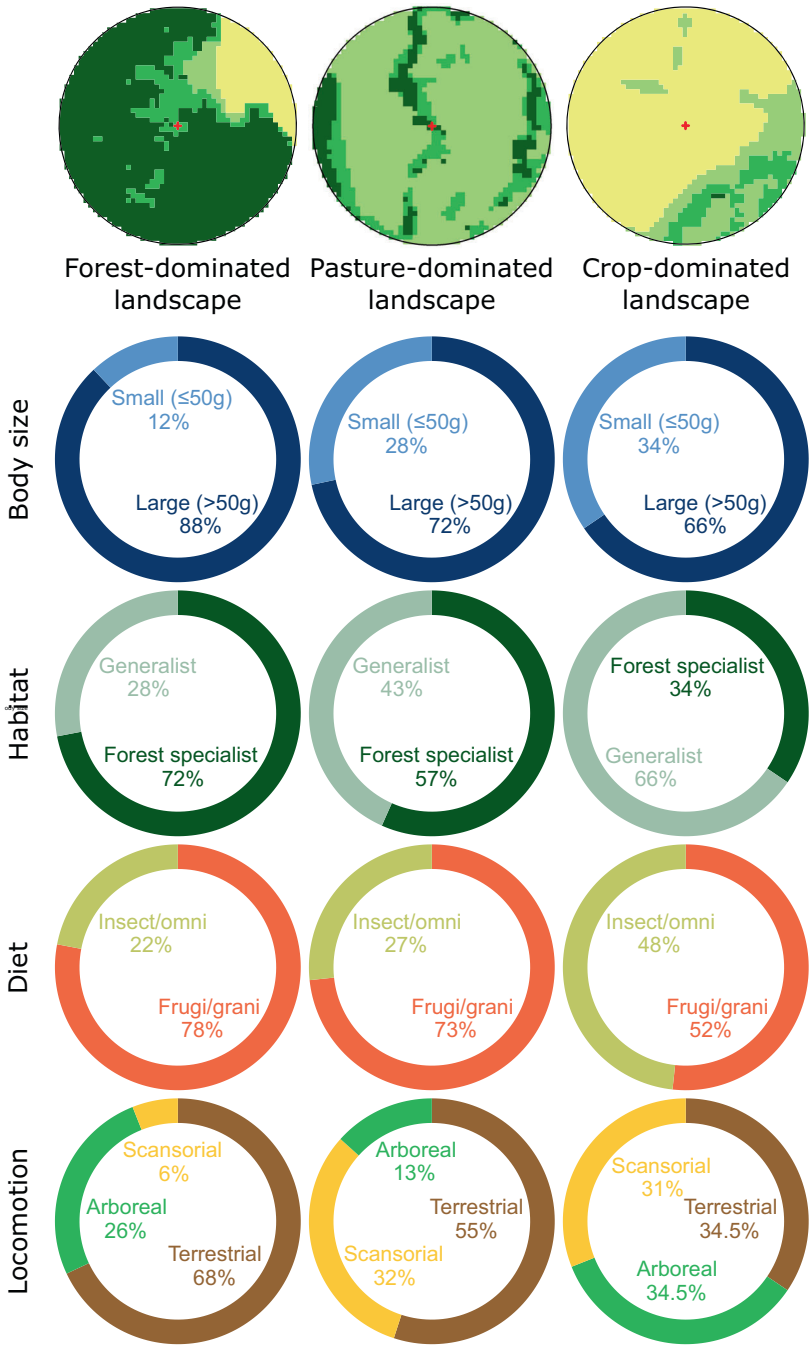

FIGURE 2 Composition of functional traits (body size, habitat, diet, and locomotion modes, see Data S1, Table A.1) of the small-mammal individuals captured across the landscape types (dominated by forest $n = 24$, pastures $n = 50$, and crops $n = 9$, see Section 2). Examples of buffers of 750 m depicting forest-, pasture-, and crops dominated landscapes are presented at the top of the figure with forest represented in dark green, native open formation in medium green, pastures in light green, and crops in yellow.

lowest in pasture-dominated and highest in crop-dominated landscapes.

3.3 | Effect of land cover according to landscape type

In forest-dominated landscapes, although the total abundance and abundance of the large species decreased with increasing crop cover (Table 2), small-mammal communities were weakly affected by variation in the non-dominant types of land cover. Despite significant *p* values, we did not consider patterns on the frugivorous/granivorous and terrestrial mammals to be robust, as the standard deviation values were higher than the estimates. The abundance of individuals of terrestrial species increased with pasture coverage (Table 2). However, these results were no longer significant when *T. fosteri* was excluded from the analyses (Table 2).

In landscapes dominated by pastures and crops, small-mammal communities changed drastically with land cover (Table 2). In pasture-dominated landscapes, total abundance (Data S1, Figure A.6a), total species richness, and abundance of individuals as well as species

TABLE 2 Effects of the non-dominant land covers (proportions of forest, native open formation, pasture, and crops) in landscapes dominated by forest, pasture, or crops, on the total species richness, total abundance, and species richness and abundance of individuals within functional groups of small mammals, using likelihood-ratio test (i.e., χ^2)

		Forest-dominated ($n = 24$)			Pasture-dominated ($n = 50$)			Crop-dominated ($n = 9$)		
Dependent variable	**Functional group**	**Open formation**	**Pasture**	**Crops**	**Forest**	**Open formation**	**Crops**	**Forest**	**Open formation**	**Pasture**
Abundance	**Body size**									
	Small							21.1 ± 4.15 (<0.001)		14.14 ± 4.10 (0.003)
	Large			−22.61 ± 11.75 (0.006)		4.08 ± 1.93 (0.036)		10.19 ± 2.16 (<0.001)	11.65 ± 5.86 (0.042)	
	Large[a]					8.68 ± 2.74 (0.001)		10.91 ± 2.03 (<0.001)		
	Habitat									
	Forest					4.67 ± 2.23 (0.039)				14.10 ± 6.94 (0.012)
	Forest[a]					18.10 ± 5.65 (<0.001)				21.52 ± 11.62 (0.006)
	Generalist				6.92 ± 2.77 (0.012)			5.27 ± 2.13 (0.008)	10.18 ± 4.12 (0.011)	
	Diet									
	Frugi/grani			−68.24 ± 122.83 (0.003)						9.46 ± 4.67 (0.028)
	Frugi/grani[a]									10.33 ± 5.37 (0.032)
	Insect/omni				6.93 ± 3.63 (0.050)	6.74 ± 3.14 (0.035)		7.59 ± 3.04 (0.004)	17.22 ± 5.85 (0.001)	
	Locomotion									
	Terrestrial		4.70 ± 2.35 (0.048)	−61.84 ± 121.43 (0.024)						14.10 ± 6.94 (0.012)
	Terrestrial[a]		Failed	Failed						21.52 ± 11.62 (0.006)
	Arboreal				7.76 ± 3.46 (0.014)					
	Scansorial							14.65 ± 2.63 (0.013)		22.79 ± 5.45 (0.027)
	Total			−15.66 ± 7.56 (0.013)	3.94 ± 1.80 (0.027)			3.10 ± 1.55 (0.049)	9.51 ± 3.54 (0.006)	
	Total[a]									

(Continues)

TABLE 2 (Continued)

Dependent variable	Functional group	Forest-dominated ($n = 24$)			Pasture-dominated ($n = 50$)			Crop-dominated ($n = 9$)		
		Open formation	Pasture	Crops	Forest	Open formation	Crops	Forest	Open formation	Pasture
Species richness	**Body size**									
	Small									
	Large									
	Habitat									
	Forest									
	Generalist				6.50 ± 2.85 (0.023)					
	Diet									
	Frugi/grani									
	Insect/omni				5.77 ± 2.51 (0.015)	6.99 ± 3.02 (0.019)				
	Locomotion									
	Terrestrial									
	Arboreal				7.76 ± 3.46 (0.014)					
	Scansorial									
	Total				3.92 ± 1.92 (0.041)					
	Total[a]									

Note: Proportion of land cover was calculated within buffers of 750 m from the centroid of live-trap transects. Slope estimates ± SE (p value) are indicated only when the variables are significant ($p < 0.05$). Blanks refer to non-significant results.

[a]Refers to analyses conducted excluding the most abundant species *Thrichomys fosteri* (see Section 2.6).

richness of habitat generalists, insectivores/omnivores, and arboreal mammals increased with increasing forest cover. The abundance of the large species, forest specialists, and the abundance and species richness of insectivores/omnivores increased as the native open formation cover increased. Except for total abundance and species richness, patterns did not change when *T. fosteri* was excluded (Table 2).

In crop-dominated landscapes, the abundance of individuals within both categories of body mass (≤50 and >50 g), habitat generalists, insectivorous/omnivorous, scansorial mammals, and total abundance (only when considering *T. fosteri*) increased when the remnant forest cover increased (Table 2). The abundance of habitat generalists and insectivores/omnivores increased with native open formation cover, as did the total abundance and abundance of the large species, but only when *T. fosteri* was included in the analyses (Data S1, Figure A.6b). The abundance of small, forest-specialist, frugivorous/granivorous, terrestrial, and scansorial species increased with pasture cover. These results were consistent when *T. fosteri* was excluded.

4 | DISCUSSION

For all the transects sampled, our study showed that the total abundance and species richness of the small-mammal communities decreased when the forest cover decreased. Our study further showed that the type of land cover surrounding forest fragments shaped the distribution of functional traits of the mammal communities. We also demonstrated that specific habitats (i.e., forests, native open formations, and pastures) mitigated the negative effects of crops on small-mammal communities in less-preserved landscapes.

4.1 | Effect of forest cover depends on functional traits

The response of small mammals to forest cover depends on functional traits. The largest species (e.g., *Thrichomys fosteri* and *Marmosa rapposa*) were particularly affected when forest cover decreased compared with smaller species (e.g., *Gracilinanus agilis*). Functional groups dependent on trees or forest conditions and resources (i.e., frugivores/granivores, arboreal species, and marginally forest specialists) also declined when forest cover decreased. However, the most abundant species, *Thrichomys fosteri*, a forest specialist (Melo et al., 2022), was responsible for driving most patterns. Carmignotto et al. (2022) showed that the overabundance of a single species associated with several rare species is typical of small-mammal assemblages in the Cerrado: *T. fosteri* (22.4% of captures) is dominant in the southwest (study region), *Necromys lasiurus* in the southeast (64%), and *Gracilinanus agilis* in the central Cerrado (63%, in Mattos et al., 2021). Therefore, our results may be specific to the small-mammal communities of the study region (Bodoquena) and reflect the effect of the loss of forested systems (e.g., forested cerrado, remnant Atlantic Forest) on forest specialists such as *T. fosteri*. It should also be noted that 47% (7 out of 15) of the species captured were represented by <5 individuals. In Carmignotto et al. (2022), 47% (27 out of 58 species) of species captured across the Cerrado were represented by <5 individuals. Consideration of these rare species is key to reliably examine the responses of small-mammal communities to land use in the Cerrado.

As expected, no effect of forest cover loss was detected on the abundance and richness of other groups, such as insectivores/omnivores and scansorial species, which were assumed to be more resilient (Cassano et al., 2014; Magioli et al., 2019). Although we cannot exclude that the non-significant trends observed in response to forest cover loss may result from a lack of statistical power, we believe that this is unlikely because such functional groups are well represented in open-formation specialists and generalists of the Cerrado (Carmignotto et al., 2022; Ribeiro et al., 2019). Previous studies have shown that frugivorous and herbivorous birds within pastures of the Brazilian Cerrado depend on the distance to the nearest forest, which offers higher fruit abundance than pastures (Godoi et al., 2017); whereas insectivores and omnivores respond positively to the increase in isolated trees and shrubs. The decrease in frugivorous/granivorous species was small (1–2 species per transect at 100% forest cover, to 0 species at 0% forest cover) and strongly influenced by *T. fosteri*. Therefore, even though this decrease in frugivores/granivores with decreasing forest cover appears to be biologically relevant, it should be interpreted with caution. It is unlikely that such decrease in frugivores/granivores will be compensated by the increase of other frugivorous/granivorous taxa (e.g., birds and bats), because of the specificity of their diet (Kurten, 2013). This lack of functional compensation may jeopardize frugivory and seed dispersal (Cazetta & Fahrig, 2022), and ultimately cascade on the composition of ecological communities and ecosystem functioning (Rogers et al., 2021).

4.2 | Landscape type and composition of functional traits

The composition of functional traits in small-mammal communities varied with landscape composition. From forest-dominated to pasture- and crop-dominated landscapes, the relative abundance of the large, forest-

specialist, and frugivorous/granivorous small-mammal species decreased and the relative abundance of the small, habitat generalist, and insectivorous/omnivorous mammals increased in the communities. This suggests that small-mammal communities are affected by land-use intensity (i.e., pesticide inputs and/or harvest frequency, Beckmann et al., 2019) increasing from pasture- to crop-dominated landscapes, and/or by the change from forest to native open formations as previously reported in the Cerrado (Furtado et al., 2021). The relative proportion of scansorial mammals also increased in less-forested farming landscapes. This was expected because of their greater flexibility and ability to use both terrestrial and arboreal modes of locomotion (Cassano et al., 2014). However, we did not expect this pattern to occur at the expense of the terrestrial mammals. In the study area, terrestrial species were mostly forest specialists (e.g., *Thrichomys fosteri* and *Hylaeamys megacephalus*). Therefore, it is more likely that their decline in response to forest cover loss from forest- to crop-dominated landscapes (Data S5), which is closely related to that of forest specialists, results from mechanisms related to their habitat specialization rather than their locomotion mode.

High tree density increases canopy connectivity and pathways for arboreal mammals (Cassano et al., 2014). However, we captured many individuals of arboreal species in less-preserved landscapes. *Gracilinanus agilis* may have contributed to this pattern. Although this mammal is associated with forest understory (Camargo et al., 2018) and is considered arboreal (Hannibal et al., 2015), it has also been reported to be strongly associated with small forest patches in the Brazilian Cerrado (Mattos et al., 2021), to be able to use open areas and landscapes with low forest cover (Melo et al., 2022; Santos-Filho et al., 2008), and to descend to the ground (37%–57% of captures in ground traps in Camargo et al., 2019). This suggests that, at least in the Cerrado biome, its classification as an arboreal may need to be revised.

Anthropogenic land cover might also create new food opportunities for small mammals. However, we do not believe that this was the case in the current study. Indeed, none of the species captured in our study were considered opportunistic, except *Calomys callosus*, which not only used but also increased its abundance in human-altered environments (Santos-Filho et al., 2008). *Didelphis albiventris*, *Oligoryzomys chacoensis*, and *Oligoryzomys mattogrossae*, which are generalists, have also been documented to use human-altered habitats (Cáceres et al., 2007; Hannibal et al., 2015).

In summary, our results suggest that the predominant land use around forest fragments drives selection pressure on mammal communities by selecting specific functional traits, thereby shaping the assemblage of ecological functions available in landscapes.

4.3 | Effect of land use in mitigating negative effect of forest cover loss

The small-mammal communities did not change much in most forested (≥50% forest) landscapes when land use varied around forest fragments, as most functional groups were not affected, and the few significant effects were driven by the forest specialist *T. fosteri* in this landscape type. This was expected because, in general, small-mammal species have been reported to be more resilient to land-use change than large mammals (Rocha et al., 2018), at least up to a given threshold of remaining native vegetation cover (e.g., 30% of remaining Atlantic Forest in Pardini et al., 2010). However, this does not imply that land use around forest fragments does not affect small-mammal communities. Notably, habitat amount is the main driver of species richness and composition in small-mammal communities (Melo et al., 2017), especially in the Cerrado where the degree of habitat specialization of small mammals is important (Mattos et al., 2021; Melo et al., 2022). However, habitat configuration may also affect species richness, particularly in most preserved landscapes (≥50% native vegetation cover, Palmeirim et al., 2019).

Most functional groups of the small-mammal communities were affected by land use in less-preserved landscapes. In pasture-dominated landscapes, the abundance and species richness of small mammals increased with increasing remnant forest and native open formation cover. This suggests that both might be compelling habitats mitigating the negative effects of anthropogenic land use on functional groups. This is particularly relevant in tropical savannas, which are characterized by a mosaic of native forest remnants, savannas, and grasslands (Carmignotto et al., 2022). Such positive effects were even more obvious in crop-dominated landscapes, in which an increase in pasture cover increased the abundance of most functional groups such as the small, forest-specialist, frugivorous/granivorous, terrestrial, and scansorial mammals. Previous studies have reported that pastures, even with exotic grass and cattle, allow the dispersion and colonization of small mammals to nearby suitable patches (Palmeirim et al., 2020; Pires et al., 2002). These pastures, contrary to crops (e.g., sugarcane), maintain the amount of food resources such as insects in extensive management systems (i.e., low inputs and cattle density, Martello et al., 2016). Overall, the removal of *T. fosteri* from the analyses had very little influence on the results in these anthropogenic

(pasture- and crop-dominated) landscapes. In most cases, the strength (i.e., the slope) of the responses was even greater when *T. fosteri* was removed. Indeed, as a strict forest specialist, this species did not increase in abundance with increasing native open formations. Therefore, because of its overabundance, *T. fosteri* partly masks the positive responses of less abundant species to native open formations and pastures. Finally, the effects on species richness were only detected in pasture-dominated landscapes, which were characterized by the largest sample size. This probably resulted from a lower statistical power in the other landscape types, exacerbated by the reduction in biological entities (species vs. individuals) considered in the species richness compared with abundance analyses. In particular, it should be noted that the patterns observed in crop-dominated landscapes were based on 9 transects of 26 live-traps (i.e., 234 traps). Further studies will be needed to confirm these patterns.

4.4 | Conservation implications and perspectives

Identifying strategies to reconcile agriculture and biodiversity in human-modified agricultural landscapes has become an urgent challenge (Ellis, 2021). We found that in preserved landscapes (≥50% forest cover), variations in anthropogenic land use surrounding forests had limited impact on small-mammal communities. Our results also suggest that in human-modified landscapes, different landscape management strategies, that is, towards the prevalence of cattle pastures or arable lands, might filter functional groups. Ideally, a minimum of 50% forest cover would maintain the diversity of all the functional groups of small mammals. Alternatively, particularly in heavily deforested agricultural landscapes, promoting mixed arable and livestock farming systems and incorporating native vegetation conservation units or pastures with scattered trees (see Prevedello et al., 2018) as the predominant cover, may be effective strategies for mitigating, balancing, or reversing the negative impacts of crops on mammal communities. Maintaining 12.5% of remnant forest or native open formation cover associated with 12.5% pasture would allow to conserve 57% of the functional groups studied. More generally, maintaining connected patches of forest, savanna and grasslands or pastures in the Cerrado, should be an effective strategy for conserving the regional pool of small-mammal species, largely represented by restricted-range endemic species with a high degree of habitat specialization (e.g., forest and open-formation specialists, Carmignotto et al., 2022; Ribeiro et al., 2020). We believe that such functional and integrated landscape planning may contribute to effective conservation of vulnerable beneficial traits and functions (e.g., seed dispersal and forest regeneration) in human-modified landscapes.

In many social-ecological systems, conservation practices and restoration actions may be constrained by food security, economic, or political issues (Colman et al., 2021). This is particularly relevant in the Cerrado biome experiencing rapid land-use change for soybean expansion (Song et al., 2021). Indeed, 47% of the native vegetation cover has already been lost (Colman et al., 2021) and 40% of the remaining native vegetation can still be legally converted (Strassburg et al., 2017). Considering the land-cover quality (e.g., diversified agriculture) and the spatial arrangement of key habitat features (i.e., size, density, and distance between patches) in the agricultural matrix surrounding connected patches of native vegetation may offer ecological opportunities to promote the conservation of functional biodiversity without increasing (though maintaining) native forest cover (see also de Souza Leite et al., 2022).

It should be noted that our results are based on small-mammal communities and may not apply to larger mammal species, which may require larger areas of native vegetation (Magioli et al., 2021). However, our findings raise concerns about (small) threatened species. While well-represented species have been affected by habitat loss and land cover surrounding forest fragments, these effects could be exacerbated for threatened species when population sizes are reduced and/or ranges are restricted. There is therefore an urgent need for conservation measures to prevent conversion of remaining native habitats and, where appropriate and possible, to restore degraded habitats (Schüler & Bustamante, 2022). Further studies combining species-level and trait-based approaches are needed to examine species, ecological functions and ecosystem services at risk, and to inform effective conservation planning in human-modified landscapes.

AUTHOR CONTRIBUTIONS

Clément Harmange: Conceptualization, Methodology, Data Curation, Investigation, Formal analysis, Writing—Original Draft. Cyntia Cavalcante Santos: Methodology, Data Curation, Writing—Review & Editing. Fabio de Oliveira Roque: Methodology, Writing—Review & Editing. Franco Leandro Souza: Methodology, Project administration, Funding acquisition, Writing—Review & Editing. Damien Arvor: Methodology, Writing—Review & Editing. Manon Bonnet: Methodology, Writing—Review & Editing. Emerson M. Vieira: Writing—Review & Editing. Olivier Pays: Conceptualization, Methodology, Investigation, Formal analysis, Writing—Review & Editing, Supervision, Project administration, Funding acquisition.

ACKNOWLEDGMENT

We thank N. C. Cáceres, W. Hannibal, R. Rocha, C. Teixeira, F. Severo-Neto, C. Amiot, B. Bellon, and P. C. Renaud for their contribution.

FUNDING INFORMATION

This study was funded by a CAPES [23038.0018 18/2020-70; Capes-PrInt 41/2017: 88881.311897/2018-01], COFECUB [Sv 875-17], CNPq [307599/2021-3], the PELD *Planalto da Bodoquena*. The UA provided additional funding supports to Olivier Pays, Clément Harmange, and Manon Bonnet, and Fabio de Oliveira Roque received individual productivity grants from the CNPq [302755/2018-7]. We would like to thank the PPGEC of the UFMS, the CAPES, the COFECUB, Campus France, the FUNDECT for their institutional supports.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The dataset analyzed during the current study is available in the Open Science Framework repository, https://osf.io/nzu2r/.

ETHICS STATEMENT

The study complies with the guidelines for the use of animals in research and the Brazilian legal requirements (reference numbers of MMA-ICMBio-SISBIO authorizations: 52539-1/2016 and 52539-2/2017).

ORCID

Clément Harmange https://orcid.org/0000-0001-5207-021X
Cyntia Cavalcante Santos https://orcid.org/0000-0002-8207-9263
Fabio de Oliveira Roque https://orcid.org/0000-0001-5635-0622
Franco Leandro Souza https://orcid.org/0000-0002-7041-4036
Damien Arvor https://orcid.org/0000-0002-3017-9625
Emerson M. Vieira https://orcid.org/0000-0003-3488-621X
Olivier Pays https://orcid.org/0000-0001-8268-1804

REFERENCES

Amiot, C., Santos, C. C., Arvor, D., Bellón, B., Fritz, H., Harmange, C., Holland, J. D., Melo, I., Metzger, J.-P., Renaud, P.-C, Roque, F. O., Souza, F. L., & Pays, O. (2021). The scale of effect depends on operational definition of forest cover: Evidence from terrestrial mammals of the Brazilian savanna. *Landscape Ecology*, *36*, 973–987.

Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceauşu, S., Kambach, S., Kinlock, N. L., Phillips, H. R., Verhagen, W., Gurevitch, J., & Klotz, S. (2019). Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. *Global Change Biology*, *25*, 1941–1956.

Bonvicino, C., ... D'Andrea, P. S. (2008). Guia dos roedores do Brasil, com chaves para gêneros baseadas em caracteres externos. In *Série de Manuais Técnicos, 11*. Centro Pan-Americano de Febre Aftosa, OPAS/OMS.

Bonvicino, C. R., Lindbergh, S. M., & Maroja, L. S. (2002). Small non-flying mammals from conserved and altered areas of Atlantic Forest and Cerrado: Comments on their potencial use for monitoring environment. *Brazilian Journal of Biology*, *62*, 765–774.

Brown, D. G., Pijanowski, B. C., & Duh, J.-D. (2000). Modeling the relationships between land use and land cover on private lands in the upper Midwest, USA. *Journal of Environmental Management*, *59*, 247–263.

Cáceres, N. C., Bornschein, M. R., Lopes, W. H., & Percequillo, A. R. (2007). Mammals of the Bodoquena Mountains, southwestern Brazil: An ecological and conservation analysis. *Revista Brasileira de Zoologia*, *24*, 426–435.

Camargo, N. F., de Oliveira, H. F., Ribeiro, J. F., de Camargo, A. J., & Vieira, E. M. (2019). Availability of food resources and habitat structure shape the individual-resource network of a neotropical marsupial. *Ecology and Evolution*, *9*, 3946–3957.

Camargo, N. F., dos Reis, G. G., Mendonça, A. F., Laumann, R. A., Nardoto, G. B., de Camargo, A. J. A., & Vieira, E. M. (2022). Native marsupial acts as an *in situ* biological control agent of the main soybean pest (*Euschistus heros*) in the neotropics. *European Journal of Wildlife Research*, *68*, 62.

Camargo, N. F., Sano, N. Y., & Vieira, E. M. (2018). Forest vertical complexity affects alpha and beta diversity of small mammals. *Journal of Mammalogy*, *99*, 1444–1454.

Carmignotto, A., de Vivo, M., & Langguth, A. (2012). Mammals of the Cerrado and caatinga: Distribution patterns of the tropical open biomes of Central South America. In B. D. Patterson & L. P. Costa (Eds.), *Bones, clones and biomes: The history and geography of recent neotropical mammals* (pp. 307–350). University of Chicago Press.

Carmignotto, A. P., Pardini, R., & de Vivo, M. (2022). Habitat heterogeneity and geographic location as major drivers of Cerrado small mammal diversity across multiple spatial scales. *Frontiers in Ecology and Evolution*, *9*, 739919.

Carvalho, F. M. V., de Marco, P., & Ferreira, L. G. (2009). The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of Central Brazil. *Biological Conservation*, *142*, 1392–1403.

Cassano, C. R., Barlow, J., & Pardini, R. (2014). Forest loss or management intensification? Identifying causes of mammal decline in cacao agroforests. *Biological Conservation*, *169*, 14–22.

Cazetta, E., & Fahrig, L. (2022). The effects of human-altered habitat spatial pattern on frugivory and seed dispersal: A global meta-analysis. *Oikos*, *2022*, e08288.

Colman, C. B., Guerra, A., de Oliveira Roque, F., Rosa, I. M. D., & de Oliveira, P. T. S. (2021). Identifying priority regions and territorial planning strategies for conserving native vegetation in the Cerrado (Brazil) under different scenarios of land use changes. *Science of the Total Environment*, *807*, 150998.

Davison, C. W., Rahbek, C., & Morueta-Holme, N. (2021). Land-use change and biodiversity: Challenges for assembling evidence

on the greatest threat to nature. *Global Change Biology*, *27*, 5414–5429.

de Souza Leite, M., Boesing, A., Metzger, J., & Prado, P. (2022). Matrix quality determines the strength of habitat loss filtering on bird communities at the landscape scale. *Journal of Applied Ecology*, *59*, 2790–2802.

Dias, N. d. S., Zanetti, R., Santos, M. S., Peñaflor, M. F. G. V., Broglio, S. M. F., & Delabie, J. H. C. (2013). The impact of coffee and pasture agriculture on predatory and omnivorous leaf-litter ants. *Journal of Insect Science*, *13*, 29–11.

Ellis, E. C. (2021). Land use and ecological change: A 12,000-year history. *Annual Review of Environment and Resources*, *46*, 1–33.

Emmons, L. H., Feer, F., & Magnusson, W. E. (1997). Neotropical rainforest mammals: A field guide. *Environmental Conservation*, *25*, 175–185.

Fiske, I., & Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, *43*, 1–23.

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., … Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*, 337–342.

Fritz, S. A., Bininda-Emonds, O. R., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecology Letters*, *12*, 538–549.

Furtado, L. O., Felicio, G. R., Lemos, P. R., Christianini, A. V., Martins, M., & Carmignotto, A. P. (2021). Winners and losers: How woody encroachment is changing the small mammal community structure in a neotropical savanna. *Frontiers in Ecology and Evolution*, *9*, 774744.

Galán-Acedo, C., Spaan, D., Bicca-Marques, J. C., de Azevedo, R. B., Villalobos, F., & Rosete-Vergés, F. (2021). Regional deforestation drives the impact of forest cover and matrix quality on primate species richness. *Biological Conservation*, *263*, 109338.

Galetti, M., & Dirzo, R. (2013). Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation*, *163*, 1–6.

Godoi, M., Rudi, R., Laps, D., Ribeiro, C., Aoki, Franco, L., Souza, D., Laps, R., Ribeiro, D., Aoki, C., & Souza, F. (2017). Bird species richness, composition and abundance in pastures are affected by vegetation structure and distance from natural habitats: A single tree in pastures matters. *Emu-Austral Ornithology*, *118*, 201–211.

Gonçalves, L. R., Favacho, A. R. M., Roque, A. L. R., Mendes, N. S., Fidelis Junior, O. L., Benevenute, J. L., Herrera, H. M., D'Andrea, P. S., de Lemos, E. R. S., Machado, R. Z., & André, M. R. (2016). Association of Bartonella species with wild and synanthropic rodents in different Brazilian biomes. *Applied and Environmental Microbiology*, *82*, 7154–7164.

Hannibal, W., Duarte, L. A., & Santos, C. C. (2015). *Mamíferos não voadores do Pantanal e entorno*. Natureza em Foco.

Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, *27*, 929–941.

Klink, C. A., & Machado, R. B. (2005). Conservation of the Brazilian cerrado. *Conservation Biology*, *19*, 707–713.

Kurten, E. L. (2013). Cascading effects of contemporaneous defaunation on tropical forest communities. *Biological Conservation*, *163*, 22–32.

Magioli, M., de Barros, K. M. P. M., Chiarello, A. G., Galetti, M., Setz, E. Z. F., Paglia, A. P., Abrego, N., Ribeiro, M. C., & Ovaskainen, O. (2021). Land-use changes lead to functional loss of terrestrial mammals in a neotropical rainforest. *Perspectives in Ecology and Conservation*, *19*, 161–170.

Magioli, M., Moreira, M. Z., Fonseca, R. C. B., Ribeiro, M. C., Rodrigues, M. G., & de Barros, K. M. P. M. (2019). Human-modified landscapes alter mammal resource and habitat use and trophic structure. *Proceedings. National Academy of Sciences. United States of America*, *116*, 18466–18472.

Martello, F., Andriolli, F., de Souza, T. B., Dodonov, P., & Ribeiro, M. C. (2016). Edge and land use effects on dung beetles (coleoptera: Scarabaeidae: Scarabaeinae) in Brazilian cerrado vegetation. *Journal of Insect Conservation*, *20*, 957–970.

Mattos, I. d., Zimbres, B., & Marinho-Filho, J. (2021). Habitat specificity modulates the response of small mammals to habitat fragmentation, loss, and quality in a neotropical savanna. *Frontiers in Ecology and Evolution*, *9*, 751315.

Melo, G. L., Cerezer, F. O., Sponchiado, J., & Cáceres, N. C. (2022). The role of habitat amount and vegetation density for explaining loss of small-mammal diversity in a south American woodland savanna. *Frontiers in Ecology and Evolution*, *10*, 740371.

Melo, G. L., Sponchiado, J., Cáceres, N. C., & Fahrig, L. (2017). Testing the habitat amount hypothesis for south American small mammals. *Biological Conservation*, *209*, 304–314.

Mendonça, A., Percequillo, A. R., Camargo, N. F., Ribeiro, J. F., Palma, A. R. T., Oliveira, L. C., Câmara, E. M. V. C., & Vieira, E. M. (2018). CERRADO SMALL MAMMALS: Abundance and distribution of marsupials, lagomorphs, and rodents in a neotropical savanna. *Ecology*, *99*, 1900.

Michalski, F., Peres, C. A., & Lake, I. R. (2008). Deforestation dynamics in a fragmented region of southern Amazonia: Evaluation and future scenarios. *Environmental Conservation*, *35*, 93–103.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.

Newbold, T., Bentley, L. F., Hill, S. L., Edgar, M. J., Horton, M., Su, G., Şekercioğlu, Ç. H., Collen, B., & Purvis, A. (2020). Global effects of land use on biodiversity differ among functional groups. *Functional Ecology*, *34*, 684–693.

Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology & Evolution*, *4*, 1630–1638.

Oakley, J. L., & Bicknell, J. E. (2022). The impacts of tropical agriculture on biodiversity: A meta-analysis. *Journal of Applied Ecology*, *59*, 3072–3082.

Paglia, A. P., da Fonseca, G. A., Rylands, A. B., Herrmann, G., Aguiar, L. M., Chiarello, A. G., Leite, Y. L., Costa, L. P., Siciliano, S., & Kierulff, M. C. M. (2012). Lista Anotada dos Mamíferos do brasil 2ª Edição/annotated checklist of Brazilian mammals. *Occasional Paper Conservation Biology*, *6*, 1–82.

Palmeirim, A. F., Figueiredo, M. S., Grelle, C. E. V., Carbone, C., & Vieira, M. V. (2019). When does habitat fragmentation matter? A biome-wide analysis of small mammals in the Atlantic Forest. *Journal of Biogeography*, *46*, 2811–2825.

Palmeirim, A. F., Santos-Filho, M., & Peres, C. A. (2020). Marked decline in forest-dependent small mammals following habitat loss and fragmentation in an Amazonian deforestation frontier. *PLoS One*, *15*, e0230209.

Pardini, R., Bueno, A. d. A., Gardner, T. A., Prado, P. I., & Metzger, J. P. (2010). Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. *PLoS One*, *5*, e13666.

Pendrill, F., Gardner, T. A., Meyfroidt, P., Persson, U. M., Adams, J., Azevedo, T., Bastos Lima, M. G., Baumann, M., Curtis, P. G., de Sy, V., Garrett, R., Godar, J., Goldman, E. D., Hansen, M. C., Heilmayr, R., Herold, M., Kuemmerle, T., Lathuillière, M. J., Ribeiro, V., ... West, C. (2022). Disentangling the numbers behind agriculture-driven tropical deforestation. *Science*, *377*, eabm9267.

Pires, A. S., Koeler Lira, P., Fernandez, F. A. S., Schittini, G. M., & Oliveira, L. C. (2002). Frequency of movements of small mammals among Atlantic coastal Forest fragments in Brazil. *Biological Conservation*, *108*, 229–237.

Prevedello, J. A., Almeida-Gomes, M., & Lindenmayer, D. B. (2018). The importance of scattered trees for biodiversity conservation: A global meta-analysis. *Journal of Applied Ecology*, *55*, 205–214.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ribeiro, J. F., Guaraldo, A., Nardoto, G. B., Santoro, G., & Vieira, E. M. (2019). Habitat type and seasonality influence the isotopic trophic niche of small mammals in a neotropical savanna. *Hystrix*, *30*, 30–38.

Ribeiro, R., Ricklefs, R. E., & Marinho-Filho, J. (2020). Partitioning beta diversity to unravel mechanisms underlying the distributions of nonvolant small mammls in Brazil's Cerrado. *Journal of Mammalogy*, *101*, 1438–1450.

Rocha, E. C., Brito, D., Silva, P. M., Silva, J., Bernardo, P. V. S., & Juen, L. (2018). Effects of habitat fragmentation on the persistence of medium and large mammal species in the Brazilian Savanna of Goiás State. *Biota Neotropica*, *18*, e20170483.

Rogers, H. S., Donoso, I., Traveset, A., & Fricke, E. C. (2021). Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *52*, 641–666.

Santos-Filho, M., da Silva, D., & Sanaiotti, T. (2008). Edge effects and landscape matrix use by a small mammal community in fragments of semideciduous submontane forest in Mato Grosso, Brazil. *Brazilian Journal of Biology*, *68*, 703–710.

Schüler, J., & Bustamante, M. M. C. (2022). Spatial planning for restoration in Cerrado: Balancing the trade-offs between conservation and agriculture. *Journal of Applied Ecology*, *59*, 2616–2626.

Song, X.-P., Hansen, M. C., Potapov, P., Adusei, B., Pickering, J., Adami, M., Lima, A., Zalles, V., Stehman, S. V., & di Bella, C. M. (2021). Massive soybean expansion in South America since 2000 and implications for conservation. *Nature Sustainability*, *4*, 784–792.

Strassburg, B. B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A. E., Oliveira Filho, F. J., Scaramuzza, C. A. M., & Scarano, F. R. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, *1*, 0099.

van der Wal, J., Falconi, L., Januchowski, S., Shoo, L., & Storlie, C. (2014). SDMTools: Species distribution modelling tools: Tools for processing data associated with species distribution modelling exercises. R Package Version 1.1-221.2.

Vieira, M. V., Almeida-Gomes, M., Delciellos, A. C., Cerqueira, R., & Crouzeilles, R. (2018). Fair tests of the habitat amount hypothesis require appropriate metrics of patch isolation: An example with small mammals in the Brazilian Atlantic Forest. *Biological Conservation*, *226*, 264–270.

Zuckerberg, B., Desrochers, A., Hochachka, W. M., Fink, D., Koenig, W. D., & Dickinson, J. L. (2012). Overlapping landscapes: A persistent, but misdirected concern when collecting and analyzing ecological data. *The Journal of Wildlife Management*, *76*, 1072–1080.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Harmange, C., Santos, C. C., de Oliveira Roque, F., Souza, F. L., Arvor, D., Bonnet, M., Vieira, E. M., & Pays, O. (2023). The pivotal role of land cover around forest fragments for small-mammal communities in a Neotropical savanna. *Conservation Science and Practice*, e13005. https://doi.org/10.1111/csp2.13005