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## Small mammals in high fragmented landscape in Cerrado/ Atlantic Forest ecotone, Southeastern Brazil

Felipe S. Machado<sup>1,2</sup> , Aloysio S. Moura<sup>2</sup> , Ravi F. Mariano<sup>2</sup> , Rubens Manoel dos Santos<sup>2</sup> ,  
Paulo O. Garcia<sup>3</sup> , Izabela R. C. Oliveira<sup>4</sup>  & Marco Aurélio L. Fontes<sup>2</sup> 

1. Governo do Estado de Minas Gerais. Escola E. Profa. Celina de R. Vilela, rua Francisco Valia, 50, Centro, 37498-000, Cordislândia, MG, Brazil. (epilefsama@hotmail.com)

2. Departamento de Ciências Florestais, Universidade Federal de Lavras, Campus Universitário, CP 3037, 37200-000 Lavras, MG, Brazil

3. IF Sul de Minas, Estrada de Muzambinho, Bairro Morro Preto, 37890-000 Muzambinho, MG, Brazil.

4. Departamento de Estatística, Universidade Federal de Lavras, Campus Universitário, CP 3037, 37200-000 Lavras, MG, Brazil.

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**ABSTRACT.** Exploratory human activities have resulted in small fragments inserted into a matrix which is inhospitable to small non-flying mammals. The effects of landscape changes alter the distribution patterns of species. Landscape fragmentation patterns for small mammals are controversial, especially considering small fragments and ecotonal regions. Based on these arguments, we investigated the diversity patterns of small mammals in small fragments in the ecotonal Cerrado/Atlantic Forest region. A total of 24 fragments (<40 ha) were studied using tomahawk, sherman and pitfall traps. We found low species richness (11 species, six marsupials and five rodents), which was not expected because it is an ecotonal region. It was verified that composition and community structure are simplified by the marked presence of generalist species and with the increase of species turnover. The small forest fragments present a microhabitat structure with lianas and streams as main environmental filters of groups with ecological similarities. Our findings suggest that these fragments must be managed in order to conserve the local biodiversity and maintain the needed characteristics to enable the occurrence of different ecological groups.

**KEYWORDS.** Endangered fragments, rodent and marsupial community, Management of small fragments.

**RESUMO.** Pequenos mamíferos em paisagem altamente fragmentada em ecótono Cerrado/Mata Atlântica, Sudeste do Brasil. Atividades humanas exploratórias resultaram na formação de pequenos fragmentos inseridos em uma matriz inhóspita para pequenos mamíferos não-voadores. Os efeitos das mudanças na paisagem alteram os padrões de distribuição das espécies. Os padrões de fragmentação da paisagem para pequenos mamíferos são controversos, especialmente considerando pequenos fragmentos e regiões ecotonais. Com base nesses argumentos, investigamos os padrões de diversidade de pequenos mamíferos em pequenos fragmentos na região ecotonal Cerrado / Mata Atlântica. Vinte e quatro fragmentos (<40 ha) foram estudados, usando armadilhas de grade, chapa e de queda. Encontramos baixa riqueza de espécies (11 espécies, seis marsupiais e cinco roedores), o que não era esperado por se tratar de uma região ecotonal. Verificamos que a composição e a estrutura da comunidade são simplificadas pela presença de espécies generalistas e com o aumento do *turnover* de espécies. Os pequenos fragmentos florestais apresentam uma estrutura de microhabitat com lianas e riachos como principais filtros ambientais de grupos com semelhanças ecológicas. Nossos resultados sugerem que esses fragmentos devem ser gerenciados para conservar a biodiversidade local e manter as características dentro dos fragmentos para possibilitar a ocorrência de diferentes grupos ecológicos.

**PALAVRAS-CHAVE.** Fragmentos ameaçados, comunidade de roedores e marsupiais, gerenciamento de pequenos fragmentos.

Habitat fragmentation is a process in which a large habitat extension is changed to a set of small areas which are isolated by a matrix composed by a different habitat from the original (FAHRIG, 2003). It not only causes habitat loss, but also changes the properties of the vegetation remnants (VAN DEN BERG & OLIVEIRA-FILHO, 2000). Fragmentation creates different-sized remnants and the effect on the area is one of the most well documented patterns in ecology, being widely recognized as one of the main threats to biodiversity (LAURANCE & BIERREGAARD, 1997; HANSKI, 2015; CROOKS *et al.*, 2017; among others).

Small mammals are non-flying animals weighing less than one kilogram, and are highly influenced either positively (*i.e.* PARDINI *et al.*, 2005) or negatively (*i.e.* LAURANCE, 1994;

HANSKI, 2015) by fragmentation. There are more resources, larger populations (HANSKI, 2015; BOVENDORP *et al.*, 2019) and consequently lower extinction risks in larger areas. On the other hand, the populations are smaller in islands or small fragments and more susceptible to stochastic events, intraspecific interactions, habitat heterogeneity, isolation, occasional disturbances, and especially environmental characteristics (LOMOLINO & WEISER, 2001).

In this context, Brazil harbors the Atlantic Forest and the Cerrado, two biodiversity hotspots (MYERS *et al.*, 2000) which have been sharply reduced, and their current remnants are small secondary fragments in their majority. Different scenarios in the Atlantic Forest are presented in official documents and scientific articles, as RIBEIRO *et*

*al.* (2009) reports that only approximately 11.26% of the vegetation still remains, with 83.4% of this total being fragments smaller than 50 hectares. However, recent data from the NGO SOS MATA ATLÂNTICA (2020) show that only 13% remain, which is of concern from the ecological and conservation points of view (RIBEIRO *et al.*, 2009). The Cerrado situation is also worrying, where more than 55% of its original range (KLINK & MACHADO, 2005) has been deforested or transformed by human action (TRIGUEIRO *et al.*, 2020), which was intensified after the approval of the forest code 2012 (VIEIRA *et al.*, 2018; TEIXEIRA *et al.*, 2018). The ecotonal regions between these two hotspots are in line with these high levels of deforestation, and studies on the mammal response to fragmentation inside these regions are incipient (see ROCHA *et al.*, 2011; MESQUITA & PASSAMANI, 2012).

The distribution patterns of small mammals in ecotonal regions in the Neotropical region are little studied, with the most common being in regions between the Cerrado and Amazon (*e.g.*, LACHER JR & ALHO, 2001; BEZERRA *et al.*, 2009; RAMOS PEREIRA *et al.*, 2013). The ecotones correspond to a meeting of two ecosystems, and the complexity of these areas generates unique characteristics such as the presence of high diversity (*e.g.* plants in MACHADO *et al.* 2016a, and Mammals in TALAMONI *et al.*, 2014; LAURINDO *et al.*, 2017) due to the overlapping distribution ranges of the species from adjacent biomes (see SOUZA *et al.*, 2020 to plants and CÁCERES *et al.*, 2007 to mammals). Thus, understanding which features influence the occurrence and distribution of organisms (PÜTTKER *et al.*, 2008) in Atlantic Forest-Cerrado ecotones, for example the microhabitat structure effects on biological communities, can generate bases for conservation plans.

The microhabitat structure is a space within an environment which includes biotic and abiotic factors that influences individual behavior of a given species (JORGENSEN, 2004), consequently changing the community parameters. Substantial effort has been focused on microhabitat studies using small non-flying mammals (NAXARA *et al.*, 2009; HODARA & BUSCH, 2010; LIMA *et al.*, 2010), because these mammals are indicators of environmental trends and conditions (LEIS *et al.*, 2008). Nevertheless, most studies are focused on medium or large fragments (*i.e.* NAXARA *et al.*, 2009; LIMA *et al.*, 2010).

Based on the above presented arguments, our objective was to evaluate the richness and structure of small non-flying mammal communities in small forests (<40 ha) along a high fragmented landscape in an ecotonal region from Atlantic Forest-Cerrado domains, analyzing the richness, composition and microhabitat structure of only small mammals. To do so, we sought to answer the following questions: i. Is the diversity of small mammals greater in ecotonal regions where there is an increased diversity in relation to other studies published in southeastern Brazil, even though it is a strongly fragmented region? ii. Is there turnover or nestedness composition of the fragments? iii. Which microhabitat characteristics influence this composition? Herein we hypothesized that: i. the diversity is greater than other locations in southeastern Brazil because it is an ecotonal environment, even though it is a highly

fragmented environment; ii. there is a high nestedness effect on the composition; and iii. the characteristics of these fragments corresponds to environmental filters which select specific species groups.

## MATERIAL AND METHODS

**Study area.** The studied forest fragments are located in a Cerrado-Atlantic Forest ecotone in southeastern Brazil, which is characterized by high human occupation and a long history of natural landscape degradation (21°18'S - 21°14'S and 44°39'W - 44°35'W) (Fig. 1). All forest fragments (<40 hectares each one – Supplementary Material Tab. A1) are inserted in a heterogeneous landscape matrix comprising crop rotations such as beans, sorghum, and maize, as well as *Eucalyptus* plantations and pastures interspersed with patches of Cerrado *sensu lato* and Semi-deciduous Atlantic Forests (Supplementary Material Tab. A2) (IBGE, 2004). The complete information regarding tree diversity can be found in MACHADO *et al.* (2016a).

Data from the Lavras weather station (35 Km from the study area) indicated that the average monthly temperature ranges from 16 to 21.8 °C, with an annual average of 19.6 °C. The average monthly precipitation ranges from 19 to 293 mm, with an annual average of 1.517 mm (VAN DEN BERG & OLIVEIRA-FILHO, 2000). The climate is defined as Cwb (mesothermal, with mild summers and dry winters) (ALVARES *et al.*, 2013) according to the Köppen classification. According to the Brazilian soil taxonomy system, the soils vary from Dystrophic Tb Haplic Cambisol in steep areas to Yellow Acric Oxisol in flat areas (EMBRAPA, 1999; HORTA *et al.*, 2009).

The study area harbors several springs in the upper reaches of the Capivari River, a tributary of the Grande River. In turn, the Grande Rive, merges with the Paranaíba River, forming the Paraná River, which is the main lotic system of the second largest basin in South America (PEREIRA *et al.*, 2006). The study area is biologically strategic because it connects two large mountain ranges with two biodiversity hotspots: the Serra do Espinhaço (Cerrado) and Serra da Mantiqueira (Atlantic Forest) mountain ranges.

The study area is located near the Perdizes Plateau, a region of “high biological importance” (DRUMMOND *et al.*, 2005) which harbors large natural areas, including one of the largest forest remnants in the southern region of Minas Gerais. Previous studies have recorded high diversity of mammals (MACHADO *et al.*, 2015, 2016b, 2017, 2018; PECORA *et al.*, 2016), bats (MORAS *et al.*, 2013), birds (MOURA & CORRÊA, 2012), dung beetles (ALMEIDA & LOUZADA, 2009) and plants (MACHADO *et al.*, 2016a).

**Sampling of small non-flying mammals.** We collected samples from October 2012 to December 2013. Monthly samples were collected for seven (using Sherman and Tomahawk traps) and four days (using pitfalls traps). The first seven months of sampling were conducted with a set of 12 fragments, and the next seven months of sampling were conducted with a different set of 12 fragments. Thus, a total of 24 fragments were sampled.

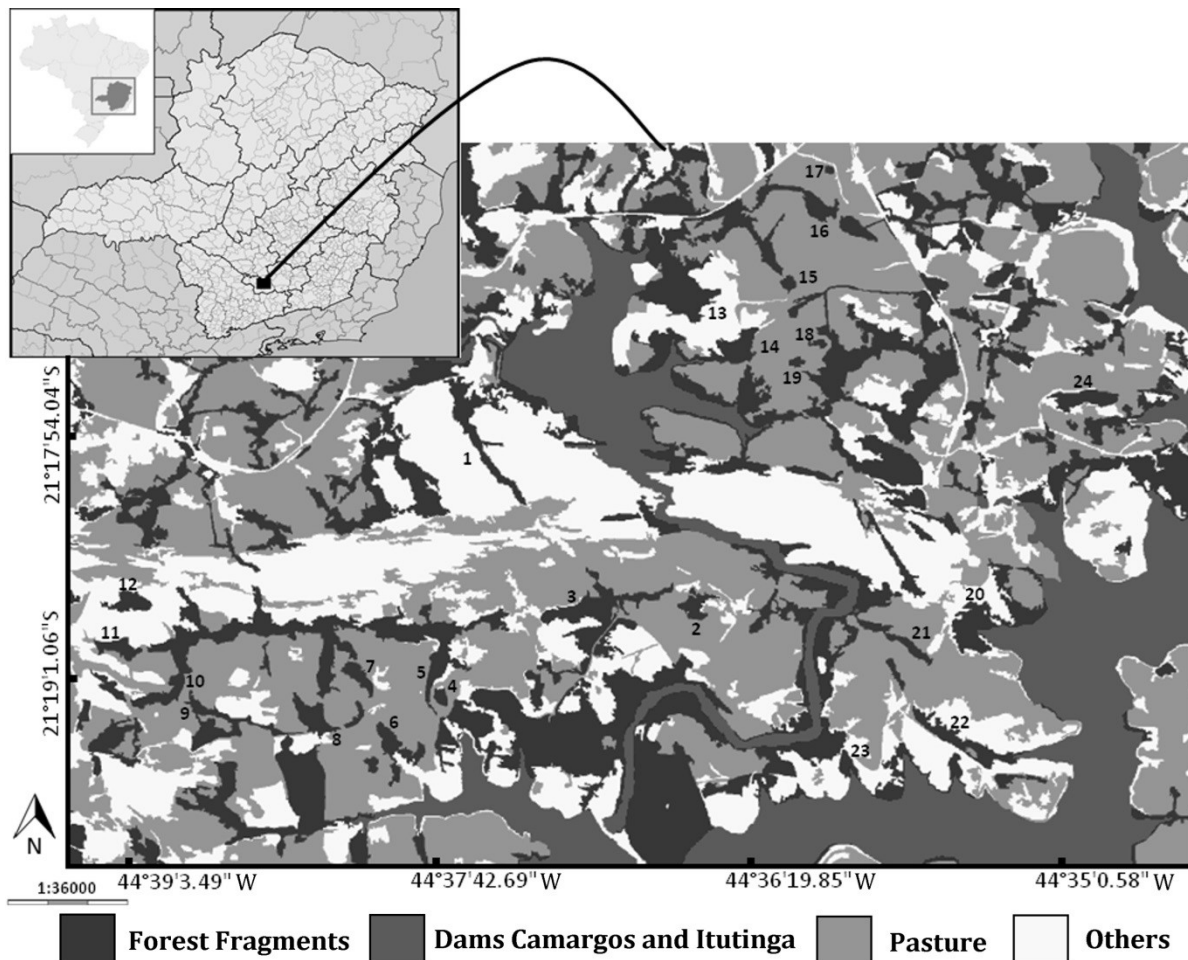


Fig. 1. Location of the forest communities studied in 24 forest fragments located in southeastern Brazil. A description of individual forest fragments can be found in Supplementary Material Tab. A1.

Two linear transects were established in each fragment and the first transect comprised ten capture points using Sherman® and Tomahawk® traps. Thus, two traps were installed at each capture point, one on the ground and one in the understory at a height of ~ 1.6 m. The collection points were located five meters apart from each other. The second transect comprised the pitfall traps, which consisted of 65-, 45- and 35-liter buckets connected by a 50 cm-high plastic fence supported by wooden stakes. The pitfall traps were arranged approximately eight meters apart from each other.

Scientific names were updated following PAGLIA *et al.* (2012). We used information from BONVICINO *et al.* (2002), HANNIBAL *et al.* (2012) and LAFERRIÈRE (1995) to classify species in altered and non-altered environments, considered in our study as generalists and specialists.

**Sampling of microhabitat variables.** Three vegetation variables and twelve environmental variables were selected to characterize the microhabitat of the small non-flying mammals and were obtained in the wet and dry seasons. The following vegetation variables were obtained in order to analyze the microhabitat: (1) richness, (2) abundance and (3) estimated height average of trees. A circular evaluation

area of 50 meters in diameter was established in the center of each of the 24 fragments to collect these data. Thus, an area of 1963.5 m<sup>2</sup> per fragment and 47124 m<sup>2</sup> in total was studied. The criterion for tree inclusion was circumference at breast height (CBH) ≥ 10 cm at a height of 1.3 m. The tree species were identified by experts using literature data and materials from the ESAL (Escola Superior de Agricultura de Lavras [School of Agriculture of Lavras]) Herbarium. Herbarium specimens of the collected source material were prepared and are currently located at the ESAL Herbarium. The classification system adopted for botanical families was Angiosperm Phylogeny Group IV (APG IV, 2016). The species list and the tree richness is in MACHADO *et al.* (2016a).

Next, five sampling points were selected within each fragment using the cardinal points along with the center of the evaluated areas to collect the environmental variables. A radius of two meters was delimited in these sampling points, and the following data were obtained: (1) canopy openness, (2) understory closure, (3) epiphyte level (except lianas), (4) liana level, (5) number of fallen dead trees, (6) presence of cattle, (7) presence of creeks and streams, (8) presence of wetlands (flooded area), (9) rocky outcrop level, (10) degree of soil exposure, (11) litter height, and (12) arthropod biomass.

The presence of cattle, streams and flooded areas were assessed in terms of their presence/absence, and other variables were obtained as the mean of the five evaluated sub-areas using the square adapted from FREITAS *et al.* (2002). This method was also used to estimate the degree of soil exposure and rocky outcrop. A single square divided into 100 minor squares was used, so the score of these small squares provided an estimate. The epiphyte and liana variables were categorized using a scale from 0 to 4, in which 0 (zero) represents an absence of individuals, 1 (one) represents one to five individuals, 2 (two) represents six to 10 individuals, 3 (three) represents 11 to 15 individuals, and 4 (four) represents greater than 15 individuals. The litter height was obtained using a graduated ruler, and the number of fallen trees was obtained by direct counting.

Canopy openness was measured with a Lemmon Convex spherical densitometer (LEMMON, 1957). The understory closure variable was assessed by vertically placing a 180 x 190 cm panel on the substrate and photographing from a distance of three meters in each sampling site. We were careful to avoid placing the panels on forest trails or paths. The forest understory was measured as the percentage of black pixels in black and white images (adapted from MARSDEN *et al.*, 2002). Four photos were obtained from each site, one for each cardinal direction, and the images were processed using SideLook 1.1.01 (ZEHM *et al.*, 2003).

The arthropod biomass was obtained using three epigeic pitfall traps per fragment. The traps consisted of bait-free plastic containers (8 cm in diameter and 12 cm in height). Saline solution (for the preservation of arthropods) and a few drops of detergent (to break the water surface tension) were placed into each container. The epigeic pitfall traps remained in the field for five days.

**Statistical analyses.** The richness of the small non-flying mammals was analyzed by species accumulation curves (with 1000 randomizations) to describe each individual fragment, fragments together and comparing first 12 fragments to last 12 fragments (COLWELL & CODDINGTON, 1994; GOTELLI & COLWELL, 2001). In addition, the species accumulation curves were compared with a first-order Jackknife estimator to assess sampling sufficiency using the EstimateS version 9.10 software program (COLWELL *et al.*, 2012).

The composition was analyzed by beta diversity ( $\beta$ ), assessing the dissimilarity and observing the turnover or nestedness (BASELGA, 2012, 2013; BASELGA & ORME, 2012). The following dissimilarity measures were used: pair wise and multiple-site Sørensen dissimilarity indexes ( $\beta_{sor}$ ), turnover (Simpson index  $\beta_{sim}$ ) and nestedness (the divergence between the  $\beta_{sim}$  and  $\beta_{sne}$  indexes -  $\beta_{sne}$  is the nestedness component of Sørensen dissimilarity).

The microhabitat structure was analyzed by Canonical Correspondence Analysis (CCA) and the Monte Carlo permutation test (TERBRAAK, 1986). This similarity analysis was used to determine which variables affected the species occurrence. Small mammal species with  $\geq 10$  individuals were used in this analysis. The PC-ORD software program (McCUNE & MEFFORD, 1999) was used to perform the CCA.

The influence of the microhabitat characteristics on the abundance and richness were investigated using models for count data. A Poisson distribution was assumed for the abundance data, whereas the Gamma-count distribution was considered for richness (WINKELMANN, 1995; ZEVIANI *et al.*, 2014). We chose eight variables with higher environmental correlation coefficient values from the two CCA ordination axes (x1: Lianas, x2: Creeks and streams, x3: Epiphytes, x4: Canopy, x5: Cattle, x6: Fallen Trees, x7: Flooded area and x8: Understory), and the best model was chosen through a backward process. This means that the first model was fitted considering all these variables as predictors. The least significant variable was removed. The process was repeated by re-fitting the reduced models until only significant variables remained ( $\alpha = 5\%$ ). Regarding the models and the abundance data, the assumption of equidispersion was proven by the likelihood ratio test, and the adjustment was compared by the Poisson model with the Negative Binomial model. No predictor variable had a significant effect on species abundance, but we used the Gamma-count model for the richness data since the data presented subdispersion. The log-link function,  $g(\mu)$ , of the initial (complete) model for both the Poisson and the Gamma-count models was:

$$g(\mu) = \beta_0 + \beta_1x_1 + \beta_2x_2 + \beta_3x_3 + \beta_4x_4 + \beta_5x_5 + \beta_6x_6 + \beta_7x_7 + \beta_8x_8$$

The Poisson models were fitted using the glm function and the Gamma-count using the gcnt function of the MRDCr R package (ZEVIANI *et al.*, 2016). We considered only the first capture of the individuals for all the analyses.

## RESULTS

A total of 387 individuals and 11 species (Tab. I) were recorded with a sampling effort of 27,552 trap-nights [4,032 pitfall-nights (168 per each fragment) and 23,520 trap-nights (980 per each fragment)]. We captured 196 individuals of six Didelphimorphia species and 191 individuals of five Rodentia species. The capture success rate was 0.018 individuals/trap-night. The most abundant species were *Didelphis albiventris* (146 individuals; 37.73%) and *Cerradomys subflavus* (84 individuals; 21.71%).

The species accumulation curve for all the areas combined did not reach the asymptote (Fig. 2). The curve of the first-order Jackknife richness estimator remained within the 95% confidence interval for the total curve but ended out of range, with an estimated richness of 12.92 species. Therefore, 85.14% of the estimated diversity of the small mammals was recorded. The curves of the fragments (Fig. 3) also failed to reach the asymptote. The richness for each fragment ranged from two to eight species, and the abundance ranged from eight to 26 individuals. Moreover, the fact that the accumulation curve for the last 12 fragments evaluated is within the confidence interval of the curve for the first 12 fragments reveals similarity of richness and abundance between them.

Tab. I. Species list of small mammals and their absolute and relative (in percentage) abundances of 24 small forest fragments in southeastern Brazil. The habitat selection is related to occurrence of the species, where A represents “Altered Environments” and N “Non-altered Environments”.

Species	Habitat selection	Abundance (Relative Abundance)
Didelphimorphia		
Didelphidae		
1. <i>Caluromys philander</i> (Linnaeus, 1758)	N	1 (0,26)
2. <i>Didelphis albiventris</i> Lund, 1840	A	146 (37,73)
3. <i>Didelphis aurita</i> Wied-Neuwied, 1826	A	10 (2,58)
4. <i>Gracilinanus microtarsus</i> (J. A. Wagner, 1842)	A	13 (3,36)
5. <i>Marmosops incanus</i> (Lund, 1840)	A	25 (6,46)
6. <i>Monodelphis kunsii</i> Pine, 1975	N	1 (0,26)
Rodentia		
Cricetidae		
7. <i>Akodon montensis</i> Thomas, 1913	A	19 (4,91)
8. <i>Cerradomys subflavus</i> (Wagner, 1842)	A	84 (21,71)
9. <i>Nectomys squamipes</i> (Brants, 1827)	A	16 (4,13)
10. <i>Oligoryzomys nigripes</i> (Olfers, 1818)	A	24 (6,2)
11. <i>Rhipidomys tribei</i> Costa, Geise, Pereira & Costa, 2011	A	48 (12,4)
Total	387 (100)	

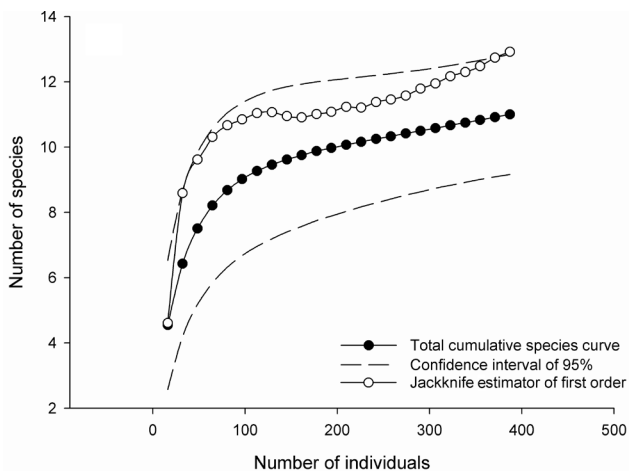


Fig. 2. Species accumulation curves to 24 fragments together for small mammals located in southeastern Brazil.

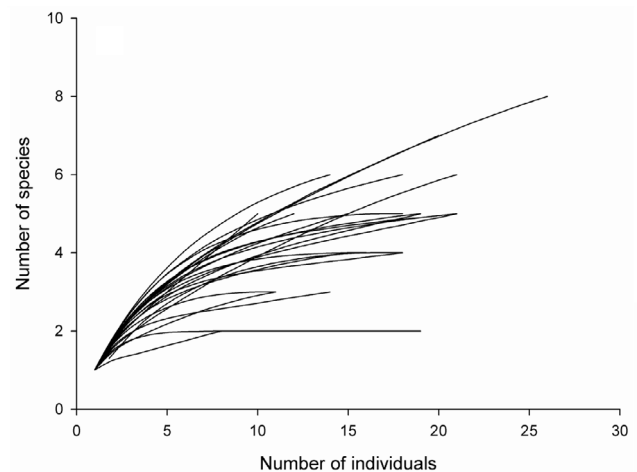


Fig. 3. Species accumulation curves to 24 fragments singly for small mammals located in southeastern Brazil.

The beta diversity is shown in Tab. A2, A3, and A4 (Supplementary Material). The results were higher for  $\beta_{sim}$  than for  $\beta_{sne}$ , indicating high species turnover. This finding was corroborated by the multiple-site dissimilarity indices (Fig. 4), and the percent species turnover was 89.53%.

The values of the environmental variables and their respective standard deviations are shown in Tab. A1 (Supplementary Material). The acronyms used in CCA are shown in Tab. II. The eigenvalues of the first two ordination axes were 0.287 and 0.153. The first three axes explained 44.6% of the variance, whereas the first and second axes explained 22.6 and 12.1% of the variance, respectively. The correlations of the environmental variables with the species

( $p = 0.017$ ) and eigenvalues ( $p = 0.008$ ) were significant at 95% probability according to the Monte Carlo permutation test. Axis 1 was correlated with the “liana”, “Creeks and streams”, “epiphyte”, “wetland” (flooded area), “canopy”, and “cattle” variables in descending order (Tab. II).

The positioning of the plots along the axis (Fig. 5) shows the presence of distinct environments at the ends of the axes. There are environments influenced by higher levels of lianas, other epiphytes and denser understory at the beginning of the first axis; while the opposite of the same axis presents environments highly influenced by water (right side of axis 1) such as streams and flooded areas, and the presence of cattle. The *Didelphis aurita*, *Didelphis albiventris*

and *Cerradomys subflavus* species were associated with the environments influenced by higher levels of lianas and other epiphytes, whereas *Nectomys squamipes*, *Oligoryzomys nigripes* and *Rhipidomys tribei* were associated with those containing cattle and water with more open canopy. It is worth noting that the presence of cattle was inversely related to the understory variables: “lianas”, “other epiphytes” and “understory density”. Axis 2 can also be interpreted as the same way, as the arthropod biomass is opposite to presence of rivers, separating *Rhipidomys tribei* from *Didelphis aurita* and *Nectomys squamipes*.

We obtained a model with significant effect which was highly correlated with lianas and streams. The negative estimate for the liana effect indicates a decrease in species richness as the values of this variable increase. On the other hand, the positive estimate for the streams indicates an increase in species richness with the increase of this variable (Tab. III, and Supplementary Material Figs A1, A2).

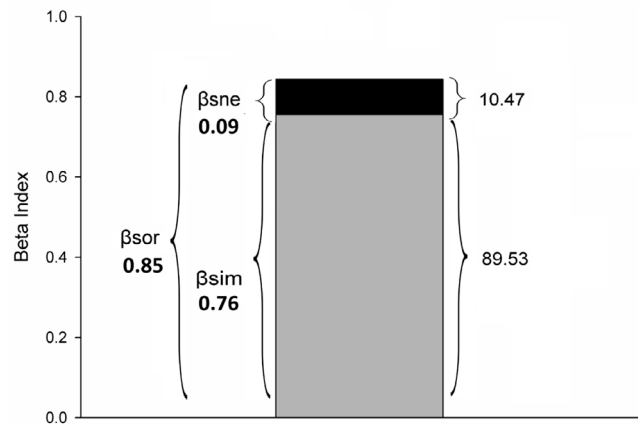


Fig. 4. Beta ( $\beta$ ) diversity values for small mammals related to nesting ( $\beta_{sne}$ ), turnover ( $\beta_{sim}$ ) and general dissimilarity ( $\beta_{sor}$ ) in the 24 small forest fragments located in southeastern Brazil. The figures on the right represent the final percentage for each index.

Tab. II. Environmental correlation coefficients and the first two ordination axes of canonical correspondence analysis of 24 small forest fragments in southeastern Brazil. The acronyms refer to the letters in CCA Fig. 5.

Variable	Acronyms	Axis 1	Axis 2
Understory Closure	uc	-0,298	0,037
Canopy openness	co	-0,341	0,238
Epiphytism	ep	-0,503	-0,012
Lianas	lia	-0,822	-0,015
Fallen trees	ft	0,211	-0,186
Cattle	ca	0,271	-0,014
Creeks and streams	cs	0,512	-0,292
Wetlands	we	0,359	0,190
Soil exposure	se	-0,028	0,005
Rocky outcrop	ro	0,029	0,015
Litter	lit	-0,027	-0,009
Arthropod biomass	ab	-0,044	0,553
Vegetal Richness	vr	-0,059	0,141
Vegetal Abundance	va	-0,221	-0,151
Average tree height	ath	0,167	-0,163

## DISCUSSION

Regarding studies with small mammals in fragmented landscapes in southeastern Brazil, ROCHA *et al.* (2011) and MESQUITA & PASSAMANI (2012) recorded 15 (10,080 trap-nights) and 11 (6,300 trap-nights) species, respectively. However, PASSAMANI & FERNANDEZ (2011) recorded a higher richness (20 species) in a fragmented landscape in Atlantic Forest domain (Santa Tereza municipality, Espírito Santo state, Brazil), with a sampling effort of 37,794 trap-nights, and MACHADO *et al.* (2013) found 26 small mammal species in a nearby large and conserved area to our study area at the Perdizes Plateau (Minduri and Carrancas cities, Minas Gerais state, Brazil) with a sampling effort of 11,880 trap-nights. It was expected that the study area would have a high

richness because it is an ecotonal region (as in TALAMONI *et al.*, 2014; LAURINDO *et al.*, 2017), however our study shows that fragmentation negatively affects the community, presenting low richness (similar to BOVENDORP *et al.*, 2019), even with a high sampling effort. The adjacent conserved area, the Perdizes Plateau, can be considered as “Testimony area” of our study due to its geographical proximity (20 km in a straight line), which harbors greater richness (MACHADO *et al.*, 2013). We attributed our result to the high degree of fragmentation (see MACHADO *et al.*, 2016a) and the small area of the fragments (PARDINI *et al.*, 2010; HANSKI, 2015), summed with the effects of other human actions such as an increase in agricultural areas, non-selective wood removal, cattle entry and vegetation loss by herbivory, among others (personal observations made during sampling).

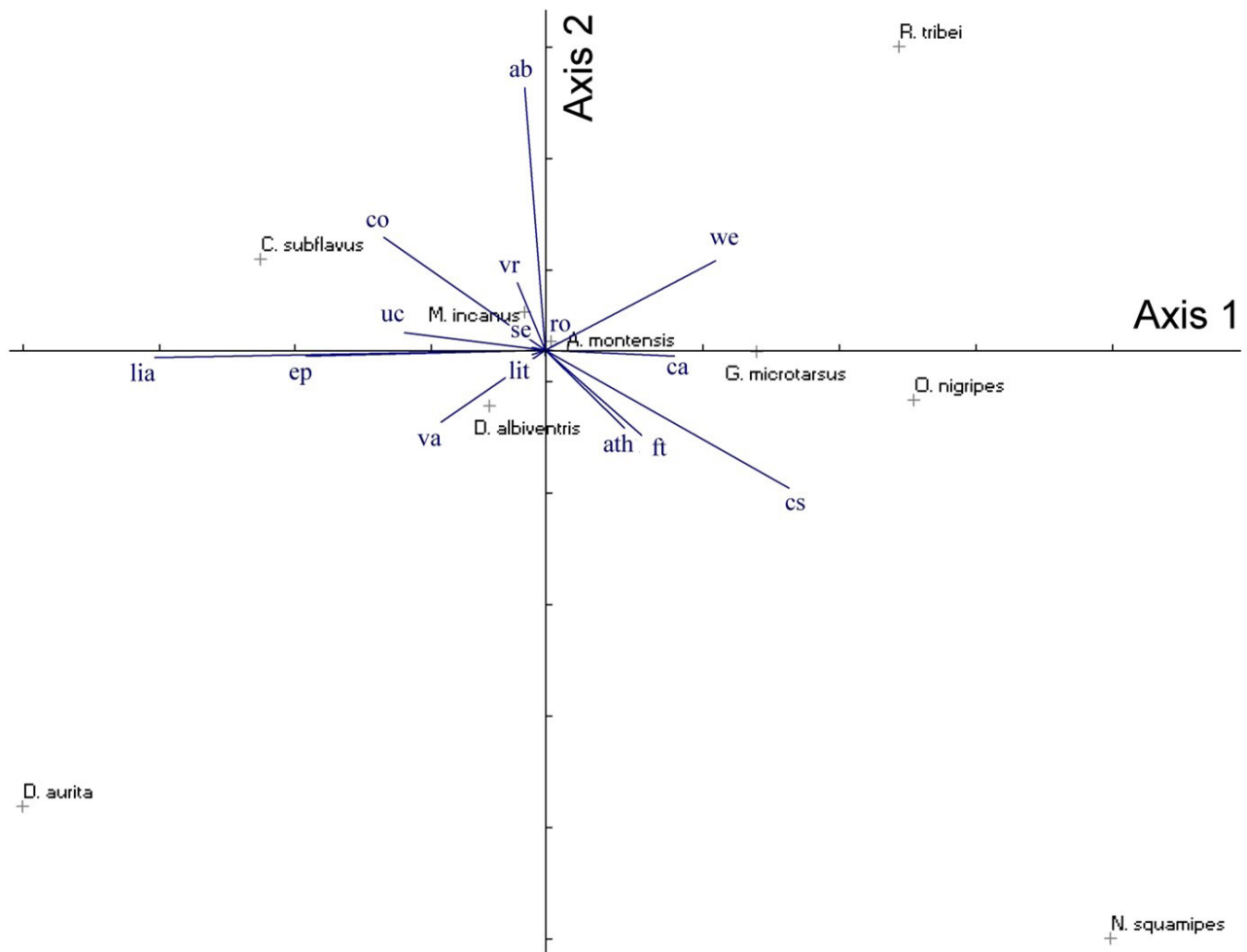


Fig. 5. Diagram of ordering of species of small mammals and environmental variables in the 24 small forest fragments in southeastern Brazil, produced by canonical correspondence analysis. The Acronyms represent “uc” to understory closure, “co” to canopy openness, “ep” to epiphytism, “lia” to lianas, “ft” to cattle, “cs” to creeks and streams, “we” to wetlands, “se” to soil exposure, “ro” to rocky outcrop, “lit” to litter, “ab” to arthropod biomass, “vr” to vegetal richness, “va” to vegetal abundance, and “ath” to average tree height.

Tab. III. Summary of fitting Gama-count models to microhabitat conditions on richness in small fragments in southeastern Brazil. The estimates refer to the dispersion parameter ( $\hat{\gamma}$ ) in the Gamma-count model and the Pr(z) to the null hypothesis of equidispersion ( $\hat{\gamma} = 1$ ).

Model	Estimate <sup>1</sup>	Std. error	Pr(z)	-2logL	AIC
richness ~ lianas + understory + epiphytism + canopy + fallentrees+ cattle + creeksandstreams + floodedarea	4.94E-11	6.76E-1	1.00	87.68	107.68
richness ~ lianas + understory + epiphytism + canopy + fallentrees + cattle + floodedarea	4.94E-11	6.76E-1	1.00	87.69	105.69
richness ~ lianas + understory + canopy + fallentrees + cattle + floodedarea	4.94E-11	6.75E-1	1.00	87.70	103.70
richness ~ lianas + understory + canopy + fallentrees + floodedarea	4.92E-11	6.71E-1	1.00	87.76	101.76
richness ~ lianas + understory + fallentrees + floodedarea	4.88E-11	6.61E-1	1.00	87.91	99.91
richness ~ lianas + understory + floodedarea	4.82E-11	6.48E-1	1.00	88.14	98.14
richness ~ lianas + understory	4.74E-11	6.33E-1	1.00	88.42	96.42
richness ~ lianas	1.17	0.32	<0.001	79.10	85.10
richness ~ creeksandstreams	1.07	0.31	<0.001	81.20	87.20
richness ~ creeksandstreams + lianas	1.18	0.32	<0.001	78.81	86.81
Null model	0.88	0.31	0.005	85.49	89.49

Studies using sampling methods commonly do not reach full diversity. This occurred in the present study, which was demonstrated by the species accumulation curve. However, an increase in sampling effort can increase the richness and abundance found in the study area (similar to mentioned by VOSS & EMMONS, 1996). The low richness found was not expected considering that ecotonal environments contain a mix of fauna elements from adjacent domains tend to have greater richness (as in TALAMONI *et al.*, 2014; LAURINDO *et al.*, 2017).

Our results showed a high turnover rate (beta diversity) of species in the studied communities (as predicted by FELINKS *et al.*, 2011). This composition with low number of specialists (18.2%) and high to generalists (81.8%) (similar to BOVENDORP *et al.*, 2019) suggest that the beta diversity was determined by the forest size (PÜTTKER *et al.*, 2015) and human actions on the fragments, which in turn generated unique characteristics based on local type of pressure on the environment. Therefore, the environmental characteristics of fragments (microhabitat structure) which correspond to biotic or abiotic factors acted in synergy to shape the richness and species composition patterns reported in our study.

A principal component analysis was performed (PCA) to try to understand the pattern of these characteristics inside forest fragments (Fig. 5) and showed two opposite environments regarding the microhabitat structure; one with open environments influenced by characteristics such as streams and flooded area, and another with closed environments influenced by lianas and epiphytes. This shift partitioned the small mammal community based on their ecological characteristics, where *N. squamipes*, *G. microtarsus*, and *O. nigripes* were correlated with environments with relatively high levels of water availability. The association of *N. squamipes* with streams and flooded environments has been reported at other sites, mostly due to the morphological, ecological and behavioral adaptations (ERNEST & MARES, 1986; BONVICINO *et al.*, 2002). The associations of *G. microtarsus* and *O. nigripes* with stream environments are not mentioned in other studies, but they were mostly associated with open sites of the nearby matrix (ROCHA *et al.*, 2011). The correlation of *C. subflavus*, *D. albiventris* and *D. aurita* with lianas, other epiphytes and denser understory suggest that these species prefer dense environments which may reduce encounters with predators and increase the probability of finding shelter sites (OLIVEIRA *et al.*, 2014).

The habitat characteristics in these fragments demonstrates that the human actions and environmental factors provide different microhabitat structures for each fragment which may not be required for a specific group of animals. Thus, it disables the use of this small fragment as housing or an ecological corridor (or stepping stones) (ROCHA *et al.*, 2011) because the microhabitat structure can function as an environmental filter, not allowing the displacement and establishment of some species. In addition, the small size (*i.e.* < 50 ha) and the distance between fragments can strongly

influence colonization and displacement rates (PÜTTKER *et al.*, 2011), affecting alpha and beta diversities.

Our models showed that there are two main filters for small mammals in the study area: streams and lianas. The presence of rivers in a landscape facilitates permeability of small mammals for both generalists and specialists of the habitat (PAISE *et al.*, 2020), increasing richness and abundance in highly fragmented environments, including in ecotonal environments (our study), as it increases the number of available habitats and resources. In addition, the lianas, associated with arboreal characteristics (WELLS *et al.*, 2004), are normally used to avoid predators and for finding shelter (OLIVEIRA *et al.*, 2014).

We highlighted that the appropriate management of these forest fragments is necessary in order to conserve the local biodiversity, considering that the presence of cattle was inversely related to the understory variables (BONESSO SAMPAIO & GUARINO, 2007): “lianas”, “other epiphytes” and “understory density”, which are determining factors of richness in the patches. Therefore, we suggest that management strategies such as to enclose the fragments to prevent cattle entry, allows the entry of native animals, and to establish linear patches (ecological corridors) to allow structural connection between them. Furthermore, rare species can occur in fragmented landscapes, which in most cases have a reduced home range (*i.e.* *C. philander* has a home range of approximately 3 ha; LAFERIERRE, 1995), which points out that the management strategies cited above are more important for these species. Therefore, incentives for maintaining such areas as legal reserves or permanent protection areas [*Reserva Legal* (RL) and *Áreas de Proteção Permanente* (APP) in Brazilian Legislation] (BRASIL, 2012), as well as habitat connection through ecological corridors are necessary (FIALHO *et al.*, 2017). Environments presenting 30% or more vegetation cover lead to increased biodiversity and the emergence of specialist small mammal species (PARDINI *et al.*, 2010). Furthermore, an increase in natural forest areas favors individuals being able to move around and increases the possibility of metapopulation persistence (PÜTTKER *et al.*, 2011).

We conclude that the richness of small non-flying mammals communities in the forest fragments studied is low as a result of the fragmentation effect on the landscape. The composition had a high number of generalist species, and an increase in species turnover. The small forest fragments in the ecotonal area of the Cerrado/Atlantic Forest domains present a microhabitat structure with lianas and streams as the main selectors for a specific group of small mammals with ecological similarities.

**Supplementary material.** The following online material is available for this article: Table A1. Identification and description of the landscape matrix of 24 forest fragments in southeastern Brazil; Table A2. List of variables used in the description of habitat microstructure as well as the average and standard deviation, in 24 small forest fragments in southeastern Brazil; Table A3. Beta diversity indexes paired (Beta Simpson) in 24 small forest fragments in southeastern Brazil; Table A4. Beta diversity indexes paired (Beta Nestedness) in 24 small forest fragments in southeastern Brazil;



Table A5. Beta diversity indexes paired (Beta Sorensen) in 24 small forest fragments in southeastern Brazil; Figure A1. The dispersion plots between the predictive variables from the models of microhabitat structure in relation to abundance within small forest fragments in southeastern Brazil. The “dados” represent data, “abundancia” represent abundance, “subbosque” represent understory, “epifitismo” represent Epiphytes, “dossel” represent Canopy, “arvorescaidas” represent fallen trees, “gado” represent cattle, “rio” represent Creeks and streams, and “alagado” represent flooded area; Figure A2. The dispersion plots between the predictive variables from the models of microhabitat structure in relation to richness within small forest fragments in southeastern Brazil. The “dados” represent data, “riqueza” represent richness, “subbosque” represent understory, “epifitismo” represent Epiphytes, “dossel” represent Canopy, “arvorescaidas” represent fallen trees, “gado” represent cattle, “rio” represent Creeks and streams, and “alagado” represent flooded area.

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