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"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

EFFECTS OF DOMESTIC MEGAFAUNA AND LANDSCAPE ON DIVERSITY OF MAMMALS IN ATLANTIC FOREST REMNANTS

LAÍS LAUTENSCHLAGER RODRIGUES

Dissertação apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Mestre em Ecologia e Biodiversidade.

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Orientador:

Prof. Dr. Mauro Galetti Rodrigues

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Resumo

A conversão de paisagens florestais para usos antrópicos é a principal causa do desmatamento das florestas tropicais em todo o mundo. Essas florestas são conhecidas por conter parte significativa da biodiversidade terrestre global, porém pouco se sabe sobre como as modificações na paisagem, como a perda de habitat para produção agropecuária e o principalmente o impacto do gado afetam a diversidade e ocupação de mamíferos resilientes nesses fragmentos. Sendo assim, nós examinamos como a riqueza de espécies e a composição de mamíferos são explicadas pela configuração da paisagem e como a presença do gado afeta a detecção de mamíferos de médio e grande porte. Foram amostradas 20 paisagens dominadas por pastagens ao longo de um gradiente de cobertura florestal (8% a 98%), no sudeste do Brasil. Nós registramos 75% das espécies de mamíferos esperadas para esta região em uma cobertura florestal de média a alta. A cobertura florestal, distância euclidiana do vizinho mais próximo e área estrutural foram as variáveis que melhor explicaram a ocorrência de algumas espécies de mamíferos dependentes de floresta. As comunidades de mamíferos exibiram um alto grau de alternação de espécies entre as paisagens, representando 95% da diversidade beta total. Os impactos da pecuária foram mostrados devido ao seu efeito negativo na detecção de espécies florestais e positivo na detecção de grupos de espécies não florestais. Discutimos a importância de manter fragmentos com alta cobertura vegetal para melhorar a conectividade entre paisagens perturbadas, favorecendo o fluxo de espécies de mamíferos, além da urgente necessidade de uma melhor compreensão dos impactos gerais do gado sobre a fauna e flora em remanescentes florestais, em uma escala mais fina que considere o interior dos fragmentos, avaliando quais os efeitos da presença do gado na alteração da qualidade desses ambientes e assim aprimorando a conservação da biodiversidade e dos recursos naturais.

Palavras-chave: *Pecuária, Fragmentação, Matriz de Pasto, Mamíferos, Armadilhas-fotográficas, Diversidade Beta.*

Abstract

The landscape conversion to anthropic uses is the major cause of deforestation worldwide. Tropical forests are known to contain a significant portion of global terrestrial biodiversity, but little is known about how changes in landscape, such as habitat loss for livestock and its impacts affect the diversity and occupation of resilient mammals in forest fragments immersed in pasture matrices. Here we examine how species richness and mammal composition are explained by landscape configuration and how cattle presence affects the detection of medium and large mammals. We sampled 20 landscapes dominated by pastures along a forest cover gradient (8% to 98%) in southeastern Brazil. We recorded 75% of the mammalian species expected for this region in a medium-to-high forest cover. Landscapes metrics, as forest cover, Euclidean distance from the nearest neighbor and structural area were the variables that best explained the occurrence of some forest mammal species. Mammalian communities exhibited a high degree of species turnover between landscapes, representing 95% of total beta diversity. Livestock impacts were shown due to its negative effect on the detection of forest-dwelling species and positive on the detection of non-forest species groups. We discuss the importance of maintaining forest fragments with high vegetation cover to improve connectivity between disturbed landscapes, favoring mammalian species flow. There is an urgent need for a better understanding of livestock general impacts inside forest remnants, considering the interior of these fragments, assessing how cattle's presence alters the quality of these habitats and thus improving the biodiversity and natural resources conservation.

Keywords: *Livestock, Fragmentation, Pasture matrix, Mammal species, Camera trapping, Beta diversity.*

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1. Introduction

Urban expansion and economic development have required large amounts of land, altering natural areas and creating anthropically modified landscapes (Melo et al., 2013). The rainforests conversion to anthropic uses represents about 80% of forest deforestation worldwide (Kissinger et al., 2012) and it has been considered the main cause of global biodiversity loss (Green et al., 2005; Laurance et al., 2006). At the moment, cattle ranching occupies 2 billion ha of global grasslands (FAO, 2018), with livestock corresponding to 60% of global vertebrate biomass (≈0.1 Gt C), being in an order of magnitude larger than all the terrestrial wild megafauna before the Quaternary Megafauna Extinction (Bar-On et al., 2018). Tropical ecosystems are being disrupted by large-scale changes, as agricultural and land conversion to pastures, suffering from several consequences as forest loss, fragmentation, logging, animal hunting and edge effects (Peres et al., 2006; Wright, 2010, Laurance et al., 2014).

The Atlantic forest of South America is one of the most endangered ecoregions worldwide, with only 11.7% of its original vegetation cover remaining, scattered in the landscape in forest patches smaller than 50 ha (Ribeiro et al., 2009). Besides, it is considered as a global priority due the highest plant and vertebrate biodiversity, including many endemic species that are seriously threatened by anthropogenic pressures (Myers et al., 2000; Galetti et al., 2009). This pressure has negative effects as habitat loss and fragmentation observed at multiple spatial scales. Changes in the configuration and structure of the landscape around fragments can affect the persistence of several species such as birds, mammals and others (Andrén, 1994). Large and specialist species, for example, tend to suffer reductions in population size, in genetic diversity, recruitment averages, increasing inbreeding and extinction rates, while generalist and small species tend to be benefited by habitat loss due the reduction and/or extinction of predators or competitors, also by the exploitation of new resources from the matrix (Michalski and Peres, 2007). Forest fragmentation also severely affects the persistence of many species, causing impacts on the composition of local community (Pardini et al., 2009), creating landscapes with impoverished communities and simplified networks interactions (Fahrig, 2003; Tylianakis et al., 2010).

In the present moment, Brazil holds the largest commercial cattle production worldwide, reaching 215 million heads of cattle in around 162 million hectares of pasture (ABIEC, 2019), being considered the country with the largest beef exports in the world with minor producing costs, according of its climatic characteristics and territorial extension (Carvalho et al., 2009; Deblitz, 2012). The historical core of livestock ranching in Brazil lies in the south and southwest

regions (de las Heras et al., 2011). With accelerated economic development of this region it has altered the original landscape during the last centuries, replacing native vegetation to livestock production and also many agricultural crops as coffee, forestry and sugarcane fields (Dean, 1996). Atlantic forest remnants are present in only 14% of São Paulo state territory (SOS Mata Atlântica, 2018) and are mainly isolated, fragmented and scattered across the landscape dominated by cultures and anthropic areas (Brown and Brown, 1992). Only a narrow fraction of these forest remnants is under restrictive protected areas (Coetzee et al. 2014), most of them are located within private landholdings surrounded by sugarcane and pasture matrices (Tabarelli et al., 2004).

Although pasture areas could be considered heterogeneous, associated with nutrients cycling, carbon stocking and plant species recruitment (Dias-Filho and Ferreira, 2008), the increasing land conversion to new cattle farming areas can result in high emission of greenhouse gases and loss of some important ecosystem services (Godfray et al. 2010; Foley et al. 2011). Only a few species can maintain viable populations in tropical livestock systems (Esquivel et al., 2008), resulting in lots of impacts on wildlife that can occur directly, through interference competition or indirectly, with changes in vegetation structure that influences the availability of natural resources and nesting areas. From all species groups, there is a lack of information about the influence of livestock on large bodied mammals, even with all importance of this taxon, since mammals cover a wide range of body sizes and diet types, also they can compete directly with cattle for food resources, particularly between large ungulates (Schieltz and Rubenstein, 2016).

Conciliating food production with biodiversity conservation has been a major challenge in tropical countries (Balmford et al. 2002; Green et al., 2005; Eisler et al., 2014). Here we asked if rainforest remnants immersed in pasture matrices can sustain an assemblage of mammals and how the landscape configuration affect these communities. Specifically, we predicted that (i) forest cover should be a predictor for higher native mammal richness, since they are most affected by the habitat loss (Andrén, 1994; Pardini et al., 2010; Fahrig, 2013), (ii) mammal communities inside forest patches immersed in pasture matrices should experience a *turnover* species process, even with habitat loss and fragmentation, these forests must retain a heterogeneous species, with replacement of species at some sites by different species at another sites (Baselga, 2010), same encountered by Beca et al. (2017) in sugarcane matrices, and (iii) livestock (cattle and horse) can negatively affect the occupancy of native mammals and positively the occupancy of exotic species (wild boars and dogs) by changing the structure of

the forest (Hegel and Marini, 2013). Finally, we propose conservation measures to these fragments surrounded by pasture, enhancing the importance of keep these forest remnants protected from livestock disturbing, favoring the local biodiversity.

2. Material and Methods

2.1 Study area

This study was carried out in 20 landscapes with forest remnants immersed in pasture matrices, distributed through southern Atlantic rainforest, São Paulo, Brazil (Figure 1; Table S1, Supplementary Material). We selected the landscapes using the map of forest remnants provided by Ribeiro et al. (in prep.), which was prepared in Albers Projection and WGS 84 Datum, with 30 m spatial resolution. Although São Paulo state presents different types of vegetation we choose to use only remnants of seasonal semideciduous forest, since this particular Atlantic forest physiognomy have been so degraded in most small fragments (50 ~ 200 ha) and still is considered essential to reduce fragment isolation among larger fragments, suggesting that they are important species stepping stones (Ribeiro et al., 2009). Each chosen landscape was in a 2 km radius buffer, with 8% to 98% forest cover gradient, so we can verify if the amount of remaining vegetation influences mammal richness. We defined this spatial extent due the responses of medium and large-sized vertebrates to landscape variables be better explained in scales of 2 km (Lyra-Jorge et al., 2010). To reduce spatial autocorrelation between our sampling scenarios the margins of each buffer have a minimum distance of 10 km from another landscape (Fortin and Dale, 2005; Beca et al., 2017).

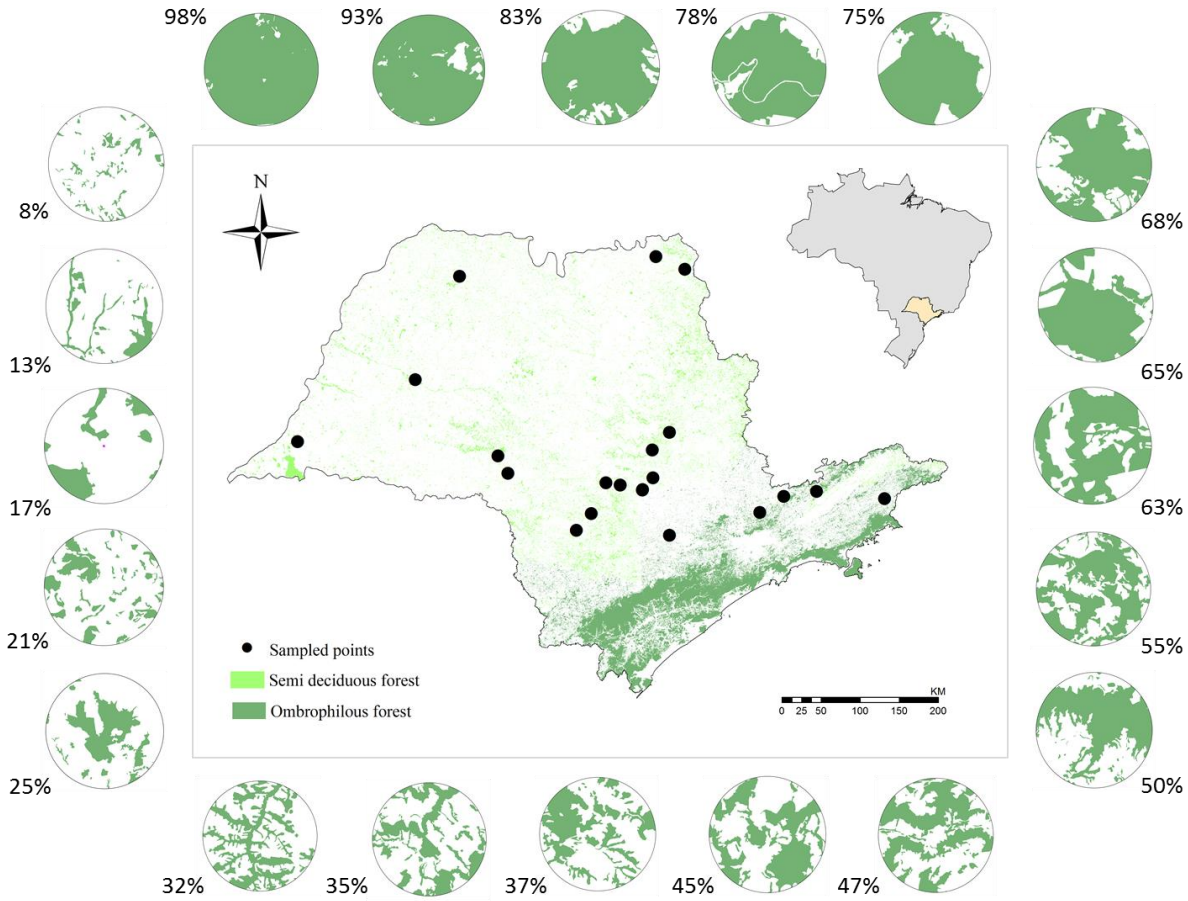


Figure 1. Forest amount in 20 landscapes survey in the Brazilian Atlantic forest. The circles have 2 km radius around the centroid of each landscape.

Since we worked with a gradient of forest cover, the landscapes were chosen from the higher cover of pastures or open areas in relation to other types of matrices, such as sugarcane, forestry and urban areas. Almost all our landscapes were private properties as family livestock farms, with only two protected areas included: Mico Leão Preto Ecological Station and the Ipanema National Forest, providing higher cover of natural forest (75% and 98% consecutively).

2.2 Mammal sampling

We used camera trapping to assess species richness and composition of medium and large-sized mammals (≥ 1 kg), due the possibility to record species with wider range of ecological and behavioral characteristics, especially in their different periods of activity (Beca et al. 2017, Lima et al., 2017). Camera traps can be considered an efficient tool for generating data about species occurrence in forest environments, including species that are elusive and

have low population density (Tobler et al., 2008; McCallum, 2013; Lima et al., 2017). Surveys were carried out from January 2018 to January 2019, with eight cameras trap (Bushnell Natureview Cam Essential HD) without baits per landscape, that were placed at different places, which could be in the same fragment or in different fragments, depending on the patch size of the forest remnant within 2 km radius buffer (Beca et al., 2017), i.e., we used a mosaic-level sampling protocol, attempting to sample the greatest number of fragments within each landscape rather than just one (Bennett et al., 2006) (Figure S1, Supplementary Material). The camera traps were exposed over a period of 30 days and spaced apart by distances ranging from 200 m to 1500 m, installed on tree trunks at 30-40 cm above ground at sites with similar local features (e.g. local animal activity, such as natural tracks or water streams, but avoiding human trail and roads). Sampling effort at each landscape was standardized at 240 camera trap/days (5,760 camera trap/hours).

2.3 Landscape metrics

For each landscape survey we performed a manual mapping to ensure greater accuracy of the forest cover gradient, which was divided into three categories: (1) Forest, (2) Pasture areas and (3) Other matrices types and land uses, using the ArcGIS ® v.10.5.0 software (ESRI, 2012) and its available system base map, at a fine scale of 1:5,000. Forest cover (%) was calculated by considering the area of all remaining semideciduous forest patches within the 2 km buffer, divided by the landscape size buffer (1,257 ha) and multiplied by 100. Forest cover is a landscape composition parameter in which the total amount of vegetation remaining is evaluated, regardless of their spatial organization (as amount of habitat, edge effect and shape) (Drinnan, 2005). Furthermore, we also calculated the edge amount (ha) and structural area (ha) of the fragments. To calculate forest edge amount, we first selected all peripheral 30m forest pixels from our raster map of all fragments in each landscape, considering the entire 2 km buffer around all fragments and then calculated their aggregate area. Assuming that terrestrial mammals can move beyond the boundaries of the 2km buffer area, particularly when forest patches exceeds this boundary, we defined the structural area as the cumulative fragment area that was intercepted by the 2 km buffer within another buffer of 5 km radius. These bigger 10km buffers were defined as five times the buffer area used to assess the effects of landscape cover on mammalian carnivores in the Atlantic forest (Regolin et al., 2017) (Figure S1, Supplementary Material). We performed a Mantel test to verify if species richness were

autocorrelated between our 20 landscapes, and it indicates that we didn't have any spatial autocorrelation (r-value = - 0.03, p = 0.57).

There are several spatial processes that modifies the land by affecting landscape in different ways, causing changes in spatial patterns and ecological processes interactions (Forman, 1995). In order to analyze these interactions, as mammal richness and diversity, spatial patterns need to be defined (Turner et al, 2001). Landscape metrics are useful tools to measure arrangement of landscape components both in time and space, being used to describe spatial patterns (Leitão and Stolfi, 2002). Since more than one metric is needed to define the landscape patterns, besides forest cover (%), edge amount (ha) and the structural area (ha) we also used 6 other landscape forest metrics (Table S2, Supplementary material), which was chosen using the FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps documentation (McGarigal, 2015), that provides a detailed description of metrics. These metrics was measured using the map of forest remnants provided by Ribeiro et al. (in prep.). We converted the entry maps into matrix format using the software GRASS GIS 7.6 (GRASS Development Team, 2017) and calculated the values using the package *landscapemetrics* (Hesselbarth et al., 2019) in software R (R Core Team, 2019).

2.4 Data analysis

2.4.1 Total mammal species richness

The total mammal species richness was defined as the number of species recorded at each landscape sampled. We built species rarefaction curves to verify if our sampling effort was sufficient at each landscape, trying to reach an asymptote, based on the number of days sampled and the number of species recorded per landscape (Gotelli and Colwell, 2001). Rarefaction curves were generated using the *iNEXT* package (Hsieh et al., 2019) with an incidence dataset. This new metric uses the observed sample of abundance or incidence data to compute diversity estimates and the associated 95% confidence intervals for two types of rarefaction and extrapolation (R/E). We also plot a sampled completeness curve, that provides a dotted bridge between the rarefaction and extrapolation curves. All analyses were conducted using the software R (R Core Team, 2019).

2.4.2 Landscape effects on mammal species

In order to verify which landscape configuration are related with mammal diversity we used the entire assembly of medium and large-sized mammals recorded, and we also create three different species groups by their desired habitat: forest-dwelling, non-forest dwelling and exotics and/or invasive species (Table S3, Supplementary Material). This classification was made using the ATLANTIC Mammals datapaper (Souza et al., 2019), where we selected only our native species recorded and calculate the proportion due the location of sampling habitat of each species, that it could be "forest interior" (considered here as forest-dwelling species) or "edge" (non-forest dwelling species). If some species was not very represented in the datapaper, we used the IUCN The Red List of Endangered Species (IUCN, 2019) website to access those species habitats information.

To evaluate how the landscape metrics affect species composition of medium and large-sized mammals in general and for that three habitat groups we generate Regularized Discriminant Analysis (RDAs), using the *vegan* package in R (Oksanen et al., 2013) and the *rda* function (Legendre and Legendre, 2012; Borcard et al., 2018). In each case, we conducted a multiple correlation coefficient analysis between spatial metrics to only use non-correlated landscape metrics. RDA analyses was based on how the predictor matrix (landscape metrics) could influence the response matrix (mammal species composition groups). In case of the RDAs generated respond statistically significatively, we then related some selected species from the group to the explanatory landscape metrics, using Generalized Linear Models (GLMs) with a binomial distribution to examine species richness (Zuur et al., 2009), selecting the most plausible models using Akaike's weights (wAICc, > 0.1) and ΔAICc (< 2.0) (Burnham and Anderson, 2002), also including a null model to represent the absence of effect on the list of competing models.

2.4.3 Beta-diversity of mammals across landscapes

To preserve biodiversity across spatial scales it is important to know the relationship between locally collected data and regional diversity dynamics, and how the mechanisms that maintain diversity vary from local to regional spatial scales (Kraft et al., 2011). Therefore, we calculated the beta (β_{SOR}) diversity among landscapes, using the Sørensen dissimilarity index (Baselga, 2010). We also decomposed the beta diversity into *turnover* of species and *nestedness* components, according to Baselga (2010). The spatial *turnover* of species is represented by *Simpson dissimilarity index* (β_{SIM}) and it occurs when species present at one site are absent at

another site, but are replaced by other species absent from the first. *Nestedness* is represented by the *nestedness index* (β_{NES}), which quantifies the dissimilarity due to the difference in species richness, and it occurs when species present at one site are absent at another but are not replaced by additional species. *Turnover* across natural sites implies that conservation must target multiple sites, while *nestedness* suggests that conservation might target the richest sites (Socolar et al., 2016). To calculate the β-diversity we used the functions *beta.multi* and *beta-pair* of the *betapart* package in R software (Baselga and Orme, 2012). We also tested if the two β-diversity components (β_{SIM} and β_{NES}) for landscape-level mammal assemblages differed from those expected by chance, creating a null model and preserving the rarity of species occurrence (i.e. by maintaining the number of times each species occurred at all 20 landscapes), and built confidence intervals for both β_{SIM} and β_{NES}, whereby values outside those confidence intervals indicated divergence from random expectations.

In order to examine the effects of landscape metrics chosen and geographic distances on the β-diversity and its two components (β_{SIM} and β_{NES}) we used Multiple Regressions on distance Matrices (MRM; Lichstein, 2007), using the distance matrices as the response matrices, and landscape metrics and geographic distances as explanatory matrices. MRM analysis can deal with linear, non-linear and non-parametric relationships between matrices, and is considered a more flexible approach than the often-used Mantel test. Estimates of MRM tests were carried out using the *ecodist* package in R (Goslee and Urban, 2007), testing the significance of R2 values with 100 permutations.

2.4.4 Evaluating livestock effects through occupancy modelling

We conduct Single Species - Single Season occupancy modellings (Mackenzie et al., 2006) to understand if the detection (P) or occupation (Psi, ψ) of cattle inside the forest fragments affect the probability of detection and/or occupation of mammals. These occupancy modelling approaches dynamics are very useful for identify the underlying processes that generate patterns in occupancy of species (e.g., metapopulations) (Mackenzie and Nichols, 2004). Here, we used those three habitat groups' species with three detection (1) and non-detection (0) matrices with the total encounter history of 30 occasions, each representing one day of camera trapping (24 hours), and the number of heads of cattle (considering *Bos taurus* and *Equus caballus*, that was recorded on camera-traps in each landscape during the camera-trapping period) and the landscape metrics (forest cover (%) and pasture cover (%)) as co-variates. The modelling analysis was made using the software MARK (MacKenzie et al. 2006).

To rank the best models, we used the Akaike's Information Criterion corrected for small sample sizes (AICc - Hook and Regal, 1997). Those with ΔAICc < 2 and > 0.01 AICc weight were considered the best models, because of their higher level of empirical support (Burnham and Anderson, 2004).

3. Results

3.1 Medium and Large-sized Mammal Richness

We had a total effort of 111.600 hours in 20 landscapes sampled (mean 5.580 h per landscape) and found 31 species of medium and large-sized mammals, including four exotic species (domestic dog (*Canis lupus familiaris*), wild boar (*Sus scrofa*) and domesticated farm species: cattle (*Bos taurus*) and horse (*Equus caballus*)) (Figure 2; Table S3, Supplementary Material). On average, we recorded 11 mammal species per landscape, with a minimum of 7 and maximum of 17 species. The most common and widespread species was the white-eared opossum (*Didelphis albiventris*) which was recorded at all landscapes and the nine-banded armadillo (*Dasypus novemcinctus*) recorded at 19 of 20 landscapes. The bush dog (*Speothos venaticus*), neotropical otter (*Lontra longicaudis*), jaguarundi (*Puma yagouaroundi*), striped hog-nosed skunk (*Conepatus semistriatus*) and the black-fronted titi monkey (*Callicebus nigrifrons*) were the rarest species, recorded only once. Although the rarefaction curves that estimates species richness per survey-day failed to reach an asymptote in most of our 20 landscapes, our extrapolated richness was not much different from what we found, same in our sampling completeness curves and confidence intervals encountered and expected (around 0.90%) (Figure S2, Supplementary Material).

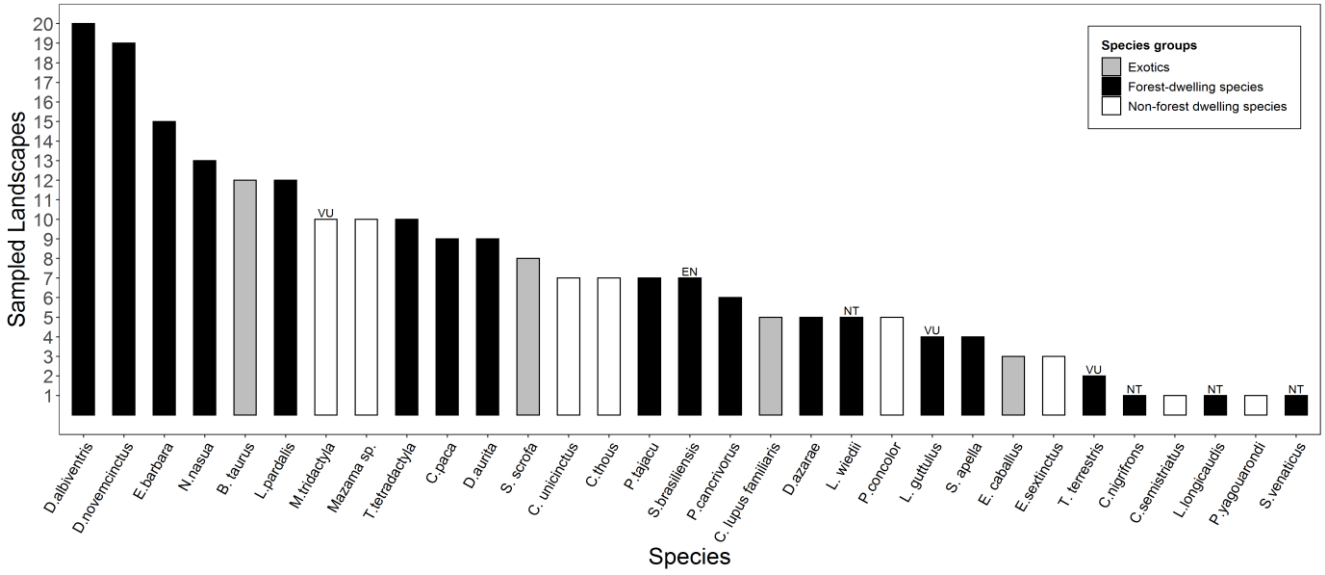


Figure 2. Representation of 31 medium and large-sized mammal species recorded at 20 semideciduous forest remnants, in São Paulo state, Brazil. Black bars represent the forest-dwelling species, white bars represent non-forest dwelling species and gray bars represent exotics and/or invasive species. Endangered (EN), Vulnerable (VU) and Near Threatened (NT) species were indicated, according to IUCN Red List of Threatened Species.

3.2 Effects of landscape metrics on mammal assemblages

We found that landscapes with medium-to-high forest cover (>55% to 80%) retained the highest richness of mammals (13 and 17 species), although we recorded our lower richness number (7 and 9 species) at the two areas with more than 90% of natural cover, indicating that only forest cover does not explain the species richness in Atlantic forest fragments immersed in pasture.

We performed four RDAs (one for each species groups, including the total richness) and only the RDA for forest-dwelling species showed a significant relationship between the mammal composition and the landscape variables (R^2 = 0.38, p-value = 0.04) (Figure S3, Supplementary Material). The first ordination axis (RDA1) explained 51% of the data variation, with the patch area metric, followed by number of cattle (28%). The second ordination axis (RDA2) was explained by structural area (72%) and forest cover (71%). Thus, to access which landscape metrics better explained specific mammal species, we generated one GLM to each forest-dwelling species (19) using those six landscape variables. Using a model selection, we observed five principal mammal species which some landscape metric better explained instead of the null model (Table 1). We encountered that for each species a different landscape metric explained better. The occurrence of *Cuniculus paca* was best explained by the Euclidean nearest neighbor distance (ΔAICc = 0.0, wAICc = 0.43); to *Leopardus pardalis* it was the edge area of the fragments (ΔAICc = 0.0, wAICc = 0.28); *Pecari tajacu* was best explained by forest cover in the landscape (ΔAICc = 0.0, wAICc = 0.46); the *Tamandua tetradactyla* was related with the landscape structural area (ΔAICc = 0.0, wAICc = 0.76) and *Tapirus terrestris* was explained by the amount of edge area (ΔAICc = 0.0, wAICc = 0.78).

Table 1. Summary of the set of candidate models fitting the five forest-dwelling species related to the landscape variables. The ΔAICc is Akaike differences, df is degrees of freedom of the model and wAICc is Akaike weights. Plausible models for explain each response variable are in bold.

Response variables	Model	ΔAICc	df	wAICc
Cuniculus paca	**Euclidean nearest neighbor**	**0.0**	**2**	**0.43**
	Cattle number	0.6	2	0.32
	Null	3.4	1	0.08
Leopardus pardalis	**Edge area**	**0.0**	**2**	**0.28**
	Null	0.2	2	0.25
	Euclidean nearest neighbor	1.7	1	0.12
Pecari tajacu	**Forest cover**	**0.0**	**2**	**0.46**
	Null	2.1	1	0.16
	Patch area	2.8	2	0.11
Tamandua tetradactyla	**Structural area**	**0.0**	**2**	**0.76**
	Forest cover	3.2	2	0.15
	Null	6.9	1	0.02
Tapirus terrestris	**Edge area**	**0.0**	**2**	**0.78**
	Cattle number	4.2	2	0.09
	Null	5.8	1	0.04

3.3 Beta Diversity of mammal communities

The variation in beta diversity among the assemblages of medium and large-sized mammals was mainly explained by the turnover of species (β_{SIM}, 80%) in the 20 landscapes, with a small part explained by the nestedness (β_{NES}, 4%). According to our MRM analysis, since the landscapes were not spatially auto-correlated, we only used the landscape variables as explanatory matrices. However, none of the β indices (β_{SOR}, β_{NES} (nestedness) and β_{SIM} (turnover)) were explained by the landscape metrics (Table 2).

Table 2. Beta diversity partition, showing Sørensen dissimilarity index (β_{SOR}), species turnover (β_{SIM}) and nestedness patterns (β_{NES}), with the chosen landscape variables, including heads of cattle.

	Confidence interval	Landscape Variables	Slope	p-value
βSOR (*Sørensen*) 0.84		Forest cover	1.477038e-05	0.98
		Cattle	-1.174599e-04	0.59
		Edge area	-7.804544e-03	0.75
		Structural area	1.772928e-04	0.24
βSIM (*turnover*) 0.80	0.8013316 ± 0.8002522	Forest cover	2.717196e-04	0.73
		Cattle	-4.920051e-05	0.93
		Edge area	5.381869e-04	0.99
		Structural area	1.498477e-04	0.37
βNES (*nestedness*) 0.04	0.04276332 ± 0.04168391	Forest cover	-2.569492e-04	0.49
		Cattle	-6.825938e-05	0.64
		Edge	-8.342731e-03	0.57
		Structural area	2.744513e-05	0.84

3.4 Livestock effects under mammal detection

According to the occupancy modelling we found that the presence of cattle in forest patches can negatively affect the probability of detection of forest-dwelling species' groups, with positively detection probability of this group according to higher forest cover (p-value = 0.003, P = 0.48 and Ψ = 1.00).

With the non-forest dwelling species we observed a positive effect of the presence of cattle in their detection probability, with more heads of cattle increasing the detection of species from this group (p-value = 0.0003, P = 0.16 and Ψ = 1.00), with the pasture cover affecting negatively their detection.

Finally, we encountered a negative effect of heads of cattle in the probability of detection of exotic species, going differently to what we expected from this group (p-value = 0.02, P = 0.17 and Ψ = 0.55). In this case, we found a positively effect of pasture cover, increasing the detection of exotics species (Figure 3; Table S4, Supplementary Material). In all our significant best models the occupancy parameter was constant (.), even testing each co-variate to see if affects the occupancy. The p-values was obtained comparing with the null model (P(.), ψ (.), being "." = constant).

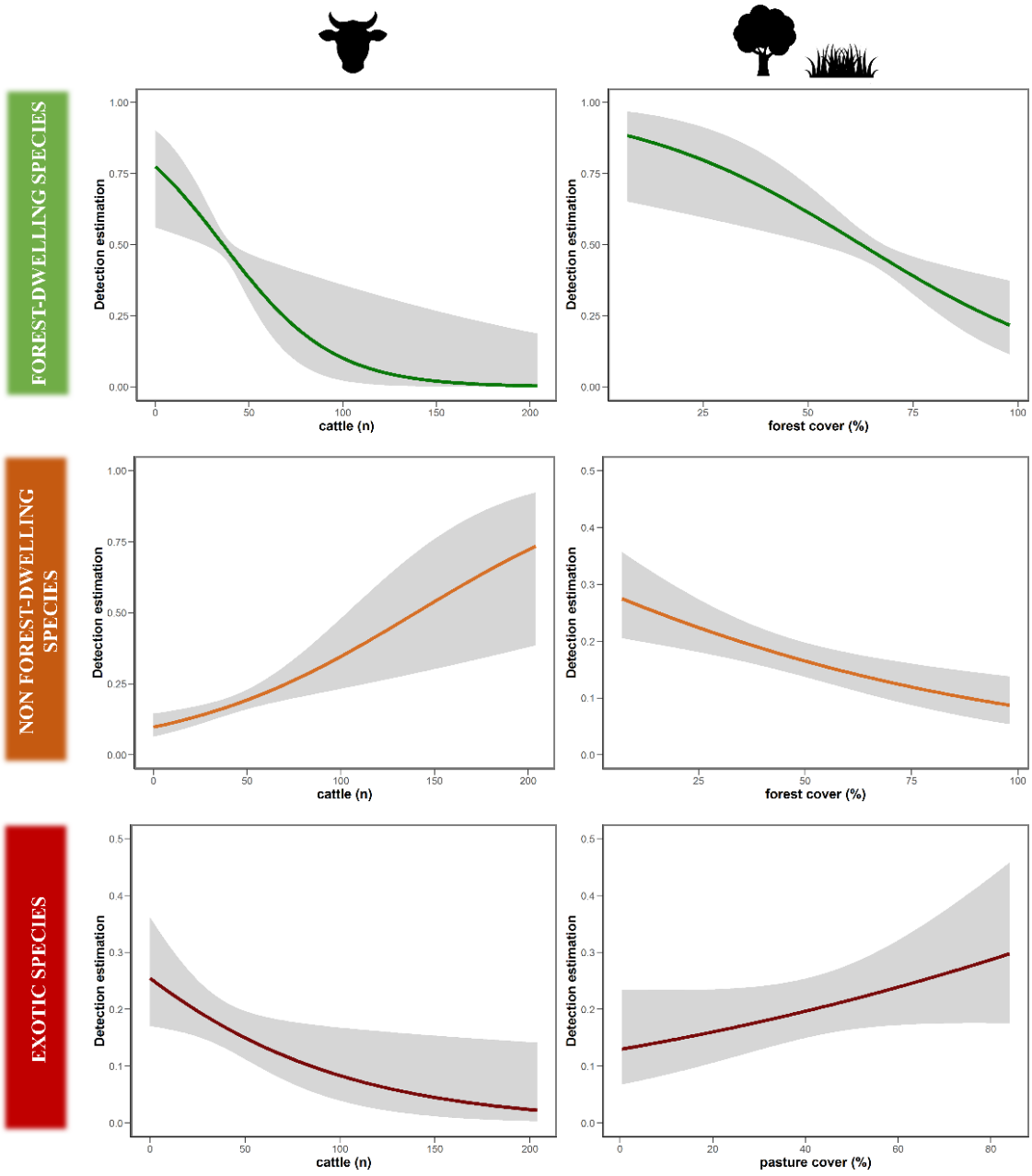


Figure 3. Summary of the relationship among the three mammal groups species (Forest-dwelling, Non-forest dwelling and Exotic species, with the landscape co-variates (heads of cattle (n), forest cover (%) and pasture cover (%).

4. Discussion

The negative impact of livestock on mammal composition inside forest patches immersed in pasture matrices can be considered as consequences from their disturbances in the habitat, that includes impoverishing fundamental natural resources, changes in the vegetation structure (Stern et al., 2002), by consuming seedlings (Santos et al., 2007) and fruits (Eaton et al., 2016), opening the area due the biomass of the cattle's herd and also contaminating water springs (Strauch et al., 2009), creating a disturbed habitat for native species, principally for forest-dwelling species, considered as disturbances sensitives.

Overall, we show that tropical rainforests patches immersed in pasture matrices maintain an impoverished assemblage of mammals, dominated by species that rather occur in open areas (such as *M. tridactyla* or *C. unicinctus*, around 26%) and exotic species (*S. scrofa* or *C. lupus familiaris*, 13%). This species tends to be more tolerant of habitat disturbance, therefore being more capable of colonizing forest remnants in altered landscapes (Swihart et al., 2003), since they are not so affected by habitat loss, even increasing its populations in these landscapes (Stuart et al. 2004; Pardini et al. 2010). Even so, these forests still retain almost the same richness (S = 29) of native medium and large-sized mammal species compared to the largest semideciduous remnant in Atlantic forest of São Paulo state (S = 31), with 23 equal species (75%) (Morro do Diabo State Park, Faria and Pires, 2006). Several other studies in disturbed areas of Atlantic forest have found similar medium to large-sized mammal richness. Dotta and Verdade (2012) encountered a richness of 25 species in agricultural landscapes; Magioli et al. (2014) at the Area of Ecological Interest Matão de Cosmópolis found a richness of 21 species, and Beca et al. (2017) in sugarcane matrices recorded a richness of 27 mammal species, showing that there were no regional-scale extinctions considering all landscapes combined, even with different matrices and locations.

The highest species richness occurred in landscapes with medium-to-high forest cover (> 50%), similar to other studies (Beca et al., 2017, Regolin et al., 2017). Some species of ungulates, such as tapir (*T. terrestris*) and collared peccary (*P. tajacu*) have only been recorded in landscapes with 45% - 80% forest cover, indicating that habitat amount is important for the occurrence of these species.

4.1 Landscape metrics effects

Only the RDA analysis for forest-dwelling species presented a statistical significance between the composition of medium and large-sized mammals and the landscape variables that we measured. When we analyze our GLMs made for specific forest species, we encountered that different landscape metrics explained different mammal species. For the three forest species (*C. paca*, *P. tajacu* and *T. tetradactyla*) explicit forest metrics explained better with a positive relation, being Euclidean nearest neighbor distance, forest cover and structural landscape area, respectively. Forest cover and structural area are both related with the amount of forest remnants, inside the sampled buffer (2km) and within the biggest buffer (5km), indicating that these species depend on landscapes with preserved forest habitats areas (Keuroghlian et al. 2004; Trovati and Brito, 2009). The Euclidean nearest distance metric is a simple measure of patch context and has been used extensively to quantify patch isolation, defined as the distance from a patch to a neighboring patch of the same or different class (McGarigal, 2015). The farther distance from a forest patch to another, more isolated that community will be, negatively affecting *C. paca* species due to their low home range capacities (Beck-King et al., 1999).

For the ocelot (*L. pardalis*) it seems positively affected by the amount of edge in the landscapes, increasing its occurrence in disturbed forests with higher edge areas. This feline species, even being considered as sensitive to habitat loss, it is known that they can be found in a variety of habitats, persisting in disturbed landscapes and since their diet, it indicates their plasticity and resilience to survive in modified landscapes (Magioli et al., 2019), such as in forest patches that cattle have access. Their diet consists principally birds and small mammals (Silva-Pereira et al., 2010; Seibert et al., 2015). With cattle disturbance inside the forest fragment and pasture matrices, this species has more food resources available, as small marsupials and rodents, that were an abundant group recorded during our sampling.

Otherwise, the amount of edge negatively affects the tapir (*T. terrestris*). This relation was already expected since these ungulates have large home ranges and are highly dependent on forested habitats (Fragoso et al., 2003), mainly for obtain fruits due to its predominant frugivorous diet (Dirzo and Miranda, 1990). Therefore, if the landscape has forest fragments with a high edge area, it means that these remnants are severely degraded and affected by edge effects or, in our case, probably by cattle impacts, decreasing the natural and preserved forest habitat that tapirs need to occur.

4.2 Highly turnover of mammal species

Our β-diversity analyses shown a high degree of species *turnover* (β_{SIM}) between forest remnants immersed in pasture matrices landscapes, which represent 95% of the whole mammal β-diversity. This indicates that each landscape presents a fairly distinct subset of species, although altered ecosystems typically retain a non-random set of species that are often constituted by generalists and disturbances tolerant (Michalski and Peres, 2005; Lyra-Jorge et al., 2010).

For decades it is discussed what affects species turnover and nestedness processes, and it includes environmental heterogeneity, biotic interactions, landscape structure, dispersal capacities, disturbance regimes, species area/time relationships and so on (Ricklefs, 1987, Soininen et al., 2007; Kraft et al. 2011; Socolar et al., 2016). The landscape configuration such as forest cover and connectivity can also be considered an important factor to species turnover (besides any of our metrics did not explain our beta-diversity indices), since it influences the dispersion of species, in a manner to facilitate it or not, according to the ability of each species to move between the fragments (Michalski and Peres, 2007; Lyra-Jorge et al., 2010). To maintain biodiversity within pasture-dominated landscapes its indispensable to retain a diverse and dense tree configuration, besides to restore natural tree regeneration (Mayfield and Daily, 2005). Forest patches within pastures can contribute to the conservation of plant and animal diversity by providing habitats and resources, increasing the structural and floristic complexity of the landscape and enhancing connectivity (Harvey et al., 2004).

4.3 Impacts of livestock presence on different mammal habitat groups

Our results show that the livestock presence affects negatively the detection of forest-dwelling species. Overall, negative impacts of cattle on native fauna is a result from habitat and vegetation alterations, causing diet overlap with native grazers and browzers, and alterations in behavior or habitat use associated with avoidance of cattle (Elliott and Barrett, 1985; Moser and Witmer, 2000; Chaikina and Ruckstuhl, 2006).

Forest-dwelling species are known to be sensitive to habitat losses and disturbances, often characterized by their limited movement capabilities through the matrix (Lindenmayer et al., 1990), being reluctant to cross (even not crossing) large areas of cleared land, such as pastures areas. According to Eaton et al. (2016), cattle's presence can negatively affect ground-dwelling frugivores, with overlap in use of fruit resources and/or alterations of behavior and habitat use, with the native fauna avoiding areas where cattle has high impacts, or shift their

spatial/temporal feeding patterns due the presence of cattle. In that case, the authors distinguished three groups of mammal species based on their responses to increasing levels of cattle impact: (1) species that were intolerant of cattle impact (as *Mazama spp*., *P. tajacu*, *L. pardalis* and two armadillos species), (2) species that appeared unaffected by cattle impact (as *D. azarae* and *N. nasua*) , and (3) species with different responses to cattle impact depending on the food resource (as *T. pecari*).

Surprisingly, the exotics group were also negatively affected by livestock presence in our occupancy modelling analyses. This goes differently to what we expected, since wild boars (*Sus scrofa*) and domestic dogs (*Canis lupus familiaris*, the two exotic species from this group), are considered invasive, generalist and even domesticated species (in case of domestic dogs). Wild boars seem to be unaffected by cattle activity or presence (Eaton et al., 2016), even sometimes overlapping their foraging areas in some cases. However, Barasona et al. (2014) showed that, in southern Spain, the spatial interactions between wild boars and cattle were explained by a relative habitat selection among different seasons of the year. Cattle showed an avoidance of areas with a higher proportion of dense shrub, areas that was related to wild boar, with overlapping on their home ranges only to use water resources during the dry season or when food resources are insufficient. These differences in home ranges may be related to food availability, population density, activity behavior and/or composition of social groups by species (Massei et al., 1997).

Finally, the livestock positively affects the detection of non-forest dwelling species. These species, originally associated with savanna and open area physiognomies have been losing their natural habitat. Extensive areas occupied by Cerrado domain, also known as the neotropical savanna, has been converted into pasture and agricultural land in recent decades (around 76Mha of Brazilian savanna are planted pasture lands) (Klink and Machado, 2005; Aguiar et al., 2016; Strassburg et al., 2017). Moreover, there are biological evidences from the "savannization" in the tropical forests in Brazil (Salazar et al. 2007), indicating a process of biotic reorganization especially of fragmented Atlantic forests, where land use changes and incidence of fire replaces pristine forests by early successional ones (Joly et al. 2014). Thus, non-forest dwelling species (as brocket species, the giant anteater or even maned wolf) are expanding their geographical distribution due the fragmentation and land conversion of agricultural and livestock systems, since they are adapted to open areas and are commonly encountered in altered landscapes (Coelho et al., 2008; Lyra-Jorge et al., 2010).

5. Conclusion

The global increase in livestock production and overall landscape changes are converting natural habitats, driving the loss of species with cascading effects on biodiversity and ecosystem functioning, including negative impacts on water quality and resources availability through a wide range of processes such as forest loss and degradation, land-use intensification, exotic plant invasions, seedling consumption and soil erosion, as it has been found in other studies. We found that cattle invasion in forest patches has a negative effect of the mammalian community in the Atlantic forest, principally for forest-dwelling species, and we assume that it occurs because these cattle has indirect impacts on wildlife natural habitats.

We understand the difficulties in analyzing the entire mammal community since it was composed of species with distinct life and habitat requirements, in different spatial locations with different land-use histories, principally in forest remnants with open areas and pastures as matrices. Nevertheless, we recorded a high richness of medium and large-sized mammal species, concluding that these patches still retain an important set of species that are affected by landscape configuration in varied ways. The fragmentation of habitat into patches is a landscape-level process that requires multiscale studies to understand biological dynamics in time and space, including the pasture permeability comprehension, that clearly affects patch occupancy, since some species that can across the matrix or exploit its resources often occupy a larger number of patches. Some landscape metrics as forest cover, structural landscape area and also the distance by nearest forest patch neighbor were the principal landscape configuration that best explains a few forest-dwelling mammals' species occurrence, predicting the importance of preserve large amounts of natural vegetation.

Here we showed that cattle can alter the detection of different mammal species, with negative effects on forest-dwelling species and enhancing the detection of non-forest species. We highlight an urgent demand in studies that includes all negative impacts of livestock inside forest remnants, including abiotic and biotic factors, so we can pressure the environment departments to include in the Brazilian forest code (law no. 12.651) the obligation of landowners to fence their forest remnants and legal reserves, forbidding the cattle to access forest resources, thus protecting their water springs and biodiversity present.

Appendix A. Supplementary data

The Supplementary data used in this study is right above References section.

6. References

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7. Appendix A. Supplementary data

Table S1. Coordinates (in decimal degrees), forest cover (%) and total species richness at each of our 20 study landscapes.

Landscapes ID	*Municipal district*	*Latitude*	*Longitude*	*Forest cover (%)*	*Total species richness*
P01	Paranapanema	-23.347202	-48.792991	31.84	12
P02	Alvinlândia	-22.474961	-49.745232	25.23	13
P03	Cesarino Afonso (EEc)	-22.227009	-52.227466	74.60	9
P04	Piracaia	-23.013777	-46.204182	68.63	13
P05	Piacatu	-21.591378	-50.680331	78.50	15
P06	Piracicaba	-22.766981	-47.820128	55.25	13
P07	Cristais Paulista	-20.379832	-47.384203	34.79	13
P08	Iperó (FLONA)	-23.443846	-47.638283	98.40	7
P09	Buritizal	-20.227689	-47.742156	47.05	8
P10	Valentim Gentil	-20.398004	-50.152154	13.21	12
P11	Charqueada	-22.452002	-47.818782	50.55	9
P12	São Pedro do Turvo	-22.684989	-49.619231	64.8	9
P13	Anhembi	-22.849218	-48.241028	37.57	10
P14	Corumbataí	-22.249638	-47.613615	7.96	11
P15	Cunha	-23.032504	-44.956943	21.09	8
P16	Itatinga	-23.162279	-48.624395	45.38	17
P17	Baguari	-22.904680	-47.969060	19.42	13
P18	Botucatu	-22.814583	-48.404308	62.73	11
P19	Monteiro Lobato	-22.961052	-45.806865	83.50	10
P20	Atibaia	-23.200473	-46.519288	93.39	9

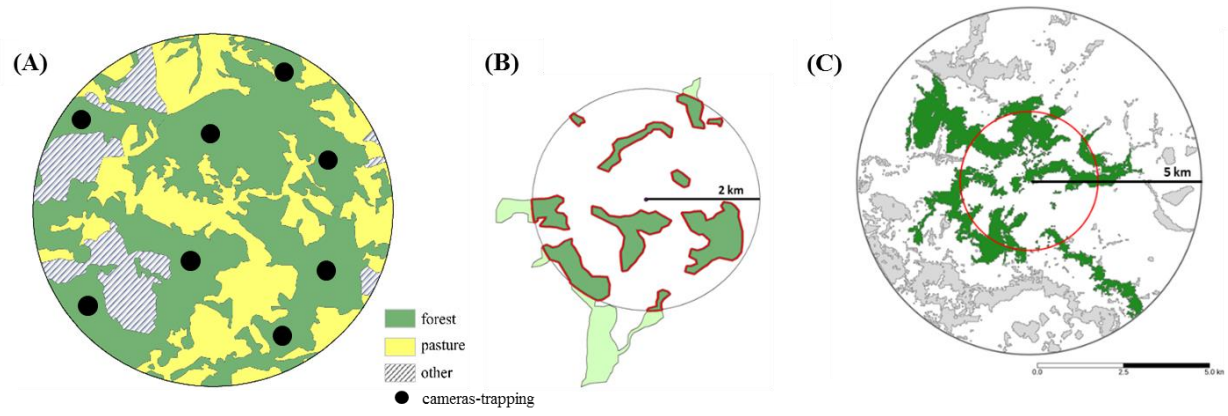


Figure S1. Representation of (A) a landscape with the three categories mapped (Forest cover in green, Pasture cover in yellow and Other types of land use in gray lines) and the eight cameras-trap disposition around the landscape (black dots); (B) Edge cover of each forest fragment within a buffer of 2km radius (red line represents the edge areas with 30 m) and (C) Structural area of forest fragments inside the 2km radius buffer but within 5km radius buffer.

Table S2. Landscape metrics used to calculate the landscape effects on mammal's richness and diversity, obtained from FRAGSTATS Help documentation.

Metrics names	*Type*	*Description*
edge area	area and edge metric	density (m/ha) of edge of a particular or all patch types
core area	core area metric	interior patch area that is unaffected by the edges
landscape shape index	aggregation metric	provides a simple measure of class aggregation or clumpiness
connectance	aggregation metric	number (%) of functional joinings between patches of the corresponding patch type, based on a user-specified distance criterion
patch area	area and edge metric	area (ha) of each patch
euclidean nearest neighbor distance	aggregation metric	often used to evaluate patch isolation
structural area	--	area (km^2) of each patch within 5km radius buffer
forest cover	--	cover (%) of semideciduous patches within 2km radius buffer
pasture cover	--	cover (%) of natural or planted pastures within 2km radius buffer
cattle_n	--	heads of cattle (n) recorded by camera-traps per landscape inside forest fragments

Table S3. The community (31 species) of medium and large-sized mammals recorded at 20 landscapes (P01 – P20) in São Paulo state, Brazil. Colored backgrounds represent different habitat groups: gray – Exotics, green – Forest-dwelling and orange – Non-forest dwelling species. Check Table S1 to landscapes identification.

Species	Landscapes recorded																				IUCN	Habitat
	P01	*P02*	*P03*	*P04*	*P05*	*P06*	*P07*	*P08*	*P09*	*P10*	*P11*	*P12*	*P13*	*P14*	*P15*	*P16*	*P17*	*P18*	*P19*	*P20*		
Bovidae																						
Bos taurus	*x*	*x*	-	*x*	-	*x*	*x*	-	*x*	*x*	*x*	-	*x*	*x*	-	*x*	-	*x*	-	-	NA	Exotic
Equidae																						
Equus caballus	-	-	-	-	-	-	-	-	-	*x*	-	-	*x*	*x*	-	-	-	-	-	-	NA	Exotic
Suidae																						
Sus scrofa	*x*	-	-	*x*	*x*	*x*	-	*x*	-	*x*	*x*	-	-	-	-	*x*	-	-	-	-	NA	Exotic
Canidae																						
Canis l. familiaris	*x*	-	-	*x*	-	-	*x*	-	-	-	-	-	-	*x*	*x*	-	-	-	-	-	NA	Exotic
Cerdocyon thous	*x*	*x*	-	-	-	-	*x*	-	-	*x*	-	-	-	*x*	-	-	-	-	*x*	*x*	LC	Non-forest
Speothos venaticus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*x*	-	-	-	-	NT	Forest
Cervidae																						
Mazama sp	-	*x*	*x*	*x*	*x*	*x*	-	-	-	*x*	-	-	*x*	*x*	-	*x*	-	*x*	-	-	NA	Non-forest
Cebidae																						
Sapajus apella	-	*x*				*x*	*x*	-	-	-	-	-	-	-	-	*x*	-	-	-	-	LC	Forest
Cuniculidae																						
Cuniculus paca	*x*	-	-	-	*x*	-	-	-	-	-	-	-	*x*	-	*x*	*x*	*x*	*x*	*x*	*x*	DD	Forest
Chlamyphoridae																						
Euphractus sexcinctus	-	-	-	-	*x*	-	-	-	-	*x*	*x*	-	-	-	-	-	-	-	-	-	LC	Non-forest
Dasyproctidae																						
Dasyprocta azarae	-	-	*x*	*x*	*x*	-	-	-	-	*x*	-	-	*x*	-	-	-	-	-	-	-	DD	Forest
Dasypodidae																						
Cabassous unicinctus	-	-	*x*	-	*x*	-	*x*	*x*	-	-	-	-	-	-	*x*	-	*x*	-	*x*	-	LC	Non-forest
Dasypus novemcinctus	*x*	*x*	*x*	-	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	LC	Forest
Didelphidae																						
Didelphis albiventris	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	LC	Forest
Didelphis aurita	*x*	*x*	-	*x*	-	*x*	-	*x*	-	-	-	-	-	-	*x*	*x*	-	-	*x*	*x*	LC	Forest
Felidae																						
Leopardus guttulus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*x*	-	*x*	-	-	*x*	VU	Forest
Leopardus pardalis	*x*	*x*	-	*x*	-	*x*	*x*	-	*x*	-	-	*x*	-	*x*	-	*x*	*x*	-	*x*	*x*	LC	Forest
Leopardus wiedii	-	*x*	-	-	-	-	-	-	-	-	*x*	*x*	-	-	-	-	*x*	-	*x*	-	NT	Forest
Puma concolor	-	-	*x*	-	-	*x*	-	-	-	-	-	-	-	-	-	*x*	*x*	*x*	-	-	LC	Non-forest
Puma yagouaroundi	-	-	-	*x*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LC	Non-forest
Leporidae																						
Sylvilagus brasiliensis	-	*x*	*x*	-	*x*	*x*	-	-	*x*	*x*	-	-	-	-	-	-	-	*x*	-	-	LC	Forest
Mephitidae																						
Conepatus semistriatus	-	-	-	-	-	-	*x*	-	-	-	-	-	-	-	-	-	-	-	-	-	LC	Non-forest

Species	Landscapes recorded *(Table S3 - continued)*																				
	P01	***P02***	***P03***	***P04***	***P05***	***P06***	***P07***	***P08***	***P09***	***P10***	***P11***	***P12***	***P13***	***P14***	***P15***	***P16***	***P17***	***P18***	***P19***	***P20***	**IUCN**	**Habitat**
Mustelidae																						
Eira barbara	-	*x*	-	*x*	*x*	*x*	*x*	*x*	-	-	*x*	*x*	*x*	*x*	-	*x*	*x*	*x*	*x*	*x*	LC	Forest
Lontra longicaudis	-	-	-	*x*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	NT	Forest
Myrmecophagidae																						
M. tridactyla	*x*	-	-	-	*x*	-	*x*	*x*	*x*	*x*	-	*x*	-	-	-	*x*	*x*	*x*	-	-	VU	Non-forest
Tamandua tetradactyla	*x*	*x*	-	-	*x*	-	*x*	-	*x*	*x*	-	*x*	-	*x*	-	*x*	*x*	-	-	-	LC	Forest
Pitheciidae																						
Callicebus nigrifrons	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*x*	-	-	-	-	-	NT	Forest
Procyonidae																						
Nasua nasua	*x*	*x*	-	*x*	*x*	-	*x*	-	*x*	-	*x*	*x*	*x*	*x*	-	*x*	*x*	*x*	-	-	LC	Forest
Procyon cancrivorus	-	-	-	-	-	*x*	-	-	-	-	*x*	-	*x*	-	-	-	*x*	*x*	-	*x*	LC	Forest
Tapiridae																						
Tapirus terrestris	-	-	*x*	-	*x*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	VU	Forest
Tayassuidae																						
Pecari tajacu	-	-	*x*	*x*	*x*	*x*	-	-	-	-	-	*x*	-	-	-	*x*	-	-	*x*	-	LC	Forest

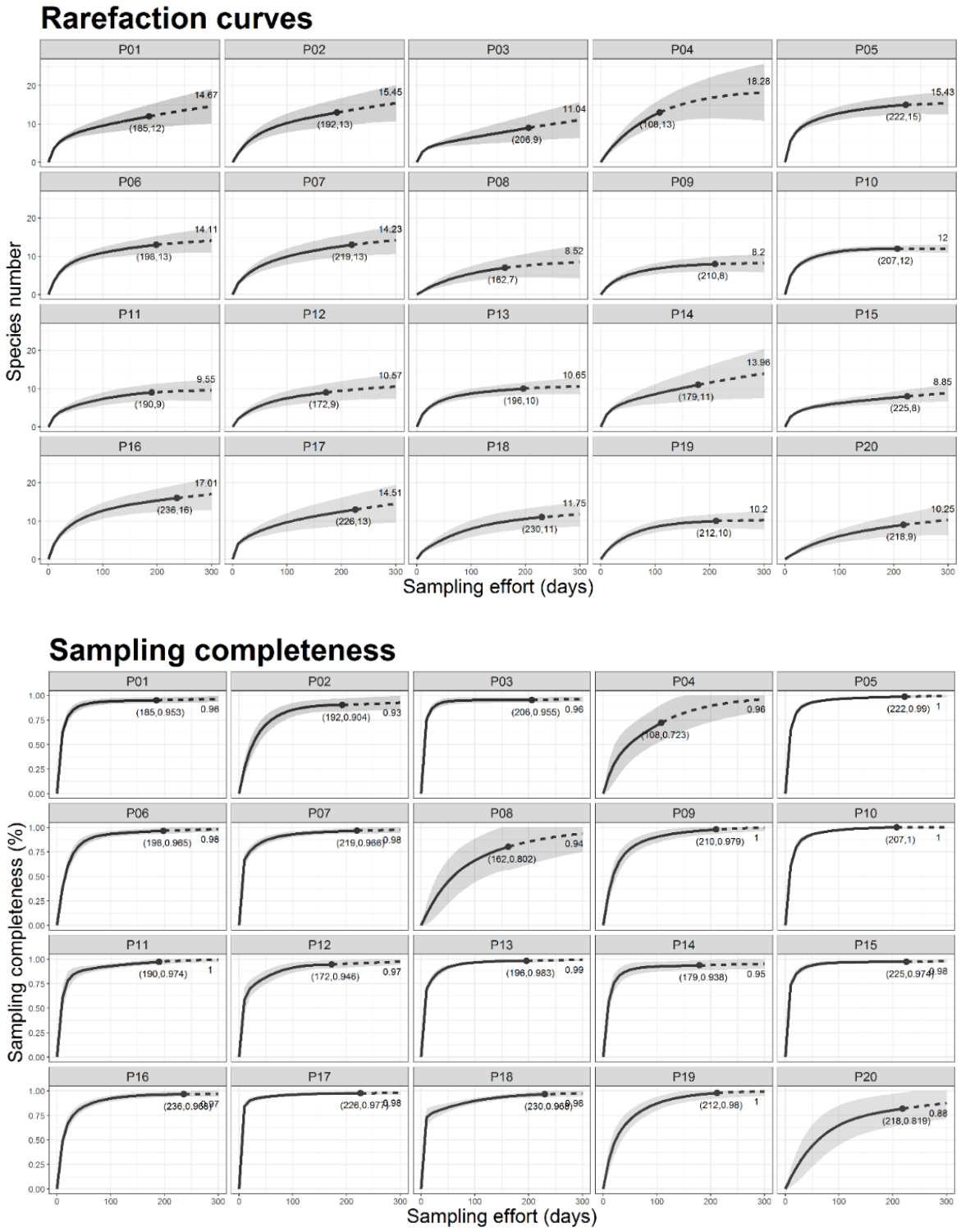


Figure S2. Rarefaction and sampling completeness curves based on the sampling effort (days) and the species number recorded in each of our 20 landscapes (January 2018 to January 2019). Each rarefaction curves includes a sampling extrapolation with the expected richness if continuing the sampling. Completeness curves also shows the extrapolated effort to reach higher confidence intervals (> 95%).

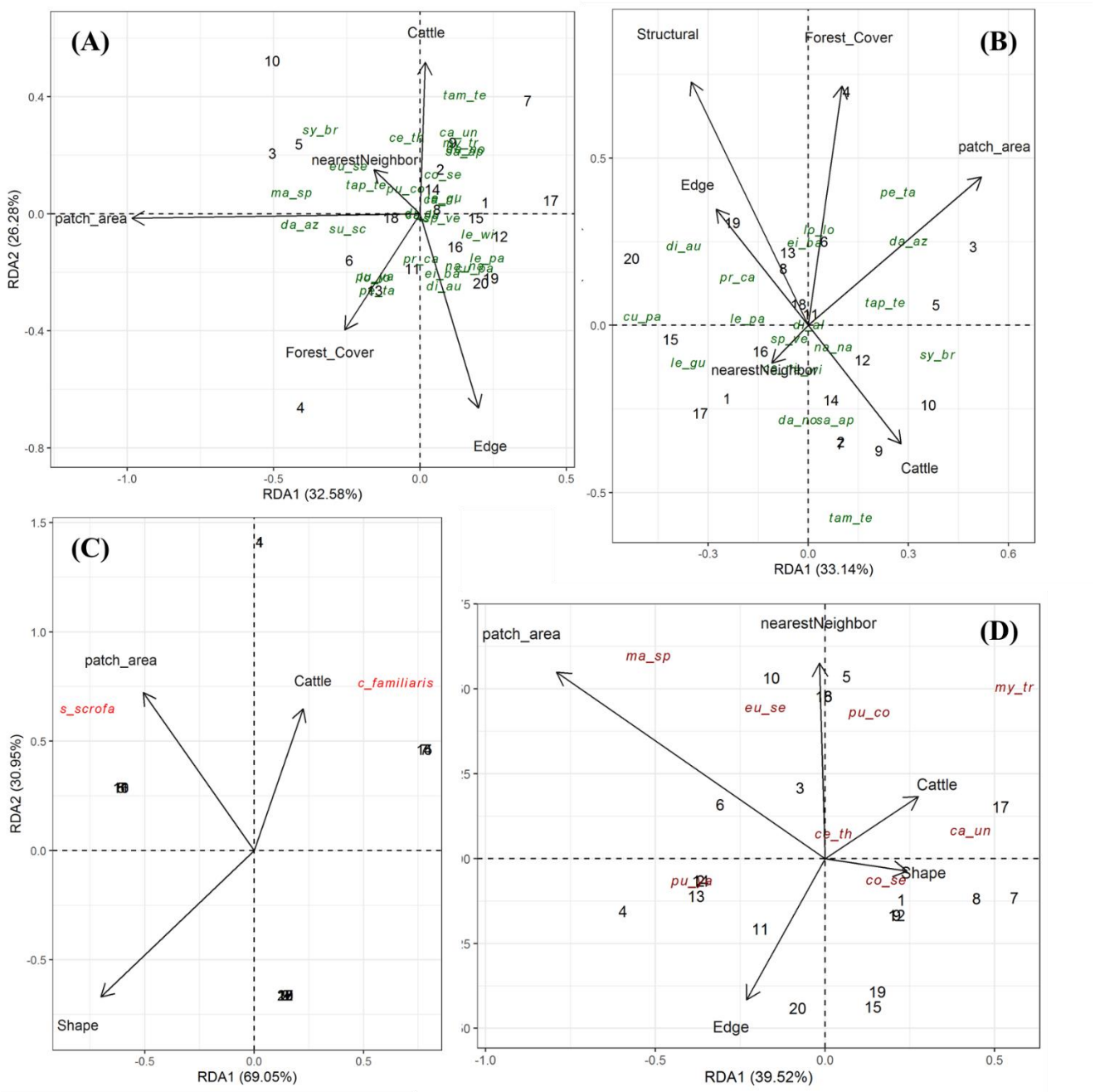


Figure S3. Redundancy analysis of (**A**) total community of medium and large-sized mammals (p-value = 0.44, R2 = 0.26), (B) forest-dwelling species (**p-value = 0.04**, R2 = 0.38), (C) exotic and/or invasive species (p-value = 0.34, R2 = 0.17), and (D) non-forest dwelling species (p-value = 0.20, R2 = 0.30).

Table S4. Best two models of each of the three sets of Single Season, Single Species Occupancy analyses: 1. Forest-dwelling species group and co-variates; 2. Non-forest dwelling species group and co-variates, and 3. Exotic species group and co-variates. We considered the best models as ΔAICc (< 2.0) and Akaike's weights (AICc Weights, > 0.1), according to Burnham and Anderson (2002).

1. *Forest dwelling species*	**AICc**	**ΔAICc**	**AICc Weights**	**Num. Par**	**Deviance**
P (forestcover + cattle), ψ (.)	858.44	0.00	0.40	4	847.77
P (forestcover + pasturecover), ψ (.)	860.63	1.19	0.13	4	849.96
2. *Non-forest dwelling species*	**AICc**	**ΔAICc**	**AICc Weights**	**Num. Par**	**Deviance**
P (forestcover+ cattle), ψ (.)	561.92	0.56	0.20	4	551.26
P (forestcover), ψ (.)	562.09	0.73	0.18	3	554.59
3. *Exotic species*	**AICc**	**ΔAICc**	**AICc Weights**	**Num. Par**	**Deviance**
P (cattle), ψ (.)	340.75	0.00	0.21	3	333.25
P (cattle + pasturecover), ψ (.)	341.26	0.51	0.16	4	330.59