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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE**

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**GABRIELLE CRISTINA BECA**

**INFLUÊNCIA DA PAISAGEM SOBRE A PERSISTÊNCIA  
DE MAMÍFEROS TERRESTRES EM FRAGMENTOS DE  
MATA ATLÂNTICA**



Rio Claro  
Janeiro 2016

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INFLUÊNCIA DA PAISAGEM SOBRE A PERSISTÊNCIA DE  
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*Dedico este trabalho a minha amada família,  
e aos mamíferos de médio e grande porte,  
que tornaram o meu trabalho mais feliz!*

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*Terra!*

*És o mais bonito dos planetas  
Tão te maltratando por dinheiro  
Tu que és a nave nossa irmã...*

*Beto Guedes*



## RESUMO

A crescente demanda por fontes alternativas de energia tem contribuído para o aumento da produção de biocombustíveis, levando a fragmentação dos habitats naturais. No entanto, paisagens naturais imersas em matrizes agrícolas podem reter uma diversidade de espécies considerável, mas os efeitos da mudança no uso do solo para a produção de biocombustíveis sobre a persistência das espécies nessas paisagens ainda permanecem incertos. A Mata Atlântica, ecossistema mais fragmentado do Brasil, tem apenas cerca de 12% de sua cobertura vegetal original. A maioria destes remanescentes estão distribuídos em fragmentos pequenos e isolados devido à expansão agrícola, especialmente pela monocultura de cana-de-açúcar. No presente estudo examinamos a riqueza e a composição de mamíferos de médio e grande porte, e quantificamos a contribuição da cobertura florestal, da área estrutural e da quantidade de borda sobre a persistência desses animais. Amostramos 20 paisagens fragmentadas, em um gradiente de cobertura florestal (3% a 96%), imersas em plantações de cana-de-açúcar. Registramos apenas 50% das espécies esperadas de mamíferos de médio e grande porte em todas as 20 paisagens, em comparação com o maior remanescente de floresta semidecídua, o "Parque Estadual Morro do Diabo". Isso nos mostra que esses remanescentes de Mata Atlântica estão altamente empobrecidos, restando apenas 25% de espécies especialistas florestais, e a maioria dos mamíferos registrados são espécies generalistas, exóticas e típicas de cerrado. A cobertura florestal foi importante para explicar apenas a presença de alguns ungulados e um roedor de médio porte. As comunidades de mamíferos responderam à substituição de espécies entre as paisagens, que representou 94% da  $\beta$ -diversidade total. Nosso estudo é novo em mostrar que a riqueza de mamíferos não foi afetada pela quantidade de habitat. É importante implementar medidas eficazes de conservação das áreas naturais em paisagens agrícolas, a fim de desenvolver medidas de restauração da cobertura florestal dos fragmentos, pois estes são cruciais para manter populações viáveis de espécies que dependem da floresta e ainda persistem nesses ambientes modificados.

**Palavras Chave:** fragmentação florestal, impacto da cana-de-açúcar, substituição de espécie, armadilhas fotográficas.

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# LANDSCAPE INFLUENCE ON THE PERSISTENCE OF TERRESTRIAL MAMMALS IN ATLANTIC FOREST FRAGMENTS

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## Abstract

The growing demand for alternative energy sources has contributed to increased biofuel production, leading to fragmentation of natural habitats. However, natural landscapes immersed in agricultural matrices can retain a considerable diversity of species, but the effects of the change in land use for the production of biofuels on the persistence of the species in these landscapes remain unclear. The Atlantic Forest, the most fragmented ecosystems in Brazil, has only about 12% of its original vegetation cover. The most of these remnants are distributed in small and isolated fragments due to agricultural expansion, especially by the sugarcane monocultures. In the present study we examined the richness and composition of medium and large sized mammals, and quantify the contribution of the forest cover, the structural area and the edge amount over persistence of these animals. We sampled 20 fragmented landscapes on a forest cover gradient (3% to 96%), immersed in sugarcane plantations. We recorded only 50% of expected species of medium and large sized mammals in all the 20 landscapes, compared to the largest remnant of semideciduous forest, the "Morro do Diabo State Park". This shows that the Atlantic Forest remnants are highly depleted, with only 25% of forest-specialist species and most of the mammals registered are generalist species, exotic and typical from savana. Forest cover was important to explain only the presence of some ungulates and a medium sized rodent. The mammal communities responded to a high turnover of species between the landscapes, which represented 94% of the total  $\beta$ -diversity. Our study is novel in showing that mammal richness was not affected by the habitat amount. It is important to implement effective conservation measures in natural areas in agricultural landscapes in order to develop measures of restoration of forest cover of the fragments, because they are crucial to maintain viable populations of forest-dependent species and still persist in these modified environments.

**Key Words:** forest fragmentation, sugarcane impact, species turnover, camera-trapping.

## Introduction

Biofuels are the most land-intensive form of energy production (McDonald *et al.*, 2009). The land conversion to agricultural ecosystems accounts for 80% of global deforestation (Kissinger *et al.*, 2012), and is the major cause of the current rates of global biodiversity loss (Tscharntke *et al.*, 2005; Green *et al.*, 2005), leading to decline of natural habitats and ecosystem functioning, and affecting the provision of ecosystem services (Turner *et al.*, 2007; Steffan-Dewenter & Westphal, 2008). According to International Union for Conservation of Nature (IUCN), 53% of terrestrial species are assessed as threatened due the negative impacts of agriculture intensification. These impacts have already been documented for birds (Donald *et al.*, 2001), mammals (Sotherton, 1998), and insects (Benton *et al.*, 2002), at regional and landscape level.

One of the main agricultural crops in the world is the sugarcane (*Saccharum* spp.), cultivated in over 100 countries. In tropical countries, as Brazil, the production has started in the XVI century mainly for sugar, but after in 1970 it became one of the most valuable biofuels (Melo & Fonseca, 1981; Brandão, 1984). The remnants of native forest are mostly present within private landholdings, embedded in matrices of sugarcane and pasture (Tabarelli *et al.*, 2004; Manzatto, 2005). Such agricultural areas act as a selective filter on the movement of species across the landscape (Gascon *et al.*, 1999; Chiarello, 2000), that influence the displacement from one fragment to another according the capacity of each individual (Laurance, 1999). The amount of edge can also influence the response of native species (Laurance, 1997; Lyra-Jorge *et al.*, 2010), as it may facilitate the entry of domestic dogs and the invasion exotic species in the fragments, resulting in the competition and changes in the structure of communities (Laurenson *et al.*, 1998; Galetti & Sazima, 2006; Gardner *et al.*, 2009).

This prolonged human disturbance transforms many landscapes in Atlantic Forest in experimental sites for understanding the long-term impacts caused by human activities on natural areas. For example, in the Atlantic Forest, there is only 12% of the original vegetation cover, from which 86% of the remnants are fragments smaller than 50 hectares (Ribeiro *et al.*, 2009). These remnants are mostly isolated due to agricultural expansion, influencing the number of species which are able to survive in the fragments (Saunders *et al.*, 1991; Silva *et al.*, 2015). The action of these multiple factors has resulted in high levels of defaunation

(Galetti *et al.*, 2009; Canale *et al.*, 2012; Jorge *et al.*, 2013), especially by the loss of large-bodied mammals, which may lead to serious consequences in the composition of forests and their functional aspects through ecological cascade effects (Galetti & Dirzo, 2013; Dirzo *et al.*, 2014).

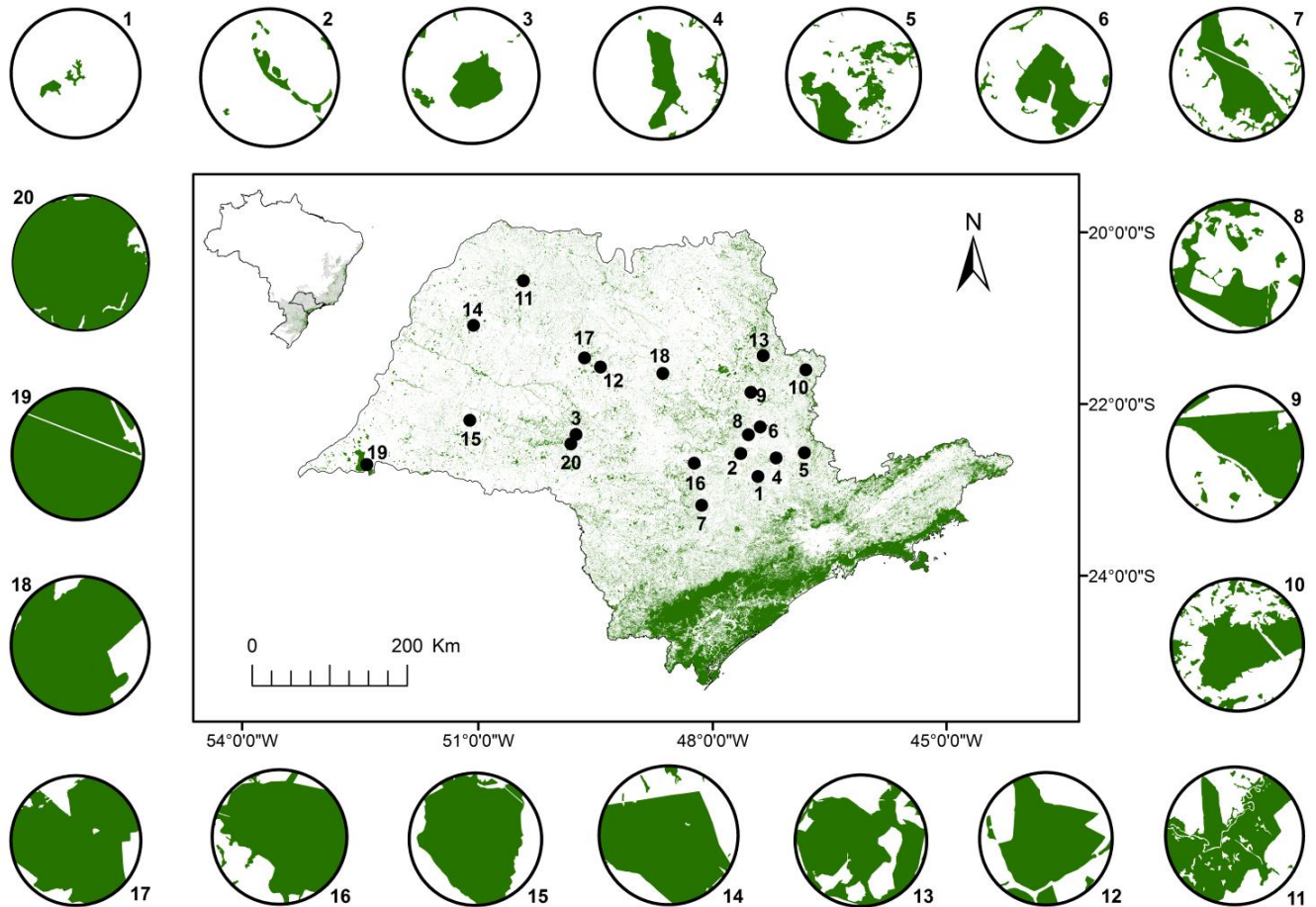
Due the importance of habitat alteration to biodiversity, there is an urgent need for information regarding the potential consequences of increased biofuel production on biodiversity (Robertson *et al.*, 2008). Here we set out to answer: What explains the richness of medium and large sized mammals in fragmented landscapes dominated by sugarcane plantations? Our main objective is to identify how the landscape variables influence the number and composition of species of medium and large sized mammals in these landscapes. Based on the literature, we developed two hypotheses: (1) The habitat amount should be a good predictor for mammal richness, since they are most affected by the habitat loss (Andr n, 1994; Pardini *et al.*, 2010; Fahrig, 2013). Therefore, we expect that the overall mammal richness would increase in response to habitat amount. On the other hand, (2) the edge amount should have a neutral effect for mammal richness, since it can be beneficial for some species or be damaging for others (Kremsater & Bunnell, 1999; Lyra-Jorge *et al.*, 2010).

## **Material and Methods**

### *Study Area*

This study was carried out in 20 landscapes immersed mainly in sugarcane plantations in southeastern Brazil (Figure 1, Supplementary Material, Table S1). The selection of landscapes was conducted using the map of forest remnants of the State of S o Paulo, which was generated using from Landsat 5 satellite images with 30 meter of spatial resolution in the scale 1: 25.000, and corrected using Google Earth images in the Open Layer plug-in by the software QGIS 1.8.0 (QGIS Development Team 2014). Although the mapping presents different vegetation types of the state of S o Paulo, in this study we used only the remnants of semideciduous forest. The selection of landscapes was performed to guarantee a forest cover gradient (from 3 to 96%) within a buffer of 2 km radius around the centroid of each landscape. We chose this spatial extent because the responses of medium and large

vertebrates to landscape variables are better explained in scales of 2 km (Lyra-Jorge *et al.*, 2010). To minimize the spatial autocorrelation between our sampling landscapes, the margins of each landscape buffer zone were located with a minimal distance of 10 km from the margin of another landscape (Fortin & Dale, 2005).



**Figure 1.** Location of landscapes (black dots) in Atlantic Forest remnants, São Paulo, Brazil. Around, in clockwise, the landscapes are shown in ascending order of forest cover. The black circles have 2 km radius around the centroid of each landscape.

### *Mammals Sampling*

We used two sampling techniques, camera trapping and sign surveys, to estimate the species richness of mammals of medium and large sized (species  $\geq 1$  kg, see Srбек-Araujo & Chiarello, 2005; Galetti *et al.*, 2009). These methods were selected because they are able to record species with a wide range of ecological and behavioral characteristics, especially in

their different activity times (diurnal, nocturnal and cathemeral, see Dirzo & Miranda, 1990; Srbek-Araujo & Chiarello, 2005). Surveys using camera traps were carried out between January 2014 to September 2015, using eight camera traps which were installed simultaneously at each landscape per time. From January 2014 to February 2015, we utilized Reconyx (Hyperfire and RapideFire), and from May 2015 to September 2015, Bushnell (Trophy Cam HD Essential). The eight cameras were used monthly (30 days per month) in each landscape, without baits, and with a minimum between-camera distance of 200m and maximum of 1500 m. We performed a mosaic-level sampling with sample points in a single type of patch, the semideciduous forest, trying to sample the maximum of fragments within each landscape and not just one (Bennett *et al.*, 2006). The cameras were installed on tree trunks at 30 cm from the ground, on sites with similar features (for example, local activity of animals, such as natural tracks, avoiding roads, see Srbek-Araujo & Chiarello, 2013). The sampling effort was standardized in 240 traps/day, or 5760 hours in each landscape. The search for sign surveys, as feces, footprints and carcasses, was carried out on the edge of the fragments sampled in the 20 landscapes. We assumed that the detection of all species were the same in all landscapes.

#### *Landscape Variables Calculation*

We use Mantel test (Fortin & Dale, 2005) in order to verify if the species richness between our 20 landscapes were autocorrelated, and our results indicate that there was no spatial autocorrelation ( $R^2 = 0.041$ ;  $p = 0.31$ ). For each landscape, we calculated the forest cover (%), the edge amount (ha) and the structural area (ha). The forest cover and the edge amount were calculated within a buffer of 2 km radius (Supplementary Material, Figure S1). The forest cover (%) was calculated considering all the patches of semideciduous forests present within the buffer of 2 km radius. To calculate the edge amount, we selected 30 meters (one pixel of our raster map) from the edge of all the fragments present in each of 20 landscapes within the buffer of 2 km radius, and then we summed all these values. As we consider that mammals are able to move beyond the buffer of 2 km, particularly when the forest patches extrapolate this buffer limit, the structural area was calculated within a buffer of 10 km radius (see Supplementary Material, Figure S1 for a schema of this calculation). This scale was used to account for the fragments that had been intercepted by the buffer of 2 km

radius. We also conducted a correlation analyses between the landscape variables to check for collinearity, and none of them were correlated (with Pearson's  $r < 0.7$ ; Zuur *et al.*, 2009).

## *Data Analysis*

### *Total Mammal Richness*

We built accumulation curves based on the number of days sampled and the number of species recorded in each landscape, to estimate the richness in all landscapes, and verify the sufficiency of the sampling effort in relation to its shape, seeking to reach the asymptote (Gotelli & Cowell, 2001). The curves were generated using the ‘vegan’ package in R, using the *specaccum* and *specpool* functions (Oksanen *et al.*, 2013). The result was compared with the prediction of the estimator "first-order Jackknife" estimator (Jackknife 1), to estimate the expected richness to the landscapes sampled (Smith & Pontius, 2006). This non-parametric estimator is based on the number of unique species contained in each observation (Smith & Pontius, 2006), and it performs better than other estimators for data sets derived from large numbers of camera days (Tobler *et al.*, 2008). We also selected this estimator for its reduced bias and because it is based on the presence or absence of a species rather than on the abundance of the species (Smith & Pontius, 2006).

### *Partial Mammal Richness*

In order to analyze only the terrestrial and forest specialist species, we excluded the arboreal mammal species (porcupines), exotic species (wild boars), rare species which were recorded in only one landscape (bush dog), aquatic habitat specialists (capybaras, pacas and raccoons, see Emmons & Feer, 1997), and savanna mammals (nine and six-banded armadillos, giant and collared anteaters, pumas, jaguarondis, crab-eating foxes, maned wolves and brown brocket deer), since it was not the purpose of this study to sample areas close to watercourses or non forest animals (Supplementary Material, Table S3). For the classification of savanna species we consider their life history, anatomy, morphology, physiology, feeding habits and behavior (Eisenberg & Redford, 1999; Emmons & Feer, 1997; Galetti *et al.*, in prep).



### *Landscape Effects on Mammal Richness*

We related the total and partial richness, with the explanatory variables (forest cover, structural area and edge amount). We used generalized linear models (GLM) utilizing the Poisson family distribution (counting data; Zuur *et al.*, 2009). We selected best models, including the null model (which represent the absence of effect; Martensen *et al.*, 2012), based on their Akaike's weights (wAICc) and the  $\Delta\text{AICc}$ . We considered that models with  $\Delta\text{AICc} < 2.0$  and  $\text{wAICc} > 0.1$  are equally plausible to explain observed pattern (Burnham & Anderson, 2010).

### *Landscape Effects on Mammal Composition*

We used redundancy analysis (RDA) to evaluate how the landscape variables affect the composition of medium and large sized mammals. This analysis is based on two data matrices: the response matrix (mammal composition) and the predictor matrix that influences the response matrix (landscape variables). We used the 'vegan' package (Oksanen *et al.*, 2013) in R, and the *rda* function (Borcard *et al.*, 2011; Legendre *et al.*, 2012). We related some selected species according to associative results by the RDA, with the explanatory variables (forest cover, structural area and edge amount), also using generalized linear models (GLM), utilizing the Binomial family distribution (presence/absence data; Zuur *et al.*, 2009). Again we selected best models, including the null model (which represent the absence of effect; Martensen *et al.*, 2012), based on their Akaike's weights (wAICc) and the  $\Delta\text{AICc}$ . We considered that models with  $\Delta\text{AICc} < 2.0$  and  $\text{wAICc} > 0.1$  are equally plausible to explain observed pattern (Burnham & Anderson, 2010).

### *Beta Diversity*

We calculated the beta 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 ( $\beta_{\text{sim}}$ ) and the nestedness is represented by nestedness index which quantifies the dissimilarity due to the difference in species richness

between pair-wise ( $\beta_{sne}$ ; see Baselga, 2010). Turnover occurs when species present at one site are absent at another site, but are replaced by other species absent from the first. Nestedness occurs when species present at one site are absent at another, but are not replaced by additional species. Beta diversity was estimated using the ‘betapart’ package in R (Baselga & Orme, 2012). Additionally, we tested if the components of beta diversity of medium and large sized mammals differ from the expected by chance. For this purpose, we created a null model, saving the rarity of the species occurrence. Then, we built confidence intervals with  $\beta_{sim}$  and  $\beta_{sne}$ . Values outside the interval meant that they differed from the expected by chance.

We calculated the dissimilarity of landscape variables among the pairs of sites using Euclidean distances. The distance calculations were conducted using the *vegdist* function of the package in R (Oksanen *et al.*, 2013). We used multiple regressions on distance matrices (MRM; see Lichstein, 2007) to analyze the effect of landscape variables on the components of beta diversity. Beta diversity and its components ( $\beta_{sim}$  and  $\beta_{sne}$ ) were used as the response distance matrix and landscape variables as the explanatory matrices. The MRM is thought to be a more flexible test than the often-used Mantel test as it can cope with linear, nonlinear and nonparametric relationships between matrices. We tested the significance of  $R^2$  values with 100 permutations. Estimates of MRM tests were carried out using the ‘ecodist’ package in R (Goslee & Urban, 2007).

## Results

### *Mammal Richness*

The total sampling effort in the 20 landscapes was 115,200 hours. We recorded 28 medium and large sized mammals from 15 families, including two exotic species, the domestic dog (*Canis lupus familiaris*) and the wild boar (*Sus scrofa*; Supplementary Material, Table S2). The domestic dog was registered in 11 of our 20 landscapes and wild boar in 9. The average number of species recorded by landscape was 12, with a minimum of seven and maximum of 17. The most common species was the nine-banded armadillo, which was registered in all 20 landscapes, followed by raccoon (15 landscapes), and the coati (14). The

bush dog and tree porcupine were the rarest species, both recorded only once each, followed by the white-lipped peccary (Supplementary Material, Table S2). Although the mean accumulation curve that estimated species richness per survey day did not reach an asymptote, the sampling effort was sufficient, according to the first order jackknife (Supplementary Material, Table S3 and Figure S2).

### *Landscape Effects on Mammal Richness*

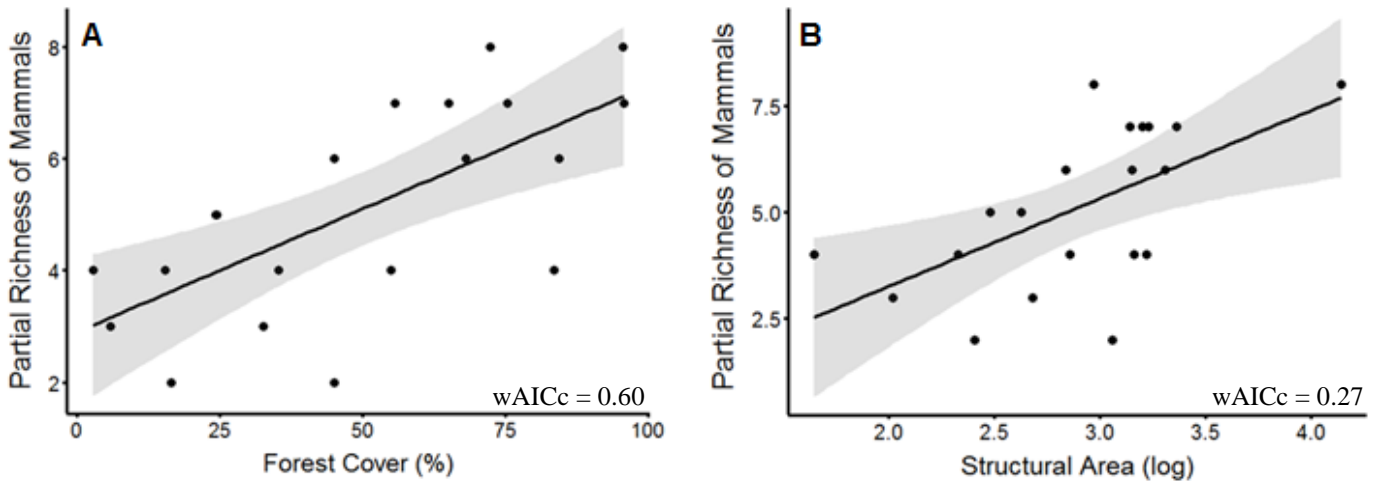
The landscape with 72% of forest cover recorded the highest number of species ( $S = 17$ ), followed by one landscape with 55% of forest cover ( $S = 15$ ). The landscape with the lowest record of species was the landscape with 16% of forest cover ( $S = 7$ ), followed by one landscape with 45% of forest cover ( $S = 7$ , see Supplementary Material, Table S3).

None of the variables explained the total richness of species, since the null model was among the best model to explain the variance in total species richness (Table 1). By other side, the partial richness was better explained by forest cover and structural area ( $wAICc = 0.60$  and  $wAICc = 0.27$ , respectively), and both models were equally plausible to explain the richness of these animals (Table 1, Figure 2).

**Table 1.** Summary of the set of candidate models fitting the total and partial richness of mammals of medium and large sized in response to landscape variables sampled in 20 landscapes of semideciduous forest in São Paulo, Brazil. The  $\Delta AICc$  is Akaike difference,  $df$  is degrees of freedom of the model, and  $wAICc$  is Akaike weight. Plausible models for explain each response variable are in bold.

<b>Response Variable</b>	<b>Model</b>	<b><math>\Delta AICc</math></b>	<b><math>df</math></b>	<b><math>wAICc</math></b>
<b>Total Richness</b>				
	<b>Null</b>	<b>0.0</b>	1	<b>0.44</b>
	<b>Forest Cover</b>	<b>1.4</b>	2	<b>0.22</b>
	<b>Structural Area</b>	<b>1.5</b>	2	<b>0.21</b>
	Edge Amount	2.4	2	0.13
<b>Partial Richness</b>				
	<b>Forest Cover</b>	<b>0.0</b>	2	<b>0.60</b>
	<b>Structural Area</b>	<b>1.6</b>	2	<b>0.27</b>

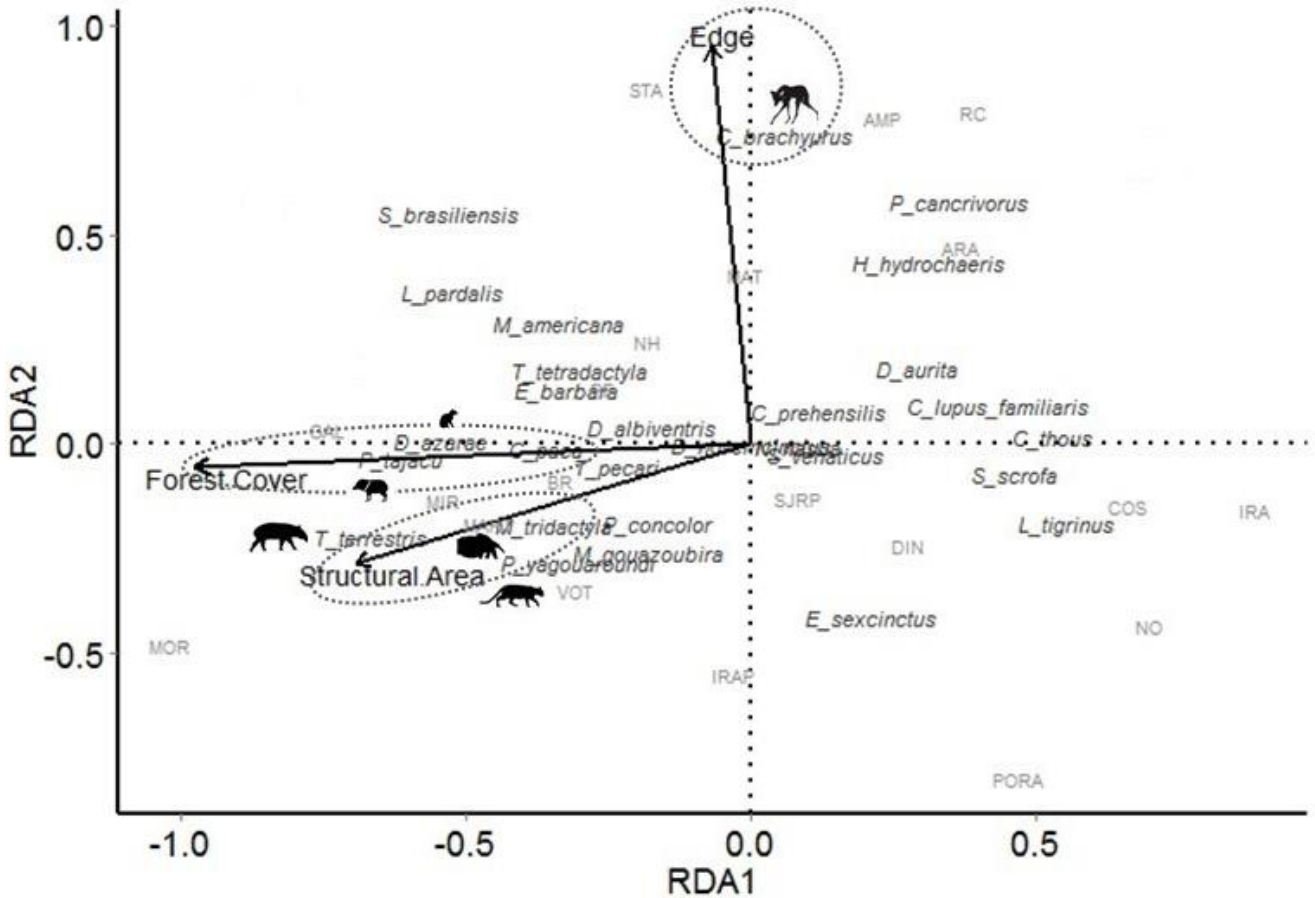
Null	3.9	1	0.08
Edge Amount	5.6	2	0.03



**Figure 2.** Partial richness of medium and large sized mammals in response to (A) forest cover (%) and (B) structural area (ha in log scale) in 20 landscapes of semideciduous forest in São Paulo, Brazil. Confidence intervals are represented by the gray shadow.

#### *Landscape Effects on Mammals Composition*

The RDA showed significant relationship between the composition of mammals of medium and large sized and the landscape variables ( $R^2 = 0.19$ ;  $p = 0.04$ , Figure 3). The first ordination axis (RDA1) explained 68% of the data variation, where the variable that most contributed was the forest cover followed by the structural area. The second ordination axis (RDA2) explained 22% of the data variation, and had a major contribution of the edge amount.



**Figure 3.** Diagram of ordination of the RDA of medium and large sized mammals in relation to the landscape variables in 20 landscapes of semideciduous forest in São Paulo, Brazil. The dotted circles represent the most related species with the landscape variables.

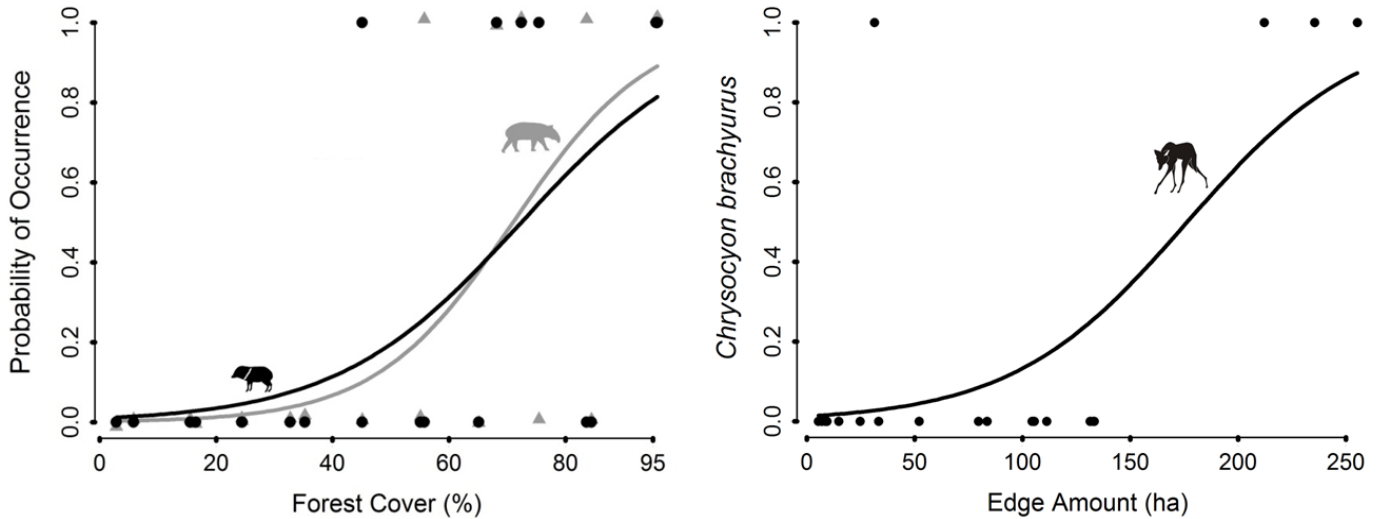
The occurrence of collared peccaries (*Pecari tajacu*) and agoutis (*Dasyprocta azarae*), were positively influenced positively mostly by the forest cover. Tapirs (*Tapirus terrestris*), giant anteaters (*Myrmecophaga tridactyla*) and jaguarundis (*Puma yagouaroundi*) were more associated to structural area. The edge amount had a positive influence on the maned wolf (*Chrysocyon brachyurus*). Based on the result of RDA, we selected those species that were more strongly related with landscape variables, and conducted logistic regressions with them (Table 2, Figure 3).

The occurrence of tapirs (*Tapirus terrestris*), collared peccaries (*Pecari tajacu*) and agoutis (*Dasyprocta azarae*) were best explained by the forest cover (wAICc = 0.82, 0.71 and 0.43, respectively), although the structural area was also important to explain the occurrence of this last species (wAICc = 0.36). None of the variables explained the occurrence of

jaguarundi (*Puma yagouaroundi*) and giant anteater (*Myrmecophaga tridactyla*) since the null model was among the best models. Maned wolf's occurrence (*Chrysocyon brachyurus*) was best explained by edge amount (wAICc = 0.90; Table 2).

**Table 2.** Summary of the set of candidate models fitting the species related to the landscape variables, according the RDA. The  $\Delta$ AICc 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 Variable	Model	$\Delta$ AICc	df	wAICc
<i>Tapirus terrestris</i>				
	<b>Forest Cover</b>	<b>0</b>	2	<b>0.82</b>
	Structural Area	3.4	2	0.15
	Null	8.1	1	0.01
	Edge Amount	10.3	2	0.00
<i>Pecari tajacu</i>				
	<b>Forest Cover</b>	<b>0</b>	2	<b>0.71</b>
	Structural Area	2.3	2	0.22
	Null	5.4	1	0.04
	Edge Amount	7.9	2	0.01
<i>Dasyprocta azarae</i>				
	<b>Forest Cover</b>	<b>0</b>	2	<b>0.43</b>
	<b>Structural Area</b>	<b>0.3</b>	2	<b>0.36</b>
	Null	2.9	1	0.10
	Edge Amount	3	2	0.09
<i>Myrmecophaga tridactyla</i>				
	<b>Structural Area</b>	<b>0</b>	2	<b>0.36</b>
	<b>Null</b>	<b>0.3</b>	1	<b>0.31</b>
	<b>Forest Cover</b>	<b>0.9</b>	2	<b>0.23</b>
	Edge Amount	2.7	2	0.09
<i>Puma yagouaroundi</i>				
	<b>Structural Area</b>	<b>0</b>	2	<b>0.38</b>
	<b>Null</b>	<b>0.3</b>	1	<b>0.32</b>
	<b>Forest Cover</b>	<b>1.4</b>	2	<b>0.19</b>
	Edge Amount	2.4	2	0.11
<i>Chrysocyon brachyurus</i>				
	<b>Edge Amount</b>	<b>0</b>	2	<b>0.90</b>
	Null	5.5	1	0.05
	Forest Cover	7.6	2	0.02



**Figure 3.** Logistic regression plots of mammals occurrence, over forest cover (%) and edge amount (ha) in 20 landscapes of semideciduous forest in São Paulo, Brazil: (A) *Tapirus terrestris* (gray triangles) and *Pecari tajacu* (black circles), and (B) *Chrysocyon brachyurus*.

### Beta Diversity

The variation in beta diversity among the communities of medium and large sized mammals was mainly explained by the turnover of species ( $\beta_{sim}$ , 94%) in our 20 landscapes. A small part was explained by the nestedness ( $\beta_{sne}$ , 6%). All values differed from the expected distribution for the null model (Table 3). Since the landscapes were not spatially correlated ( $R^2 = 0.041$ ;  $p = 0$ ), only the landscape variables were used as explanatory matrices. Both Sørensen dissimilarity index ( $\beta_{sor}$ ) and species turnover ( $\beta_{sim}$ ) were affected by the interaction with the forest cover. Nestedness pattern ( $\beta_{sne}$ ) was not explained by any variable (Table 3).

**Table 3.** Beta diversity partition, showing Sørensen dissimilarity index ( $\beta_{sor}$ ), species turnover ( $\beta_{sim}$ ) and nestedness patterns ( $\beta_{sne}$ ), with the landscape variables that most affected the beta diversity (in bold).

	Confidence Interval	Landscape Variables	Slope	<i>p</i>
<b>β<sub>sor</sub></b>				
0.8411				
		<b>Forest Cover</b>	1.82e <sup>-01</sup>	<b>0.03</b>
		Edge Amount	-1.74e <sup>-04</sup>	0.47
		Structural Area	-5.17e <sup>-06</sup>	0.35
<b>β<sub>sim</sub></b>				
0.7998	0.8029 ± 0.8019			
		<b>Forest Cover</b>	2.06e <sup>-01</sup>	<b>0.01</b>
		Edge Amount	-1.27e <sup>-04</sup>	0.64
		Structural Area	-4.76e <sup>-06</sup>	0.30
<b>β<sub>sne</sub></b>				
0.0413	0.0392 ± 0.038			
		Forest Cover	-2.38e <sup>-04</sup>	0.45
		Edge Amount	-4.74e <sup>-05</sup>	0.80
		Structural Area	- 4.03e <sup>-07</sup>	0.90

## Discussion

Our study region has a long history of agricultural use, and the remaining forests are already heavily fragmented. We recorded only 50% of expected species of medium and large sized mammals in all the 20 landscapes, compared to the largest remnant of semideciduous Atlantic forest which may reach up to 32 of terrestrial species (Morro do Diabo State Park; Cullen, 1997; Cullen *et al.*, 2004; Faria, 2006; Galetti *et al.*, 2009). We also show that the landscapes immersed in sugarcane represent an impoverished part of the original community. We found that the biodiversity of these landscapes has been replaced by species typical of open areas and exotic species, i.e., species that tend to be more tolerant of habitat disturbance, therefore being more capable of colonizing novel agricultural habitats (Swihart *et al.*, 2003).

The total richness of medium and large sized mammals in forest patches immersed in sugarcane plantations had no relationship with the landscape variables that we measured (forest cover, structural area and edge amount). However, we know the difficulties in analyzing the entire mammal community since it was composed of species with different habitat requirements and life histories, which may have covert our analysis, not confirming our initial hypothesis. Thus, the total species respond to fragmentation, but not limited to



spatial configuration like strict habitat specialists, such that the change in total species richness reflect the various responses of all species in the community (Hanski, 2015). When we used a partial richness, removing the arboreal species, exotics, rare, aquatic habitat specialists, and savanna species, leaving only the terrestrial and forest specialists, we encountered a plausible effect of the forest cover and the structural area, than was best explained, corroborating with our initial hypothesis. This means that mainly the terrestrial and forest specialists are affected by habitat fragmentation, since those species depend on the amount of forest to occur (Terborgh, 1992; Keuroghlian *et al.*, 2004; Jorge *et al.*, 2013).

The highest species richness occurred in landscapes with intermediate and high forest cover. This means that what matters for an increased richness is the total forest cover within the landscape, corroborating Fahrig (2013). Some species of ungulates, such the tapir (*Tapirus terrestris*), collared peccary (*Pecari tajacu*) and white-lipped peccary (*Tayassu pecari*), have only been recorded in landscapes over 45% forest cover, indicating that the habitat amount is important for the occurrence of those species, as well as for the agouti (*Dasyprocta azarae*), which occurrence was also explained by the structural area. This relation was already expected because these ungulates have large home ranges and are highly dependent on forested habitats (Fragoso *et al.*, 2003; Keuroghlian *et al.*, 2004). The agouti, although it was related to the habitat amount, it was observed in this study in landscapes with low forest cover, what corroborate with others studies that found agouti in highly anthropogenic disturbed landscape (Santos-Filho & Silva, 2009; Michalski & Peres, 2005). However, as the tapir and the peccaries, it also requires forest areas for obtaining fruits, due its frugivorous diet (Dirzo & Miranda, 1990), and this can explain why it is correlated to increase of habitat amount.

Although the RDA showed a positive relationship between the structural area with the tapir (*Tapirus terrestris*), jaguarundi (*Puma yagouaroundi*) and giant anteater (*Myrmecophaga tridactyla*), this variable was not plausible to explain the occurrence of these animals in the landscapes, as according to our predictions, since the jaguarundi (*Puma yagouaroundi*) and giant anteater (*Myrmecophaga tridactyla*) are generalists regarding to habitat use and more abundant in open areas due to higher resource of prey (Oliveira, 1998; Eisenberg & Redford, 1999; Mourão & Medri, 2007). The edge amount was what best explained the maned wolf (*Chrysocyon brachyurus*). This response agrees with the generalist behavior of the species, as well as the relationship with open areas, since it is a typical

savanna species considered to be a flagship species for this biome (Dietz, 1984). Studies that found the same patterns of use of the landscape for this animal (Lyra-Jorge *et al.*, 2010; Coelho *et al.*, 2008), also showed that it has a low sensitivity to landscape change or disturbance (Devictor *et al.*, 2008), therefore adapted to the edge amount.

We found a high turnover of species ( $\beta$ sim) between landscapes, which represented approximately 94% of the total  $\beta$ -diversity. This indicates that each landscape presented a distinct group of species, although a typical group of species is surviving in these agrosystems, replacing previously unique biological communities, as specialists in diet and habitat (Michalski & Peres, 2005; Lyra-Jorge *et al.*, 2010). The turnover of species was influenced by the forest cover and can be associated with the dispersal ability of these animals (Qian, 2009), especially of generalist species. The landscape-level configuration, such as the connectivity, is also an important factor because they directly influence 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 & Peres, 2007; Lyra-Jorge *et al.*, 2010), since the sugarcane matrix may not be permeable to all mammals. The generalist species, for example, are adept at occupying more than one area (Marvier *et al.*, 2004), which facilitates their presence and movement within the landscapes (Gatti *et al.*, 2006; Lyra-Jorge *et al.*, 2010). This species are more likely to survive in fragmented landscapes (Gascon *et al.*, 1999), and maybe representing the surviving animals after the advance of habitat fragmentation. In addition, savanna species as the maned wolf (*Chrysocyon brachyurus*) and the brown brocket deer (*Mazama gouazoubira*), are expanding their geographical distribution due the fragmentation of the Atlantic forest to conversion of agricultural ecosystems, since they are adapted to open areas and anthropic landscapes, which resembles their habitat type (Coelho *et al.*, 2008; Moreira *et al.*, 2008; Lyra-Jorge *et al.*, 2010; Rodrigues *et al.*, 2014).

The invasion of domestic and exotic species may also alter the composition of the biological community with loss of native species in the invaded areas and change in species composition (McKinney, 2004). Our study indicates that this may be happening, due the occurrence of the domestic dogs (*Canis lupus familiaris*), that interacts negatively with native wildlife at multiple levels (Galetti & Sazima, 2006; Srбек-Araujo & Chiarello, 2008), and the wild boar (*Sus scrofa*), which is occurring where large ungulates are no longer present. The consequence of the absence of these ungulates, as well as the jaguar, the main top predator and critically endangered in Atlantic forest, is the loss of ecological services that those species

perform, such as the control of animal populations, predation and dispersal of seeds, and plowing of the soil (Dirzo & Miranda, 1990; Galetti *et al.*, 2001; Jorge *et al.*, 2013; Terborgh 2013). At the same time, the disappearance of the top predator added to the land use change, can increase the presence of other smaller predators (Crooks & Soulé, 1999; Laurance, 1994; Chiarello, 1999; Dotta & Verdade, 2007) due the increase in their food resources (Gheler-Costa, 2006; Faria *et al.*, 2006), which may cause negative impacts on communities of small mammals and birds (Crooks & Soulé 1999). Thus, it is possible that these landscapes are subject to the effects of trophic cascade (Galetti & Dirzo, 2013; Jorge *et al.*, 2013; Dirzo *et al.*, 2014).

Forest remnants surrounded by sugarcane result in a significant impoverishment of the faunal community, since about 60% of species of medium and large sized mammals are generalists, exotic and from savanna habitats. The same patterns were found in others studies carried out in agricultural landscapes (Dotta & Verdade, 2011; Gheler-Costa *et al.*, 2012), demonstrating that forest loss and fragmentation have a strong influence on mammal communities. Only 25% of species recorded, the terrestrial and forest specialists, responded to the landscape variables. However, this species can also be associated with factors as the extinction debt, i.e., the number of currently species on a landscape, but destined to extinction due the loss and fragmentation of habitat (Tilman *et al.*, 1994). Extinction debts are more likely to happen in landscapes that had an intermediary habitat loss, since in these conditions some sensible species to the fragmentation can still persist for a reasonable period of time, close to their extinction thresholds, i.e., the minimal conditions of habitat amount for the maintenance of their population (Hanski & Ovaskainen, 2002).

It is important to implement effective conservation measures in natural areas in agricultural landscapes (Metzger *et al.*, 2010) in order to develop measures of restoration of forest cover of the fragments, because they are crucial to maintain viable populations of forest-dependent species and still persist in these modified environments (Chiarello, 2000; Dotta & Verdade, 2011; Gheler-Costa *et al.*, 2012). Although most researchers have used species richness to understand the effects of habitat amount on biodiversity loss (Andrén, 1997; Fahrig, 2003, 2013; Pardini *et al.*, 2010), our study is novel in showing that mammal richness was not affected by those variables, probably due to the historical and quality of these landscapes, but also by the biological invasion of exotic species and typical from savanna.

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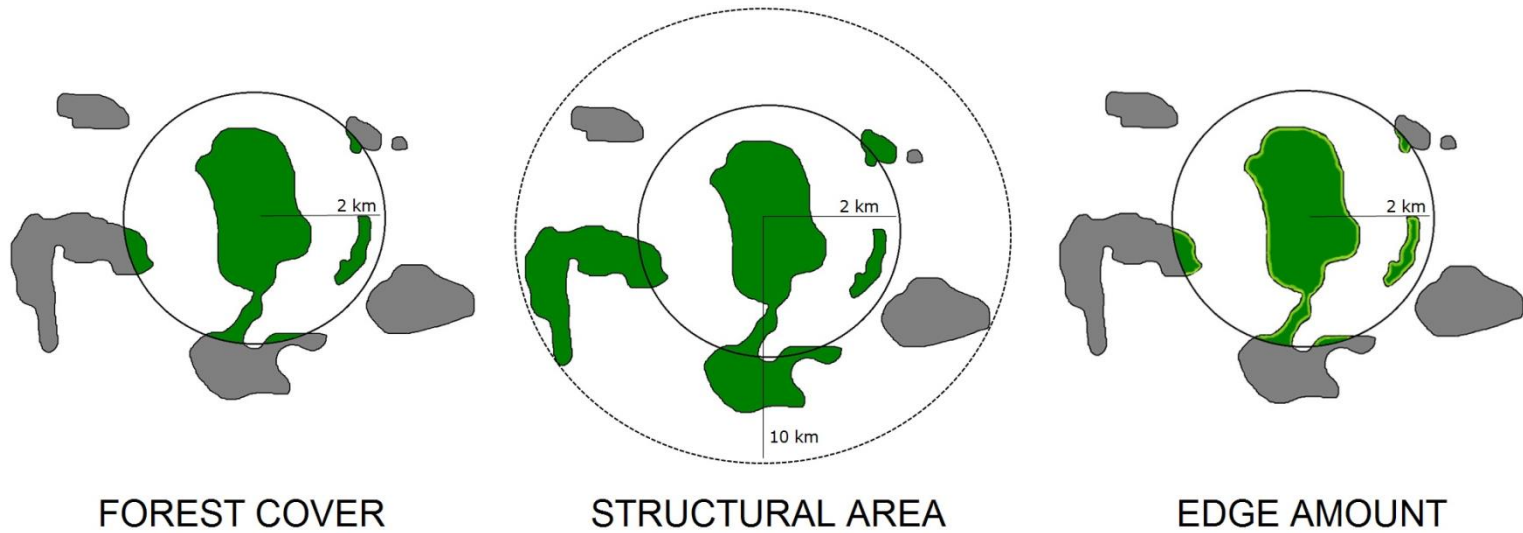


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## Supplementary Material



**Figure S1.** Representation of the calculation of landscape variables: forest cover and edge amount within a buffer of 2 km radius, and structural area, within a buffer of 10 km radius. The light grey in the edge amount represents the edge areas with 30 m.

**Table S1.**Coordinates (in decimal degrees) of the 20 landscapes where the sample of mammals of medium and large sized was performed in São Paulo, Brazil.

<b>Landscapes</b>	<b>Municipal District</b>	<b>Latitude</b>	<b>Longitude</b>
1	Nova Odessa (NO)	-22.834576	-47.366373
2	Iracemópolis (IRA)	-22.560639	-47.578775
3	Garça (DIN)	-22.299408	-49.627931
4	Cosmópolis (COS)	-22.614795	-47.134023
5	Amparo (AMP)	-22.576136	-46.786852
6	Araras (ARA)	-22.262451	-47.323744
7	Porangaba (PORA)	-23.160093	-48.078592
8	Rio Claro (RC)	-22.357462	-47.479082
9	Porto Ferreira (PF)	-21.850911	-47.430593
10	São José do Rio Pardo (SJRP)	-21.593311	-46.740981
11	Magda (VOT)	-20.499863	-50.230862
12	Novo Horizonte (NH)	-21.520642	-49.298784
13	Santa Rosa de Viterbo (STA)	-21.427606	-47.283772
14	Valparaíso (MIR)	-21.006998	-50.848169
15	Rancharia (MART)	-22.074542	-50.941241
16	Anhembi (BR)	-22.661554	-48.153833
17	Irapuã (IRAP)	-21.406376	-49.501172
18	Matão (MAT)	-21.619016	-48.537602
19	Teodoro Sampaio (MOR)	-22.532161	-52.247841
20	Gália (GAL)	-22.403835	-49.695893

**TableS2.** Records of mammals of medium and large sized by sighting (A), camera trap (C), feces (F), claws (G) and footprint (P), in the 20 landscapes of semideciduous forest in São Paulo, Brazil. The last column shows the total occurrence of each species.

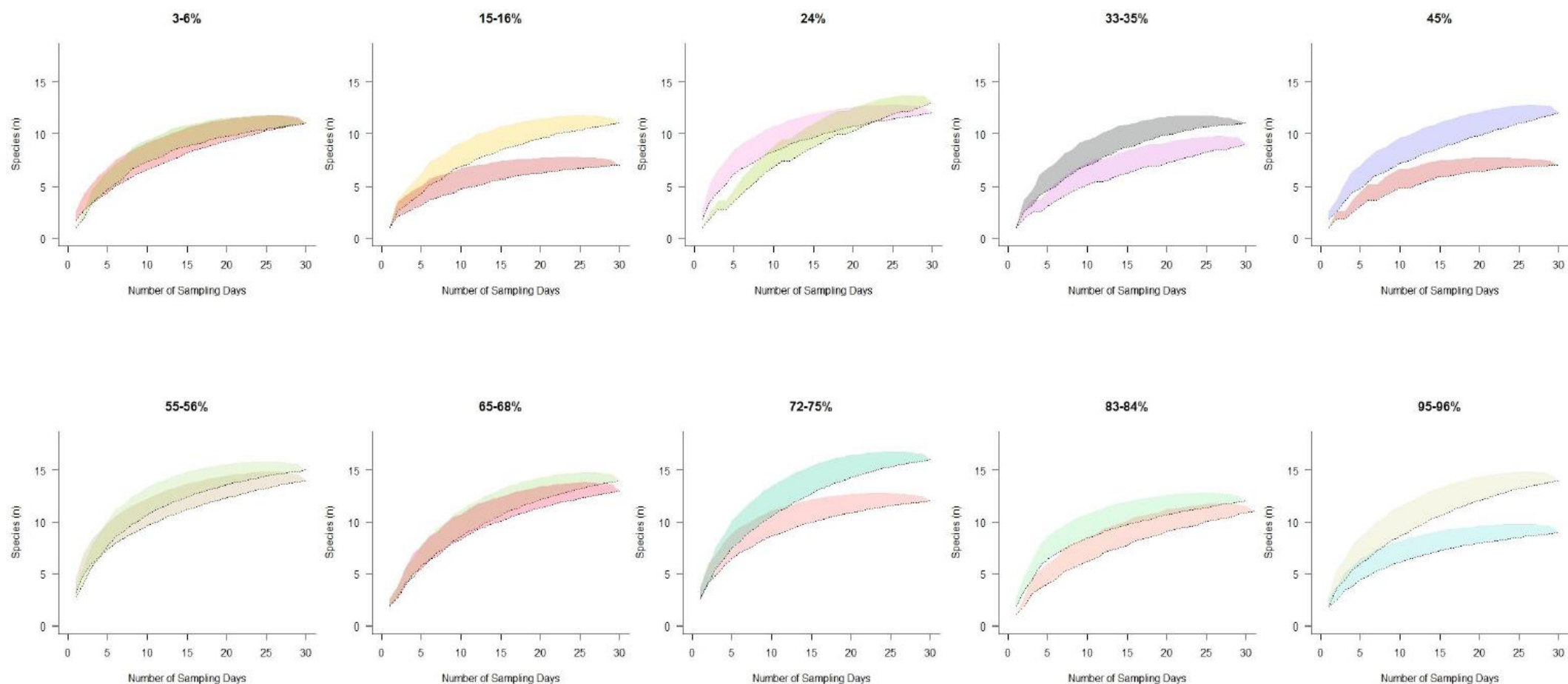
SPECIES	COMMON NAME	3-6%	15-16%	24%	33-35%	45%	55-56%	65-68%	72-75%	83-84%	95-96%	Total
<i>Didelphis albiventris</i>	White-Eared Opossum	-	C	-	-	C, P	C, P	C	C	C	C	11
<i>Didelphis aurita</i>	Big-Eared Opossum	C, P	-	C	C	-	-	C	-	C	-	7
<i>Dasypus novemcinctus</i>	Nine-Banded Armadillo	C, P	C	C, P	C	C	C, P	C, P	C, P	C	C	20
<i>Euphractus sexcinctus</i>	Six-Banded Armadillo	P	C	-	-	-	C	-	-	P	-	4
<i>Myrmecophaga tridactyla</i>	Giant Anteater	-	-	-	C	-	C, P	C, P	C, P	-	C	6
<i>Tamandua tetradactyla</i>	Collared Anteater	-	-	-	-	C	C, P	C	-	C	-	6
<i>Coendou prehensilis</i>	Tree Porcupine	-	C	-	-	-	-	-	-	-	-	1
<i>Hydrochoerus hydrochaeris</i>	Capybara	C, F, P	-	C, F	F	A, C, F, P	C, F, P	F, P	-	-	-	8
<i>Dasyprocta azarae</i>	Agouti	-	C	C	-	C	C	C	A, C	C	A, C, P	12
<i>Cuniculus paca</i>	Paca	-	C	C	-	C	C	-	C, P	-	C	9
<i>Sylvilagus brasiliensis</i>	Forest Rabbit	-	-	C	C	C	C, P	C, P	C, P	C	A, C	12
<i>Leopardus pardalis</i>	Ocelot	-	-	C	P	-	C, P	P	C, P	C	C	10
<i>Leopardus tigrinus</i>	Oncilla	C	C	-	C	C	C	-	-	-	-	6
<i>Puma concolor</i>	Puma	C, P, G	-	P	F, P	C	P	C, P	-	C, P	C	12
<i>Puma yagouaroundi</i>	Jaguarundi	-	-	-	C	C	C	-	C	-	C	7
<i>Canis lupus familiaris</i>	Domestic Dog	P	C, P	C, P	P	C	-	P	P	P	-	11
<i>Cerdocyon thous</i>	Crab-Eating Fox	C, P	C, P	F, P	C, P	-	P	P	P	P	-	13
<i>Chrysocyon brachyurus</i>	Maned Wolf	-	-	P	P	C, P	-	F, P	-	-	-	4
<i>Speothos venaticus</i>	Bush Dog	-	C	-	-	-	-	-	-	-	-	1
<i>Nasua nasua</i>	Coati	C, P	C	C, G	C, P	C	C	C	C	A, C	C	15
<i>Procyon cancrivorus</i>	Racoon	P	C	P	P	P	P	P	P	P	-	14
<i>Eira barbara</i>	Tayra	C	P	C, P	-	C, P	-	C, P	C, P	P	C, P	11

<i>Tapirus terrestris</i>	Tapir	-	-	-	-	-	C, P	C, F, P	C, F, P	A, C, F, P	C, F, P	6
<i>Sus scrofa</i>	Wild Boar	C, P	-	C, F, P	C	-	C, P	-	C, P	C, P	-	9
<i>Tayassu pecari</i>	White-Lipped Peccary	-	-	-	-	-	-	-	C, P	-	C, P	2
<i>Pecari tajacu</i>	Collared Peccary	-	-	-	-	C	-	C, P	C, P	-	C, P	6
<i>Mazama americana</i>	Red Brocket Deer	-	-	-	-	-	C	C	C	-	C	4
<i>Mazama gouazoubira</i>	Brown Brocket Deer	A, C	-	C	C	-	C	C	C	C	C	8

**Table S3.**Total richness, partial richness and richness estimated by first order jackknife estimator for the total richness in each of our 20 landscapes in São Paulo, Brazil, according to the forest cover (%).

Forest Cover (%)	Total Richness	Partial Richness	First Order Jackknife CI $\pm$ 95%
3	11	4	07.19 $\pm$ 22.54
6	11	3	10.61 $\pm$ 17.18
15	11	4	09.63 $\pm$ 18.16
16	7	2	06.25 $\pm$ 11.61
24	12	5	09.15 $\pm$ 20.64
24	13	5	13.44 $\pm$ 26.08
35	11	4	10.07 $\pm$ 13.86
33	9	3	09.59 $\pm$ 18.06
45	12	6	12.15 $\pm$ 21.44
45	7	2	06.07 $\pm$ 09.86
56	14	7	13.67 $\pm$ 21.16
55	15	4	14.07 $\pm$ 21.65
65	14	7	11.19 $\pm$ 21.53
68	13	6	12.19 $\pm$ 21.53
72	17	8	14.63 $\pm$ 23.16
75	12	7	11.25 $\pm$ 16.61
83	11	4	10.79 $\pm$ 20.88
84	12	6	11.61 $\pm$ 18.18
96	9	7	08.61 $\pm$ 15.18
96	14	8	14.07 $\pm$ 21.65





**Figure S2.** Accumulation curves based on the number of days sampled and the number of individuals recorded in each landscape, grouped according to the forest cover (January 2014 to September 2015), including the upper bounds of the 95% CI.