Forest cover influences occurrence of mammalian carnivores within Brazilian Atlantic Forest

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Habitat fragmentation reduces biodiversity and affects ecological processes that are fundamental for maintaining ecosystem services. We investigated how landscape structure—percent forest cover, patch density, percent cover by edge, perimeter-area ratio, and spatial heterogeneity—affects the diversity of mammalian carnivores at multiple extents within 22 Atlantic Forest landscapes. We hypothesized that 1) species richness of carnivores is positively related to forest cover; and 2) the occurrence of species will vary according to its sensitivity to forest loss and its preference for forest or open areas. Species richness, composition, and occurrence of mammalian carnivores were correlated with several landscape structure metrics. Due to a high correlation among the metrics, we adopted forest cover as the principal predictor variable. We compared a forest cover model to a null model using Akaike Information Criterion (AICc), and evaluated other fragmentation metrics using a redundancy analysis. Carnivore species richness was positively related to forest cover and negatively associated with other fragmentation metrics. However, the responses to landscape structure differed among species, possibly due to their differences in habitat use. Landscape configuration is an important factor influencing carnivore species composition. Forest cover can explain some, but not all, carnivore species occurrence. Our results reinforce the protection of forests as fundamental to the conservation of carnivore species and the ecological processes in which they participate.

O processo de fragmentação de habitat reduz a biodiversidade e afeta processos ecológicos fundamentais para a manutenção de serviços ecossistêmicos. Nós investigamos como as métricas de estrutura da paisagem—cobertura florestal, densidade de manchas, cobertura porcentual de borda, relação perímetro-área e heterogeneidade espacial—afetam a diversidade de mamíferos carnívoros em múltiplas extensões em 22 paisagens da Mata Atlântica. Orientamo-nos pelas seguintes hipóteses: a) a riqueza de carnívoros é relacionada positivamente com a cobertura florestal; b) a ocorrência das espécies varia de acordo com a sua sensibilidade à perda de floresta e à preferência por florestas ou áreas abertas. Riqueza, composição e ocorrência de mamíferos carnívoros foram relacionadas com várias métricas da paisagem. Devido à alta correlação entre as métricas, adotamos a quantidade

de floresta como principal variável preditora. Nós comparamos modelos de cobertura florestal com modelos nulos usando o Critério de Informação Akaike corrigido (AICc) e avaliamos outras métricas da estrutura da paisagem usando análise de redundância. A riqueza de espécies de carnívoros está positivamente relacionada à cobertura florestal e negativamente associada à fragmentação. Porém, as respostas à estrutura da paisagem diferiram entre as espécies, possivelmente devido às diferenças quanto ao uso de habitat. Configuração da paisagem é importante para explicar a composição de espécies de carnívoros. A cobertura florestal pode explicar a ocorrência de algumas espécies, mas não todas. Nossos resultados reforçam que a proteção das florestas é fundamental para a conservação das espécies de carnívoros, e os processos ecológicos nos quais participam.

Habitat fragmentation reduces biodiversity and affects ecological processes that are fundamental for maintaining ecosystem services (Haddad et al. 2015). Fragmentation modifies the landscape through the loss and subdivision of habitat, reducing the quantity of available habitat and increasing the isolation of patches, the area under edge effect (Fahrig 2003), and the heterogeneity of the habitat mosaic (Brady et al. 2011). The effects of fragmentation can cause changes in the richness, composition, abundance, distribution, and genetic diversity of species; these changes affect a variety of ecological processes (Fahrig 2003; Valiente-Banuet et al. 2015). An understanding of the degree to which species are sensitive to the effects of habitat fragmentation is necessary to guide strategies for conservation of biodiversity and ecosystem services. Nonetheless, few studies have assessed the relationship between tropical forest fragmentation and the diversity of carnivorous mammals.

For decades, the island biogeography model (MacArthur and Wilson 1967) was adopted to explain population and community patterns in remnants of natural areas in terrestrial ecosystems; the model supports the prescription of conservation actions such as the planning of protected areas (Fahrig 2013). In this context, an exaggerated importance was attributed to patch size and distance from the mainland in predicting the richness patterns, abundance, and occurrence of mammal species (Chiarello 1999; Virgós et al. 2002; Swihart et al. 2003; Michalski and Peres 2005, 2007; Silva-Jr. and Pontes 2008). However, most animals are not isolated in habitat patches; rather, they can move through the mosaic of landscape units and can obtain resources in the matrix (Umetsu et al. 2008; Brady et al. 2011; Magioli et al. 2014). Therefore, the patch should not be used as an independent natural unit of measurement (Fahrig 2013). Analysis of the effects of fragmentation should occur at the landscape level (Fahrig 2003). A landscape can be defined as an area delimited by distances that are biologically relevant to the sampling point (spatial extents), and it encompasses patches of different types and proportions of different habitats (Fahrig 2003, 2013; Jackson and Fahrig 2015).

One of the challenges of landscape-level studies is to determine the best spatial extent to consider in the analysis (Boscolo and Metzger 2009). The spatial extent at which the metrics are measured is fundamental to a correct evaluation of the relationship between species and landscape (Jackson and Fahrig 2015). Although the scale of effect—the spatial extent of analysis at which the relationship is strongest—is theoretically associated with the biological characteristics of a species, there is still little empirical evidence of this (Jackson and Fahrig 2012). To deal with this issue, landscape analysis should be done at multiple spatial extents to define the scale of effect a posteriori (Jackson and Fahrig 2012, 2015; Fahrig 2013).

In addition to assessing the quantity and spatial arrangement of habitat patches at multiple extents of the landscape, studies on the effects of habitat fragmentation need to consider the heterogeneity of altered habitats in the matrix, which generally contains a high proportion of landscapes dominated by human use (Umetsu et al. 2008). For example, Brady et al. (2011) verified that attributes of the matrix are more important than patch and landscape variables for explaining mammal richness in a subtropical area of Queensland, Australia. These authors proposed that, under the evaluated conditions, the primary measure of isolation should be the matrix because it functions as a filter for dispersal, a source of disturbances by feral animals and humans, and a supplementary source of resources.

Responses to fragmentation can vary among species due to differences in their use of habitat, acquisition of resources, niche breadth, and capacity for movement through the landscape (Virgós et al. 2002; Swihart et al. 2003). For example, Lyra-Jorge et al. (2010) observed that the best explanatory models for the frequency of occurrence differed among 3 carnivore species in southeastern Brazil. The authors reported that ocelot (*Leopardus pardalis*) occurrence was explained best by the quantity of Cerrado woodland ("cerradão") formations within a narrow extent (i.e., within a 250-m buffer around the sampling site). Conversely, they found that models of edge length within a wide extent (i.e., within a 2,000-m buffer around the sampling site) best explained mountain lion (*Puma concolor*) and maned wolf (*Chrysocyon brachyurus*) occurrences. Brodie et al. (2015) also ascertained differences in mammalian responses to fragmentation of tropical forests in Borneo. In that area, the clouded leopard (*Neofelis diardi*), the Malay civet (*Viverra tangalunga*), and the leopard cat (*Prionailurus bengalensis*) composed the group most negatively affected by landscape modifications, as they were much more abundant in primary forests, where their responses to edge effect differed. Given that species' responses can differ in relation to the structure and composition of the landscape (Virgós et al. 2002; Lyra-Jorge et al. 2010; Brodie et al. 2015), it is important that studies on the effect of habitat fragmentation include species-specific approaches.

The present study focuses on carnivorous mammals because this group includes species that are generally affected in a negative way by landscape changes, and they are also responsible for essential ecosystem functions (Crooks and Soulé 1999; Roemer et al. 2009; Oliveira et al. 2010; Jorge et al. 2013). Furthermore, carnivores can be monitored by camera traps, which are 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). Methodological advances that reduced the cost of camera traps have led to an increase in the number of studies on carnivore ecology (McCallum 2013). However, there are gaps in the information about the ecology of carnivores in many regions, and these species' responses to modification of the landscape throughout their distributions remain scarcely explored.
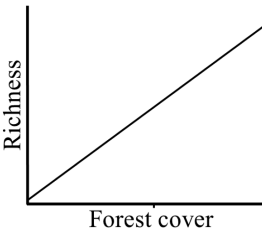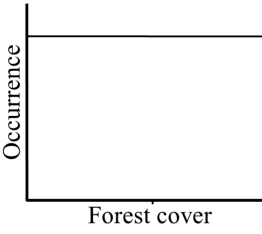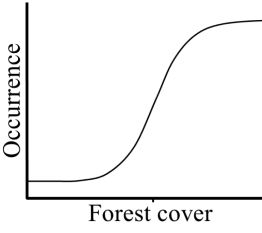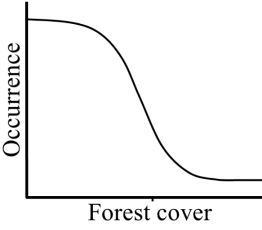
Although the Atlantic Forest is a hotspot for biodiversity conservation (Myers et al. 2000), it has been intensely degraded and currently reduced to 12% of its original vegetation cover, which is generally distributed in small, isolated remnants (< 50 ha) that are commonly not protected by Nature Reserves (Ribeiro et al. 2009).

The main objective of this study was to assess the effects of forest fragmentation on the species richness, composition, and occurrence of carnivores in the Atlantic Forest at multiple extents of landscape analysis. We hypothesized that 1) species richness of carnivores is positively correlated to forest cover and 2) the occurrence of a species will vary according to its sensitivity to forest loss and its preference for forest or open areas. To organize and facilitate the analyses, we categorized the species in our study area into 3 groups according to expected patterns of response to forest fragmentation: 1) habitat generalist species; 2) forest-preferring species; and 3) forest species tolerant of habitat degradation. These expected patterns are based on knowledge available in the scientific literature regarding the natural history of each species, and they are presented in Table 1.

MATERIALS AND METHODS

Study landscapes.—The study took place in 22 landscapes in the states of Santa Catarina and Rio Grande do Sul, southern Brazil (Fig. 1). These landscapes are situated in the Atlantic

Table 1.—Predictions for occurrence and species richness of mammalian carnivores in relation to percent forest cover in 22 landscapes within the southern part of the Brazilian Atlantic Forest.

| Response variables	Reference	Visual representation
Species richness	Chiarello (1999), Silva-Jr. and Pontes (2008)	
Habitat generalist species (group 1) *Cerdocyon thous* (Linnaeus, 1766) *Puma yagouaroundi* (Geoffroy, 1803)	Berta (1982), Michalski et al. (2006), Di Bitetti et al. (2009), Oliveira (1998a), Michalski et al. (2006), Giordano (2015)	
Forest-preferring species (group 2) *Leopardus guttulus* (Hensel, 1872) *Leopardus wiedii* (Schinz, 1821) *Eira barbara* (Linnaeus, 1758) *Leopardus pardalis* (Linnaeus, 1758) *Puma concolor* (Linnaeus, 1771)	Goulart et al. (2009), Oliveira et al. (1998b), Presley (2000), Murray and Gardner (1997), Harveson et al. (2004), Goulart et al. (2009), Mazzolli (1993)	
Forest species tolerant of habitat degradation (group 3) *Galictis cuja* (Molina, 1782) *Nasua nasua* (Linnaeus, 1766) *Procyon cancrivorus* (Cuvier, 1798)	Yensen and Tarifa (2003), Gompper and Decker (1998), Beisiegel and Mantovani (2006), Emmons and Feer (1997), Cáceres et al. (2007)	
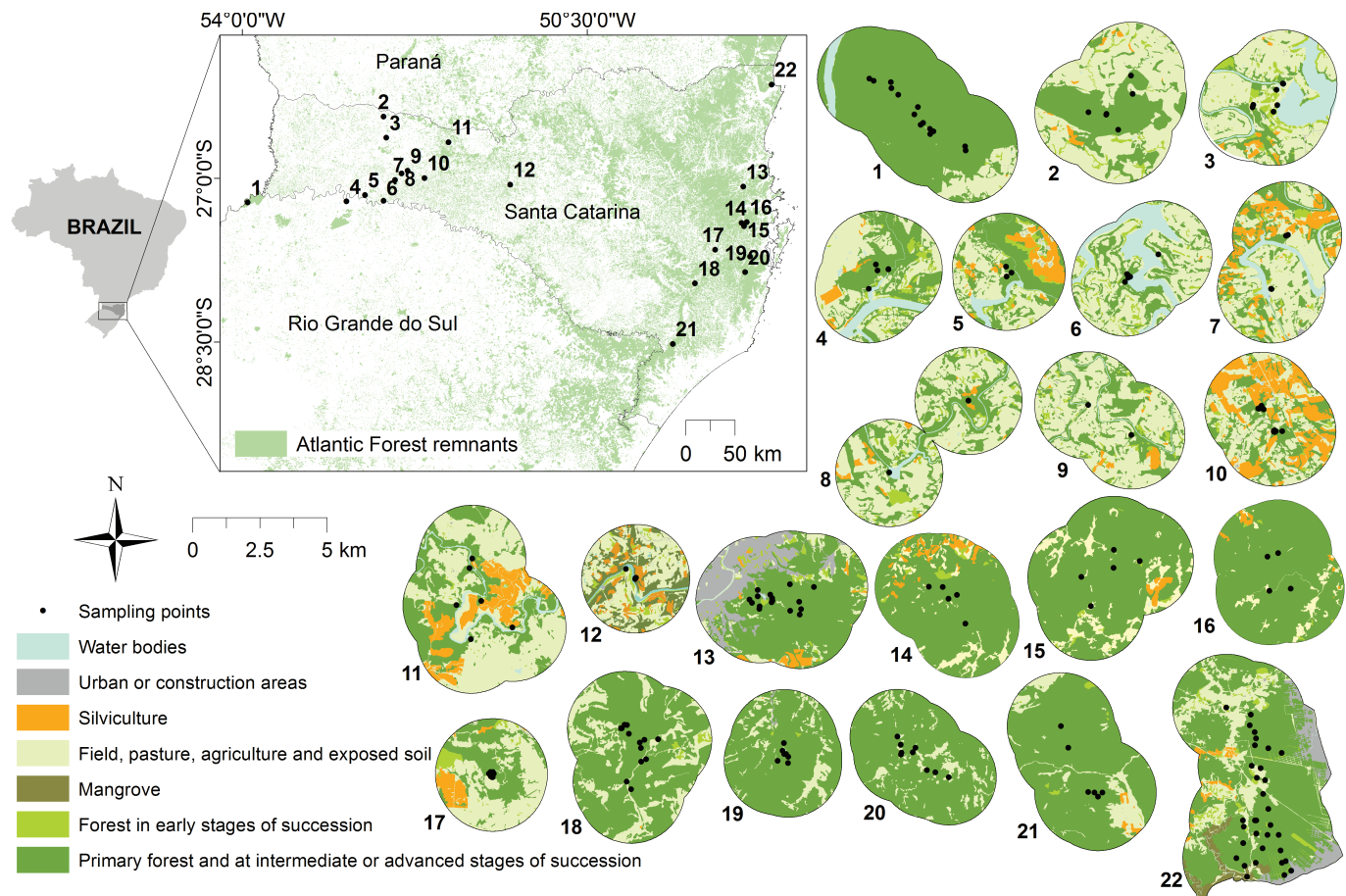
Fig. 1.—Locations of 22 study landscapes within the southern part of the Brazilian Atlantic Forest and maps of the land use and sampling points where carnivore occurrences were recorded. Study landscapes: 1) Turvo State Park; 2) Araucárias State Park; 3) Quebra Queixo Hydropower plant; 4, 5, and 6) Foz do Chapecó Hydropower plant; 7) Arvoredo Small Hydropower; 8) Plano Alto Small Hydropower; 9) Alto Irani Small Hydropower; 10) Ipumirim; 11) Passos Maia Small Hydropower; 12) Salto Góes Small Hydropower; 13) Private Natural Reserve (RPPN) Chácara Edith; 14, 15, and 16) RPPN Caraguatá; 17) RPPN Rio das Furnas; 18) RPPN Leão da Montanha; 19 and 20) Serra do Tabuleiro State Park; 21) Aguaí State Biological Reserve; 22) Itapoá Port.

Forest ecoregion (IBGE 2004) and present different degrees of anthropogenic intervention. Forest cover varies from 19% to 98% among the landscapes. The vegetation type of each landscape is presented in the Supplementary Data SD1. The area of the landscapes varies from 1,256 to 4,074 ha, with multiple collection stations in each landscape. However, we do not consider this as compromising our analyses, because the landscape metrics are not influenced by the landscape extents.

Sampling of the mammals.—Sampling of the mammals in all landscapes was accomplished through remote photography (models: Tigrinus 6.0C, Tigrinus 6.0D, Tigrinus Equipamentos para Pesquisa Ltda., Timbó, Santa Catarina, Brasil; or Bushnell HD, Bushnell Outdoor Products, Kansas City, Kansas). Sampling occurred during different periods between 2005 and 2012. Camera traps were installed within forest fragments, positioned on trails and paths used naturally by carnivorous mammals, and affixed to tree trunks at a height of 30–40 cm to maximize the chance of recording the local fauna. The traps remained operative for 24 h/day and were serviced to download the photos and to perform maintenance when necessary. The sampling effort totaled 10,544 trap-nights, varying between 180

and 910 trap-nights per landscape (Supplementary Data SD2). We verified graphically whether the difference in sampling effort between landscapes affected the results of the species occurrence analyses and observed no pattern in the relationship between species records and sampling effort (Supplementary Data SD3). To evaluate the potential influences of sampling effort on observed richness, we first calculated the regression between them. Second, we evaluated the relationship between the residuals of this regression and percent forest cover for each landscape.

Landscape metrics at multiple spatial extents.—First, we inserted the geographic coordinates of the sample points into a geographic information system (GIS), using the UTM projection, Zone 22S, Datum WGS 84. Next, we generated buffers of different sizes around these points to represent the various extents of analysis. The buffer sizes were 250, 500, 1,000, 1,500, and 2,000 m, which correspond to similar values used in a previous study that also assessed the relationship between the landscape variables and the occurrence of medium- and large-sized carnivores (Lyra-Jorge et al. 2010; Beca et al. 2017).

To calculate the landscape metrics, we interpreted high-resolution images available in the applications "Online World Imagery" in the software ArcGIS 10.2.1 (ESRI 2011) and "Google Earth" in the "Open Layer plug-in" in the software QGIS 1.8.0 (QGIS Development Team 2014). First, we defined a mapping area with 2,000-m buffer size around each sampling sites. Then, we proceeded with a visual interpretation of high-resolution imagery at the visualization scale of 1:2,500. We mapped the vegetation cover, land use, and land occupation according to the following classes: 1) water bodies; 2) urban and developed areas; 3) silviculture (mainly *Pinus* spp. and *Eucalyptus* spp. plantations); 4) field, pasture, agriculture, and exposed soil; 5) mangrove forest; 6) forest in early stage of secondary succession; 7) primary forest and forest at intermediate and advanced stages of secondary succession.

We converted the entry maps into matrix format before calculating the metrics. Landscape metrics were calculated at multiple spatial extents, using the software GRASS 6.4.3 (GRASS Development Team 2014) and some functions in ArcGIS 10.2.1 (ESRI 2011). For each landscape and spatial extent, we calculated the following metrics: forest cover (percentage of the landscape covered by primary forest and forest at intermediate and advanced stages of secondary succession); percent cover by edge (area of edge, in hectares, considering an edge depth of 50 m, divided by the landscape area); patch density (number of patches divided by the area of the landscape); perimeter-area ratio (ratio between the perimeter of the forest edge and the relative area of forest); and the Simpson landscape heterogeneity index.

Data analysis.—First, we checked our data for spatial autocorrelation through the Mantel test (Fortin and Dale 2005). The results (r 0.068; P = 0.17) showed no significant spatial autocorrelation between mammal occurrences and the spatial locations of the centroids of our 22 landscapes. Next, we checked for multicollinearity between predictor variables through the Pearson's correlation test. We found a high correlation ($R > 0.7$) between the 5 extents for all landscape metrics (Supplementary Data SD4–SD8). We then selected for each metric the extent

that best represented a gradient (the extent with the most homogeneous frequency distribution): 500 m for heterogeneity; 1,000 m for forest cover; 2,000 m for the percent cover by edge; 2,000 m for the perimeter-area ratio; and 2,000 m for patch density. We used Pearson's correlation analysis to assess the correlation between these 5 metrics in their respective spatial extents. We found a high correlation among them (Supplementary Data SD9) and selected forest cover as the main measure of forest fragmentation. We based this choice on the fact that 1) the amount of habitat is the main determinant of species richness and occurrence in the landscape (Fahrig 2013), and 2) forest is the main habitat for the 10 carnivore species studied here.

Subsequently, we adopted a redundancy analysis (RDA) to check whether species composition is explained by the landscape variables (Borcard et al. 2011; Legendre and Legendre 2012). Finally, we used generalized linear models (GLMs) to relate carnivore species richness and the occurrence of each species to the percent forest cover in the landscape. For richness and composition, we adopted a normal distribution, and for occurrence, a binomial distribution (Zuur et al. 2009). We used the identity link function for richness and composition, and the logit link function [$\log(p/1 - p)$] for species occurrence. For each response variable (species richness or occurrence of each species), we contrasted the model Y ~ forest cover (%) against the null model (representing absence of effect). Corrected Akaike Information Criterion (AICc) values were used to rank the models, and all models with ∆AIC < 2 were considered as equally plausible (Burnham and Anderson 2002). We reported the AICc weights (w_i) for both the forest cover and null models. We used the software R version 3.1.1 for the analyses (R Development Core Team 2014).

RESULTS

Species richness and forest cover.—The results partially corroborated our predictions (Table 2). We recorded 10 species of terrestrial mammalian carnivores associated with forest formations in the 22 studied Atlantic Forest landscapes.

Table 2.—Comparison between expected responses and responses obtained from the analyses to explain the species richness and carnivore occurrence in 22 landscapes within the southern part of the Brazilian Atlantic Forest.

Response variables	Expected responses	Obtained responses
Species richness	Positive	Positive
Species occurrence		
Habitat generalist species (group 1)		
Cerdocyon thous (Linnaeus, 1766)	Null	Null
Puma yagouaroundi (Geoffroy, 1803)	Null	Null
Forest-preferring species (group 2)		
Leopardus guttulus (Hensel, 1872)	Positive	Null
Leopardus wiedii (Schinz, 1821)	Positive	Null
Eira barbara (Linnaeus, 1758)	Positive	Null
Leopardus pardalis (Linnaeus, 1758)	Positive	Positive
Puma concolor (Linnaeus, 1771)	Positive	Positive
Forest species tolerant of habitat degradation (group 3)		
Galictis cuja (Molina, 1782)	Negative	Negative
Nasua nasua (Linnaeus, 1766)	Negative	Null
Procyon cancrivorus (Cuvier, 1798)	Negative	Null

Table 3.—Eleven pairs of concurrent models compared using corrected Akaike Information Criterion (AICc) to explain the species richness, composition, and occurrence of mammalian carnivores in 22 landscapes within the southern part of the Brazilian Atlantic Forest. Null model relates the species occurrence or species richness to a random value. Forest cover relates the species occurrence or species richness to the relative amount of forest in the landscape. K refers to the number of parameters (including intercept) in a model, plus 1 for the error term. ΔAICc is the difference between the model AICc and the lowest AICc in the model set. wAICc is the Akaike model weight.

| Response variables	Model	K	ΔAICc	wAICc
Richness	Forest cover	3	0.0	0.82
	Null	2	3.1	0.18
Habitat generalist species (group 1)				
Cerdocyon thous (Linnaeus, 1766)	Null	1	0.0	0.72
	Forest cover	2	1.9	0.28
Puma yagouaroundi (Geoffroy, 1803)	Null	1	0.0	0.77
	Forest cover	2	2.4	0.23
Forest-preferring species (group 2)				
Leopardus guttulus (Hensel, 1872)	Null	1	0.0	0.77
	Forest cover	2	2.4	0.23
Leopardus wiedii (Schinz, 1821)	Null	1	0.0	0.59
	Forest cover	2	0.7	0.41
Eira barbara (Linnaeus, 1758)	Forest cover	2	0.0	0.68
	Null	1	1.5	0.32
Leopardus pardalis (Linnaeus, 1758)	Forest cover	2	0.0	1.00
	Null	1	12.9	0.00
Puma concolor (Linnaeus, 1771)	Forest cover	2	0.0	0.80
	Null	1	2.8	0.20
Forest species tolerant of habitat degradation (group 3)				
Galictis cuja (Molina, 1782)	Forest cover	2	0.0	0.90
	Null	1	4.4	0.10
Nasua nasua (Linnaeus, 1766)	Null	1	0.0	0.69
	Forest cover	2	1.6	0.31
Procyon cancrivorus (Cuvier, 1798)	Null	1	0.0	0.76
	Forest cover	2	2.3	0.24
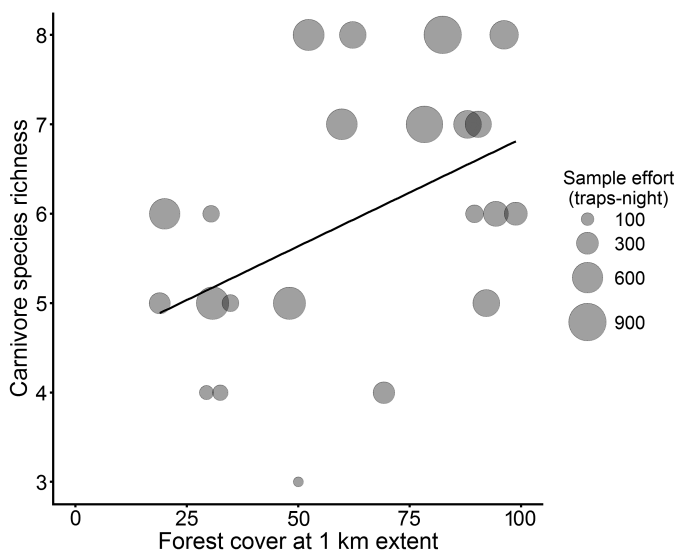
Fig. 2.—Positive relationship between carnivore species richness and a gradient of forest cover (%) at the 1-km extent for 22 landscapes in the southern part of the Brazilian Atlantic Forest.

We did not analyze records for the jaguar (*Panthera onca*) because it was detected only in the Turvo State Park landscape. We confirmed that carnivore species richness was positively related to forest cover in the 22 studied landscapes (Table 3; Fig. 2; w_i = 0.83). The relationship between the observed species richness and sampling effort was low (R = 0.30). The variance in the residuals of this regression related to forest cover was very high (F = 6.64, *d.f.* = 21, P < 0.018), which suggests that even though sampling effort influenced species richness slightly, the variation in species richness was more highly explained by the percent cover by forest. Finally, we verified that there was no relation between species richness and the number of sampling points (t = −0.092, *d.f.* = 21, P = 0.928).

Carnivore species composition and landscape metrics.— The RDA demonstrated a relationship between species composition and the landscape structure metrics (R^2 = 0.34; P < 0.001). The relationships observed in the RDA (Fig. 3) are explained mainly by the RDA 1 axis (39.9%), which represents the percent cover of forest on the landscapes. The RDA 2 axis (28.0%) was mainly correlated with landscape heterogeneity.

The RDA 1 showed a strong influence of highly forested landscapes on *Leopardus pardalis* and *Puma concolor*. *Leopardus wiedii* was slightly associated with forest cover. On the other hand, *Galictis cuja* mainly occupied more degraded landscapes.

The analysis of RDA 2 suggested that *Puma yagouaroundi* tended to occur in more heterogeneous landscapes, whereas *Procyon cancrivorus* and *Leopardus guttulus* were associated with lower landscape heterogeneity; a similar pattern was also observed for *P. concolor*. Finally, *Nasua nasua*, *Eira barbara*, and *Cerdocyon thous* were very weakly related to both axes and were therefore not strongly associated with the landscape variables.
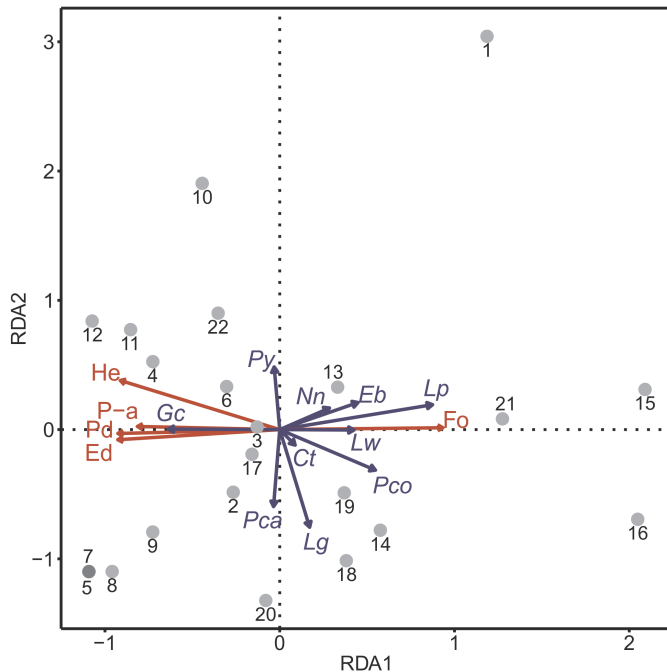
Fig. 3.—Redundancy analysis diagram of carnivore occurrence and landscape metrics. Species legend: *Ct—Cerdocyon thous, Py—Puma yagouaroundi, Pco—Puma concolor, Lg—Leopardus guttulus, Lw—Leopardus wiedii, Lp—Leopardus pardalis, Eb—Eira barbara, Gc—Galictis cuja, Nn—Nasua nasua,* and *Pca—Procyon cancrivorus.* Landscape metrics legend: He—Simpson heterogeneity index, P-a—perimeter-area ratio, Pd—patch density, Ed—percent cover by edge, and Fo—forest cover. The landscape codes are the same as in Fig. 1.

Occurrence of carnivore species and forest cover.—The pattern of occurrence as a function of the percent cover by forest on the landscape differed among the 10 analyzed species, as verified by the GLM. As expected, we found that forest cover did not contribute to the prediction of occurrence for the habitat generalist species (group 1), *C. thous* and *P. yagouaroundi* (Table 3; Fig. 4). Occurrences of forest-preferring species (group 2)—including small felines, *L. guttulus* and *L. wiedii,* and tayra, *E. barbara*—were explained best by forest cover; however, the null model was also plausible (Table 3; Fig. 4), indicating a weak relationship between the occurrence of these species and the percent forest cover on the studied landscapes. On the other hand, the large felines—*L. pardalis* and *P. concolor*—mainly occupied landscapes with a high percentage of forest cover (Table 3; Fig. 4).

Among forest species that are tolerant of habitat degradation (group 3), *G. cuja* occurrence demonstrated a negative relationship with forest cover (Table 3; Fig. 4). Finally, our results suggest that occurrences of Procyonidae—*N. nasua* and *P. cancrivorus*—were unrelated to the forest cover on the landscape (Table 3; Fig. 4), contrary to our prediction.

DISCUSSION

Species richness and forest amount.—We observed a positive influence of the percent cover by forest on the richness of carnivore species in the Atlantic Forest, which reinforces

the "habitat amount hypothesis" proposed by Fahrig (2013). According to Fahrig (2003, 2013), analysis of the effect of fragmentation must occur at the landscape level, avoiding the use of the patch as the natural unit of measure and thus weakening the power of patch size to explain species richness for medium- and large-sized mammals (as seen in Chiarello 1999; Virgós et al. 2002; Swihart et al. 2003; Michalski and Peres 2005, 2007; Silva-Jr. and Pontes 2008). Recent landscape-level studies have revealed the important influence of other landscape elements on the richness of medium- and large-sized mammal species. For example, Lyra-Jorge et al. (2010) showed that species richness is affected mainly by the area of the landscape under the influence of edge effects in a Cerrado region in southeastern Brazil. Brady et al. (2011) revealed the relevance of matrix attributes to explain the richness of mammal species in a subtropical region of Queensland, Australia.

Occurrence of carnivore species and forest cover.—In agreement with our predictions, the occurrences of *C. thous* and *P. yagouaroundi* (group 1, habitat generalist species) were not related to the percent forest cover on the landscape, supporting previous findings that both species are generalists in habitat use (Berta 1982; Oliveira 1998a; Michalski et al. 2006; Di Bitetti et al. 2009; Giordano 2016).

Contrary to our prediction, *L. guttulus* and *L. wiedii* (group 2, forest-preferring species) were not related to percent forest cover. Goulart et al. (2009) suggested that *L. guttulus* is associated with dense forest vegetation. However, this species can also occur in areas of predominantly open vegetation such as restinga (Tortato and Oliveira 2005). For *L. wiedii,* we expected greater dependence on forest cover, given that it is considered essentially, though not exclusively, a forest species (Oliveira 1998b). Ultimately, our results corroborate a study demonstrating that *L. guttulus* and *L. wiedii* forage in agricultural matrices (corn or soybean crops) of Atlantic Forest landscapes (Rinaldi et al. 2015). When examining the diets of these species, the authors found the occurrence of synanthropic prey in 44% of the fecal samples of *L. guttulus* and in 32% of those for *L. wiedii.* These findings by Rinaldi et al. (2015), together with our results, confirm the necessity of investigating the natural history of these small felines, particularly with respect to habitat use.

Contradicting our predictions, *E. barbara* (group 2, forest-preferring species) showed a tolerance of forest fragmentation. Despite the proposal by Presley (2000) that *E. barbara* is rarely found outside of forest environments, Michalski et al. (2006) reported that a tayra monitored by radiotracking did not show a preference for any habitat type available within its home range in southeastern Brazil. This species was also observed in highly disturbed and fragmented forest landscapes of southern and eastern Brazilian Amazonia (Michalski and Peres 2005). The pattern found by the last authors possibly explains the results we found in this study for *E. barbara.*

The occurrence of *L. pardalis* (group 2, forest-preferring species) was limited to landscapes with a high percentage of forest cover, as per our prediction for this species, which mainly occupies densely forested areas (Murray and Gardner
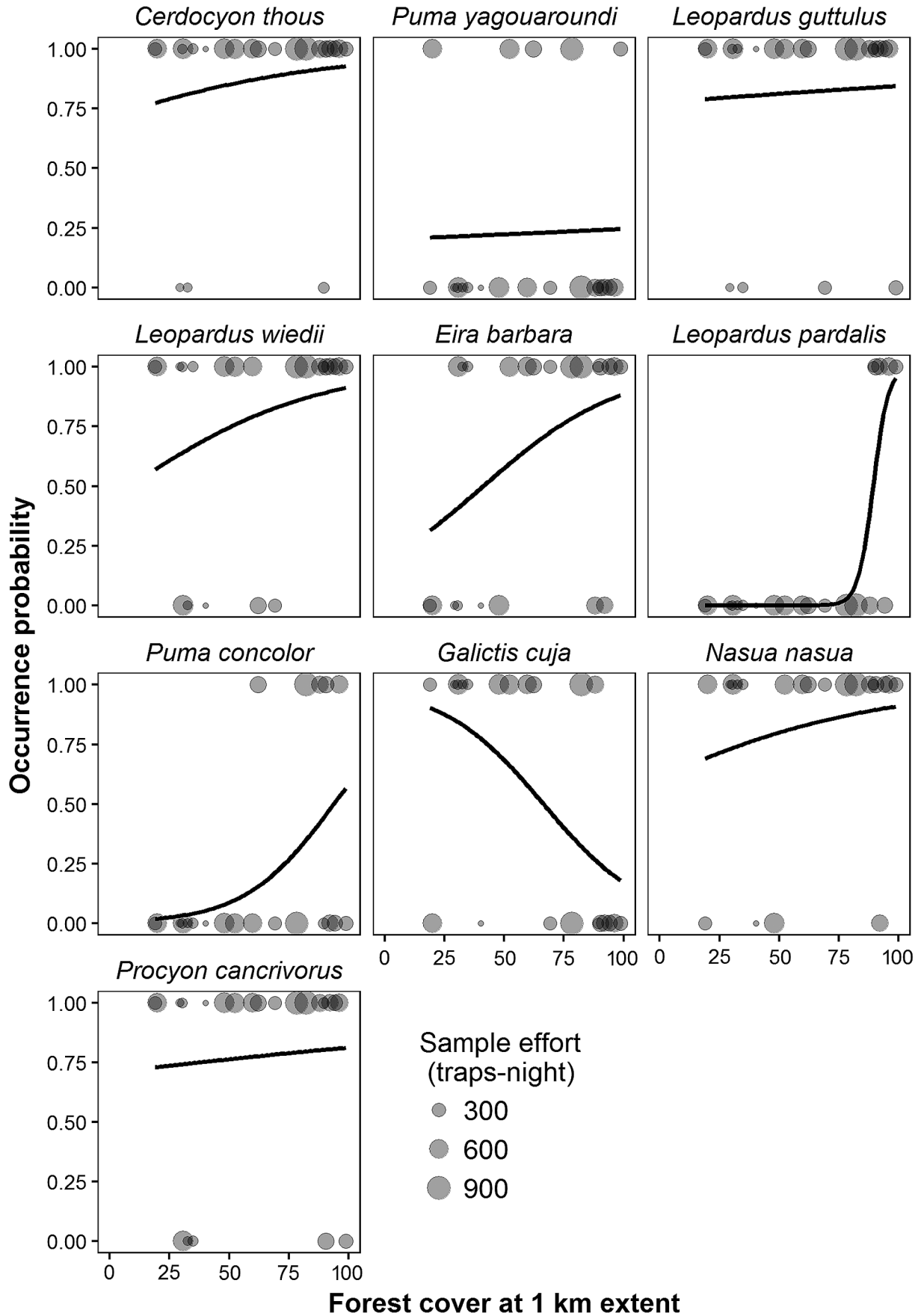
Fig. 4.—Logistic regression plots of occurrences of 10 carnivore species across a gradient of forest cover (%) at the 1-km extent for 22 landscapes in the southern part of the Brazilian Atlantic Forest.

1997; Goulart et al. 2009). Patterns similar to those we identified in the Atlantic Forest were found through radiotelemetry in Texas, where *L. pardalis* almost exclusively selected areas with high forest cover (> 95%—Harveson et al. 2004). Lyra-Jorge et al. (2010) found that the frequency of *L. pardalis* is explained by the amount of "cerradão" woodland in southeastern Brazil. Thus, we verified that *L. pardalis* is highly sensitive to the loss of forest cover in the Atlantic Forest.

Regarding *P. concolor* (group 2, forest-preferring species), despite the indication of low habitat selectivity (Lyra-Jorge et al. 2010; Magioli et al. 2014), we observed that its occurrence was strongly associated with forest cover in the Atlantic Forest landscapes of southern Brazil, as previously determined by Mazzolli (1993). This is possibly due to pressure from illegal pursuit of the species in nonprotected areas (with lower percentage of forest cover) by ranchers who seek to minimize the damages this species causes to livestock production (Mazzolli et al. 2000).

The relationship between the occurrence of *G. cuja* (group 3, forest species tolerant of habitat degradation) forest fragmentation was in agreement with our prediction. As a species that can inhabit open areas (Yensen and Tarifa 2003) and the edges of forest formations, the probability of its occurrence diminishes as a function of the amount of forest on the landscape.

The patterns of occurrence observed for *N. nasua* and *P. cancrivorus* (group 3, forest species tolerant of habitat degradation) contradict our predictions, as no relationship was observed between these species' occurrences and the percent cover of forest. Although *N. nasua* is a species that occupies mainly forested areas (Gompper and Decker 1998) and forages predominantly in the canopy (Beisiegel and Mantovani 2006), it can also obtain resources in cultivated fields and degraded and urbanized areas surrounding forest fragments, which likely explains the pattern that we found. The relationship between the occurrence of *P. cancrivorus* and forest patch density is justified by its selectivity in terms of habitat use—its occurrence is commonly associated with water courses, where it catches prey, and it rarely occupies the deep forest interior (Emmons and Feer 1997). The forest patches where we recorded *P. cancrivorus* are associated with water courses and represent ideal conditions for its occupation.

It is important to mention that the sampled landscapes consisted of more than 19% forest cover. Consequently, for cases where we found an absence of relationship between species occurrence and forest amount (i.e., when the null model was more or equally plausible compared to the model Y ~ forest cover), a minimum limit of 19% forest cover may be above the fragmentation threshold for the analyzed species.

Landscape changes, carnivore species composition, and ecological consequences.—Except for Turvo State Park, all of the study landscapes are possibly subject to the effects of a trophic cascade caused by the absence of the primary apex predator of the Atlantic Forest, the jaguar (*P. onca*), as proposed by Jorge et al. (2013). The condition of absence of an apex predator is aggravated by the fact that *P. concolor* and *L. pardalis*—the second and third largest predators, respectively, in terms of biomass (Paglia et al. 2012)—also are absent from a majority of the studied landscapes. Under these conditions, we can expect an increase in the abundance of herbivores and a consequent increase in the rate of herbivory, which affects plant communities (Roemer et al. 2009). For example, Chiarello (1999) found an elevated abundance of herbivores in landscapes with low forest cover in southeastern Brazil. The negative consequences of the increase in herbivore abundance can be even more grievous in the case of invasive exotic species, the main ones in the region being the wild boar (*Sus scrofa*) and the European hare (*Lepus europaeus*). In addition to herbivory, invasive exotic species can negatively affect native animal species through competition and the transmission of diseases and parasites (Mack et al. 2000).

Furthermore, we determined that 7 species of mesocarnivore (*C. thous*, *P. yagouaroundi*, *L. guttulus*, *L. wiedii*, *E. barbara*, *N. nasua*, and *P. cancrivorus*) occur in landscapes with varying degrees of fragmentation and therefore occupy the majority of landscapes free from the direct or indirect influence of apex predators. Under these conditions, it is expected that mesocarnivores exert a strong influence on the dynamics and structure of their prey communities (Crooks and Soulé 1999; Oliveira et al. 2010), which includes small mammals, birds, and reptiles. The consequences of this influence on these prey may include the local extinction of species and the loss of their ecological functions (Roemer et al. 2009).

Conclusions.—We verified that 1) carnivore species richness is positively related to percent forest cover and negatively associated with fragmentation; 2) landscape configuration is an important factor influencing carnivore species composition; and 3) forest cover can explain some, but not all, carnivore species occurrence. Our results reinforce that the protection of forests is fundamental for the conservation of carnivore species, ecosystems, and the ecological processes in which they participate. We also recognize the importance of complementary actions such as the restoration of degraded areas and live stock management aimed at reducing pursuit in retaliation for livestock predation (e.g., Mazzolli et al. 2000).

Additionally, we suggest that future research should analyze landscapes at larger spatial extents for a better understand of the effect of scale. Furthermore, studies should include landscapes with a very small percentage of forest cover (i.e., < 20%) to explore the widest possible gradient of forest loss. With respect to animal databases, future work should adopt a standardized sample design and analyze data through models that incorporate imperfect detection, e.g., MacKenzie et al. (2002). Finally, more studies on habitat use by carnivorous species are necessary to understand the effects of fragmentation on these species and the ecological processes in which they participate.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Vegetation type, geographic coordinates of centroids, and landscape metrics of the study areas.

Supplementary Data SD2.—Sampling details of mammals in the 22 studied landscapes.

Supplementary Data SD3.—Dotplot of carnivorous species detection, sampling effort, and type of camera-trap models.

Supplementary Data SD4.—Scatter plot matrices of the correlation of Simpson landscape heterogeneity index among 5 spatial extents.

Supplementary Data SD5.—Scatter plot matrices of the correlation of forest cover among 5 spatial extents.

Supplementary Data SD6.—Scatter plot matrices of the correlation of percent cover by edge among 5 spatial extents.

Supplementary Data SD7.—Scatter plot matrices of the correlation of perimeter-area ratio among 5 spatial extents.

Supplementary Data SD8.—Scatter plot matrices of the correlation of patch density among 5 spatial extents.

Supplementary Data SD9.—Scatter plot matrices of the correlation of Simpson landscape heterogeneity index (at 500-m extent), relative forest cover (at 1,000-m extent), percent cover by edge (at 2,000-m extent), perimeter-area ratio (at 2,000-m extent), and patch density (at 2,000-m extent).

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