

# Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil

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Received: 24 January 2009 / Revised: 6 August 2009 / Accepted: 17 September 2009 / Published online: 9 October 2009  
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**Abstract** São Paulo is the most developed state in Brazil and contains few fragments of native ecosystems, generally surrounded by intensive agriculture lands. Despite this, some areas still shelter large native animals. We aimed at understanding how medium and large carnivores use a mosaic landscape of forest/savanna and agroecosystems, and how the species respond to different landscape parameters (percentage of landcover and edge density), in a multi-scale perspective. The response variables were: species richness, carnivore frequency and frequency for the three most recorded species (*Puma concolor*, *Chrysocyon brachyurus* and *Leopardus pardalis*). We compared 11 competing models using Akaike's information criterion (AIC) and assessed model support using weight of AIC. Concurrent models were combinations of landcover types (native vegetation, "cerrado" formations, "cerradão" and eucalypt plantation), landscape feature (percentage of landcover and edge density) and spatial scale. Herein, spatial scale refers to the radius around a sampling point defining a circular landscape. The scales analyzed were 250 (fine), 1,000 (medium) and 2,000 m (coarse). The shape of curves for response variables (linear, exponential and power) was also assessed. Our results indicate that species with high mobility, *P. concolor* and *C. brachyurus*, were best explained by edge density of the native vegetation at a coarse scale (2,000 m). The relationship between *P. concolor* and *C.*

*brachyurus* frequency had a negative power-shaped response to explanatory variables. This general trend was also observed for species richness and carnivore frequency. Species richness and *P. concolor* frequency were also well explained by a second concurrent model: edge density of *cerradão* at the fine (250 m) scale. A different response was recorded for *L. pardalis*, as the frequency was best explained for the amount of *cerradão* at the fine (250 m) scale. The curve of response was linearly positive. The contrasting results (*P. concolor* and *C. brachyurus* vs *L. pardalis*) may be due to the much higher mobility of the two first species, in comparison with the third. Still, *L. pardalis* requires habitat with higher quality when compared with other two species. This study highlights the importance of considering multiple spatial scales when evaluating species responses to different habitats. An important and new finding was the prevalence of edge density over the habitat extension to explain overall carnivore distribution, a key information for planning and management of protected areas.

**Keywords** Brazilian savanna · Mammal distribution · Habitat use · Landscape ecology · Habitat heterogeneity

## Introduction

The threatening of several biological taxa facing the current process of habitat loss and fragmentation of the natural environments is a common reality worldwide. The way and intensity that native fauna use the remaining native habitats, as well as those altered or created by human, are a relevant matter to propose actions for biodiversity conservation.

Habitat loss and fragmentation are two important interacting processes that play negative impact on biodi-

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Communicated by H. Kierdorf

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versity (Fahrig 2003). Habitat cover and configuration must be considered in landscape planning and management for biodiversity conservation, mainly when natural habitats are highly fragmented or degraded (Williams et al. 2002; Lindenmayer et al. 2008). Among landscape configuration parameters, connectivity, which measures the capacity of the landscape, facilitate or impede biological fluxes (Taylor et al. 1993) is a key issue to understand species flow. Several studies have addressed to understand the effect of habitat amount and connectivity on species persistence (Fahrig and Merriam 1994), bird species richness and abundance on fragmented landscapes (Martensen et al. 2008), small mammals diversity (Umetsu and Pardini 2007), genetic diversity of toad populations (Dixo et al. 2008) and multi-taxon (trees, birds, mammals and frogs) time-lagged response to landscape structure dynamic (Metzger et al. 2009). But few efforts have been done to understand how landscape structure influences medium- and large-sized mammal's distribution on heterogeneous landscape.

Habitat use by carnivorous mammals in fragmented landscapes is quite a well-studied issue, as this group of top predator species is responsible for important ecological processes and community regulation (Miller et al. 2001). These species can be used as surrogate on consumer-resource modelling to aid reserve selection design (Rayfield et al. 2009). Most of these studies concentrate on analyzing the effects of remaining natural areas (patch size and/or quality) on carnivore populations or the use of such areas as ecological corridors (Crooks 2002; Tigas et al. 2002; Hilty and Merenlender 2004; Michalski and Peres 2005; Miotto et al. 2007). However, few studies have reported how natural and human-modified landcover/land uses influence these animals at multiple scales.

The most common landscape pattern typically found in Brazil is composed of remnant native vegetation patches immersed in anthropogenic lands (e.g. urban, exurban and agricultural) which comprises the landscape matrix. The anthropogenic matrix usually acts as a filter to species movement among native habitat patches (Boscolo et al. 2008; Hansbauer et al. 2008), thus, the persistence of native populations in fragmented environments greatly depends on the permeability of such matrices (Antongiovanni and Metzger 2005; Castellon and Sieving 2005; Umetsu and Pardini 2007; Boscolo et al. 2008; Uezu et al. 2008). Besides affecting the movement of individuals among habitat patches, the quality of the anthropogenic matrix—according to the vital resources it offers—may also determine the individuals permanence time in the landscape (Aberg et al. 1995; Ricketts 2001; Bender and Fahrig 2005; Berry et al. 2005). For instance, high-resource matrices may perform as habitat for some species, and not only as passageways connecting habitat patches (Smallwood and Fitzhugh 1995; Downes et al. 1997; Vandermeer and

Carvajal 2001; Uezu et al. 2005). As high-quality habitats are expected to be more intensely used than the poor ones (Garshelis 2000), the intensity of habitat use may indirectly indicate its environmental quality. Considering the matrix, its intense use may indicate high permeability and therefore, low contrast in terms of resources with the surrounding habitat.

The spatial scale of the species responses to different land uses and vegetation types is strongly related to some ecological attributes of the community, such as individual's frequency, species richness and local diversity, as well as to dispersal processes, movement patterns, intensities of habitat use and gene flows. The understanding of such relationships is fundamental to understand the ecosystem dynamics (Fortin and Dale 2005; Zurlini and Girardin 2008; Boscolo and Metzger 2009). Multi-scale effects have been explored in aquatic systems (Cassandra et al. 2008), landscape changing patterns (Walz 2008), impact assessment on preserved areas (Zaccarelli et al. 2008), bird incidence in fragmented landscapes (Boscolo and Metzger 2009) and chironomid taxon associations in neotropical streams (Roque et al. (in press)), however has hardly been addressed relative to medium and large mammals distribution (but see Comiskey et al. 2002).

In this study, we examined the use of native habitats and cultivated eucalypt forest by the carnivorous species. We conducted a multiple-model comparison in order to identify relationships between the landscape structure (amount and edge density of different landcover category) and species distribution. A multiple-scale approach was applied to identify the response scales of carnivorous mammals in a region that at the same time includes one of the largest protected areas in São Paulo State (Southeastern of Brazil) and a highly fragmented and anthropogenic agricultural matrix. Some of these carnivorous species are locally threatened to extinction (Lyra-Jorge et al. 2008). These information would be useful for planning and management actions. More specifically, we pursued the following three objectives: (1) to understand the relationship between response variables (species richness, carnivore frequency and frequency of *Puma concolor*, *Chrysocyon brachyurus* and *Leopardus pardalis*) and the landscape structure and (2) to assess the effect of different scales (fine=250 m, medium=1,000 m and coarse=2,000 m) on fauna response patterns.

## Materials and methods

### Study area

This study was conducted in an area of about 47,265 ha, in the Northeast of São Paulo State, Brazil (Santa Rita do Passa-Quatro and Luiz Antônio municipalities: 21°31'15"S–

47°34'42"W; 21°44'24"S–47°52'01"W), limited to the East by the Anhangüera highway, and to the South by the Mogi-Guaçu River (Fig. 1).

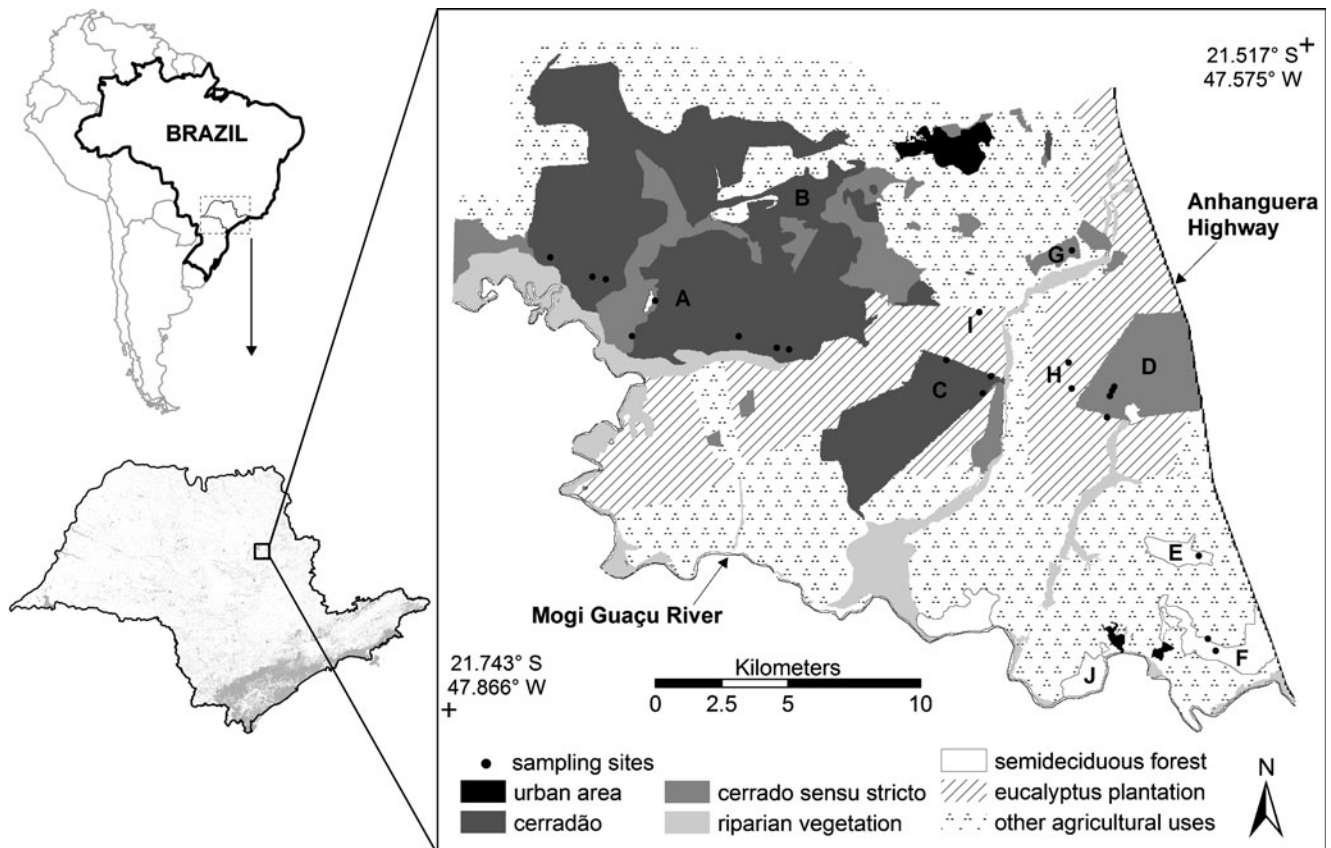
Native vegetation in the region was formerly composed of a natural mosaic of semideciduous forest (interior Atlantic Forest) and savanna physiognomies (i.e. Cerrado; Shida 2005). Among savanna physiognomies, most of the region was dominated by the *cerradão*, a sclerophyllous woodland, and the *cerrado, sensu stricto*, a typical savanna (*sensu*; Coutinho 1978; Oliveira and Marquis 2002). However, due to intense land exploitation, the region has lost most of its original landcover to intensive monospecific plantations, especially of eucalypt, sugarcane and citrus (Brannstrom 2001; Shida 2005; Durigan et al. 2007). The region is located at the boundary of Interior Atlantic Forest and Cerrado regions.

According to Ribeiro et al. (2009), only 7.1% of the original forest cover remains on interior forest, with 86% of patches smaller than 50 ha. Almost half of the remaining forest is <100 m from its edges and only 0.48% of original cover of the interior forest are protected as preserves (see Ribeiro et al. 2009 and supplementary material therein).

Two discontinuous reserves exist in the study area which shelter native vegetation fragments: (1) Jataí Ecological

Station, with two fragments predominantly covered by *cerradão* (Fig. 1, A and C) and one by regenerating *cerrado sensu stricto* (Fig. 1, B) and (2) Vassununga State Park, with one fragment covered by *cerrado sensu stricto* (Fig. 1, D) and four fragments of semideciduous forest (three of them shown in Fig. 1, E, F and J).

A landcover/land use map was derived from Landsat5-TM satellite image (dated February 22th, 2005, spatial resolution of 30 m). The image was georeferenced using the Brazilian Institute of Geography and Statistics (IBGE) topographic maps, scale 1:50,000 (IBGE 1973). We adopted the UTM coordinates system, Córrego Alegre datum, 10 m of nominal precision, and used the spectral bands TM3, TM4 and TM5. The landscape classification procedure followed five steps: (1) image segmentation; (2) non-supervised classification (ISOSEG method); (3) identification of the vegetation types; (4) map editing and (5) field validation. The map-editing step was based on both the author's knowledge of the area and on aerial photographs available on cartographical scale 1:30,000, year 2001. Steps (2) to (4) were performed using the SPRING GIS software (INPE 2005). Table 1 presents the percentage of cover of the original classes, as well as the reclassification of cover classes (hereafter referred to as cover category) used in this study. The reclassification



**Fig. 1** Study area, location and land use/landcover classes. Dots represent the sampling sites; A, B and C represent Jataí Ecological Station patches; D, E, F and J represent Vassununga State Park patches; G represents private area with “cerrado” vegetation; H and I represent eucalypt plantation

**Table 1** Cover classes derived from Landsat 5/TM image (year 2005) for the Santa Rita do Passa-Quatro and Luiz Antônio municipalities, Northeast of São Paulo State, Brazil

Original cover class	Area (hectares)	%	Cover categories
Cerradão <sup>a</sup>	9,058	19.2%	Native vegetation, Cerrado formations and Cerradão
Cerrado sensu stricto <sup>a</sup>	3,902	8.3%	Native vegetation, Cerrado formations
Eucalypt plantation	13,842	29.3%	Eucalypt plantation
Other agricultural uses	15,673	34.2%	Matrix (not analyzed)
Riparian vegetation	1,409	2.9%	Native vegetation
Semideciduous forest	1,979	4.2%	Native vegetation
Urban buildings	968	2.0%	Matrix (not analyzed)
Total	47,265	100%	

<sup>a</sup> Some original cover classes participated on more than one cover category and was included on more than one concurrent model

was performed to generate a new landcover map suitable for the objectives of this study. Some cover categories take part in more than one concurrent model, as *cerradão* which was included on models that consider native vegetation, *cerrado* formations and *cerradão* per se.

#### Mammal's survey and species description

We recorded occurrence of carnivore species on 21 points distributed in eight fragments of native vegetation (three of *cerradão*, three of *cerrado sensu stricto* and two of semideciduous forest) and two stands of homogenous *Eucalyptus* spp. plantation (Fig. 1).

To estimate habitat use intensity by carnivores, the number of species records (hereafter as frequency) was registered by camera traps during 18 months (August 2004 to January 2006), totalling 12,960 hours of exposure for all sampling points. We randomly selected the sampling sites considering the following pre-requisites: (1) placed along pre-existing trails or dirt roads, (2) with previously recorded mammals footprints on the ground and (3) protected from direct sunshine (as the cameras would set off if exposed to intense heat). Nine cameras were placed in *cerradão* patches, six in *cerrado sensu stricto* patches, two in semideciduous forest patches and four in eucalypt plantations (Fig. 1). The cameras were triggered by animal heat and/or movement and remained activated in the field through the whole sampling period; once a month they were checked to replace films and batteries.

We chose the three most abundant species (see below) as target species, as they are on the top of the food web and must be fundamental to maintain tropic chains (Miller et al. 2001; Crooks 2002). Still, these species are included on São Paulo State's red list (São Paulo State Decree n.53,494 of October 2nd, 2008).

#### Selected species

*Puma concolor* (PUMA, i.e. Cougar): is the second largest feline within the Americas, and the largest species in the

study region. It may occur in all Brazilian biomes (Oliveira and Cassaro 1999). This species has a large home range and a very high ability to move around (hundreds of kilometres), especially when dispersing. According to feeding behaviour, it is a generalist, consuming the most available food items (Moreno et al. 2006).

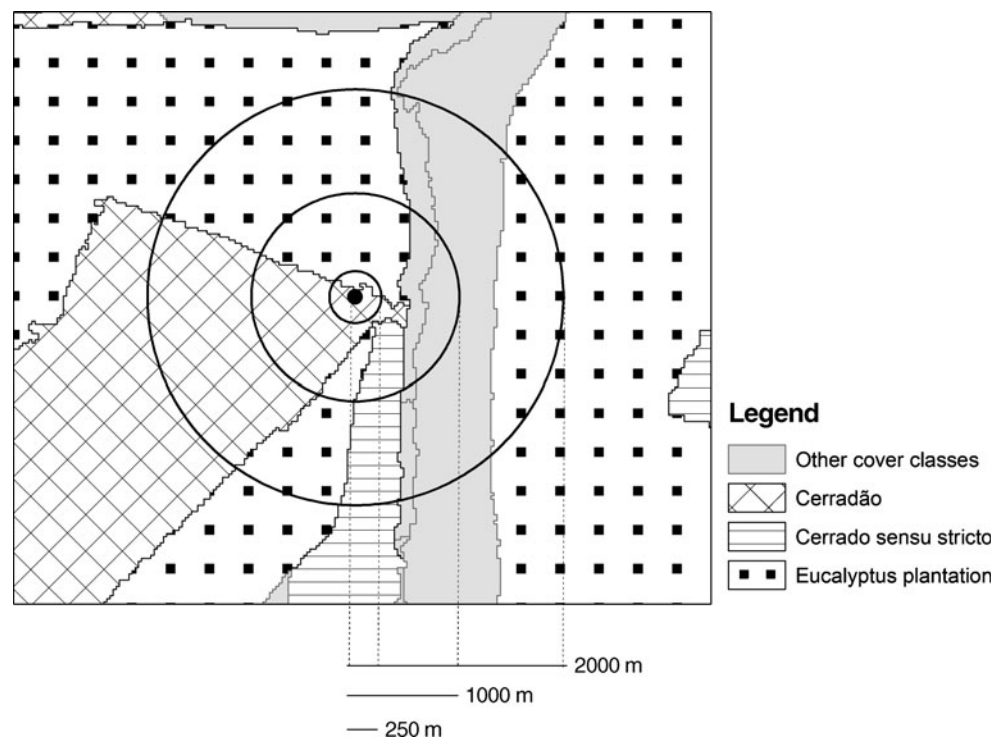
*Chrysocyon brachyurus* (CHRY, i.e. Manned wolf) is the largest South American canid. The individuals are solitary most of the year except when mating. This is a generalist species in terms of both food consumption and habitat usage. Similar to *P. concolor*, *C. brachyurus* also has large home range and is a highly vagile species (Dietz 1984).

*Leopardus pardalis* (LEOP, i.e. Ocelot) is a medium-sized feline common in the interior (e.g. deciduous and semi deciduous) forests which feeds mainly on small mammals and marsupials (Moreno et al. 2006). This species is very sensitive to habitat loss (Biatti et al. 2006) and generally avoids open areas.

#### Multi-scaled landscape metrics

In the land use/landcover map, we calculated the percentage and the edge density of four native vegetation cover categories within virtual landscapes of four sizes defined by different radii around the sampling points (see below). The analyzed cover categories were: (1) native vegetation (semideciduous forest, *cerrado sensu stricto* and *cerradão*), (2) *cerrado* forms (*cerrado sensu stricto* and *cerradão*), (3) *cerradão* and (4) eucalypt plantations. To analyze the multi-scaled effect of landscape pattern (Fortin and Dale 2005; Wagner and Fortin 2005; McAlpine et al. 2006) on response variables (species richness, carnivore frequency and frequency for the three most recorded species), we defined circular virtual landscapes around the sampling points, with varying radii (i.e. scales): 250, 500, 1,000 and 2,000 m around the sampling points (Fig. 2). The same approach was used by Boscolo and Metzger (2009) when analyzing effects of the multi-scaled landscape metrics on bird's incidence in four fragmented Atlantic Forest landscapes.

**Fig. 2** Example of virtually analyzed landscape maps for concentric scales varying from 250 to 2,000 m. Following Zuur et al. (2009)



We believe that our radius sizes are sufficient to account for the relative contribution of fine, medium and coarse landscape structures on large mammal's distribution. We did not test scales with larger radii to avoid confounding spatial auto-correlation as larger radii increased the overlapping between sampling regions (Fortin and Dale 2005, 2009). Mantel tests showed no significant spatial correlation between the sampling points distance and species richness, carnivore frequency and frequency for PUMA, CHRYS and LEOP ( $r$  varying from  $-0.09$  to  $0.12$ ;  $p > 0.05$ ). All landscape metrics were calculated using moving windows function available at GRASS GIS 6.4 (Neteler and Mitasova 2008).

#### Data analysis

Statistical analyses were performed using R language 2.9.1 (R Development Core Team 2008). Model fitting were done using `glm` and `mle2` functions available on the “base” and “bbmle” (Bolker 2008) packages, respectively. We analyzed five response variables: species richness (RICH), total frequency (TOTFREQ) and the frequency of *P. concolor* (PUMA), *C. brachyurus* (CHRYS) and *L. pardalis* (LEOP). We conducted an exploratory data analysis to select only those explanatory variables with relatively low correlation (Pearson's  $r < 0.7$ ; Zuur et al. 2009). As we had multi-models to explain the response variables, we conducted a model selection procedure based on the maximum likelihood, considering the Akaike's

information criterion corrected for small number of observations (AICc; Burnham and Anderson 2002). Under this approach, the lower the AICc, the better the model fits the data. We also calculated the difference between AICc for a model  $i$  and the lowest observed AICc (i.e.  $\Delta AICc$ ). According to Burnham and Anderson (2002), models with  $\Delta AICc < 2$  are equally plausible to explain the observed pattern as the best model. We also calculated the Akaike's information criterion weight ( $wAICc$ ), which expresses the relative contribution of the model  $i$  to explain the observed pattern. We used the concurrent model approach, and only the results for equally plausible best models ( $\Delta AICc < 2$ ) are shown (Burnham and Anderson 2002).

Since the relationship between response and explanatory variables is not always linear, we tested three curve shapes: linear, exponential (semi-log) and power ( $\sim \log\text{-log}$ ) (see Arrhenius 1921; Lomolino 2000, 2001 and Drakare et al. 2006 for details). Power models uses formula  $Y \sim a * X^b + \epsilon$ , while linear models follow the formula  $Y \sim a + X * b + \epsilon$ , where  $Y$  is the response variable,  $X$  is the explanatory variable,  $a$  and  $b$  are estimated model parameters, and  $\epsilon$  represents the error distribution. We transformed response and explanatory variables to  $X = X + 1$  to avoid log of zeros problems (Zuur et al. 2009). Response variables were best fitted by different curve shapes.

Eleven concurrent models were compared to explain our response variables. The list of competing models, grouped by type of landscape metric, landcover categories and scale (virtual landscape size in metres) is shown in Table 2.

**Table 2** Eleven concurrent models analyzed to explain the distributions of mammals on a landscape located at Northeast of São Paulo State, Brazil

250, 1,000 and 2,000 are the analyzed scales (in metres)

On model abbreviation, *PL* percentage of landscape cover, *ED* edge density, *CD* Cerradão, *NAT* native vegetation, *EP* eucalypt plantation, *CER* cerrado formations

Model number	Model abbreviation	Landscape metric	Scale	Cover category
M01	PL0250CD	Percentage cover	250	Cerradão
M02	PL0250NAT	Percentage cover	250	Native vegetation
M03	PL2000NAT	Percentage cover	2,000	Native vegetation
M04	ED0250CD	Edge density	250	Cerradão
M05	ED0250EP	Edge density	250	Eucalypt plantation
M06	ED0250NAT	Edge density	250	Native vegetation
M07	ED1000NAT	Edge density	1,000	Native vegetation
M08	ED2000CER	Edge density	2,000	Cerrado formations
M09	ED2000CD	Edge density	2,000	Cerradão
M10	ED2000EP	Edge density	2,000	Eucalypt plantation
M11	ED2000NAT	Edge density	2,000	Native vegetation

## Results

### Landcover and species frequencies

We defined seven original cover classes in the study area (Fig. 1; Table 1). The region presently has 34.6% of native vegetation, prevailing the *cerradão* (19.2%), and followed by *cerrado sensu stricto* (8.3%). The matrix is composed mainly of *Eucalyptus* plantations (29.3%), but other agricultural uses (orange plantation, sugar cane and pasture) accounts for 34.2%. Nine carnivorous mammal species belonging to four different families were recorded in *cerradão*, *cerrado sensu stricto*, semideciduous forest and eucalypt plantation (Table 3).

### Curve shape

Except for LEOP which related linearly to the explanatory variables, all other response variables (RICH, TOTFREQ, PUMA and CHRYS) were best fitted with power-shaped curves. Figure 3a–e shows the best models for each response variable ( $\Delta AICc=0$ ) and for the best curve shape only.

### Habitat cover vs edge density

Three out of 11 concurrent models were selected as best models to explain our response variables (Table 4). Edge density on coarse scale was present on four out of five analyzed variables (exception for LEOP), with  $wAICc$  varying from 0.32 (for RICH) to 0.82 (for CHRYS). Edge density of *cerradão* at fine scale was selected to explain RICH ( $wAICc=0.13$ ) and PUMA ( $wAICc=0.16$ ). Despite the edge density of *cerradão* at fine scale having  $\Delta AICc < 2$ , its  $wAICc$  was smaller than  $wAICc$  of the model representing native vegetation edge density at coarse scale. All response variables that included edge density as plausible explanatory variable showed non-linear negative response independently of the scale (see negative beta parameter "b" on Table 4). LEOP was the only variable which was best explained by the percentage of cover of *cerradão*, and the relationship between this variable and the explanatory variable was linearly positive (Table 4, Fig. 3e).

The two best explained response variables were CHRYS (sum of  $wAICc=0.82$ ) and TOTFREQ (sum of  $wAICc=0.73$ ), and the worst explained variable was RICH (sum of  $wAICc=0.45$ ; Fig. 3a).

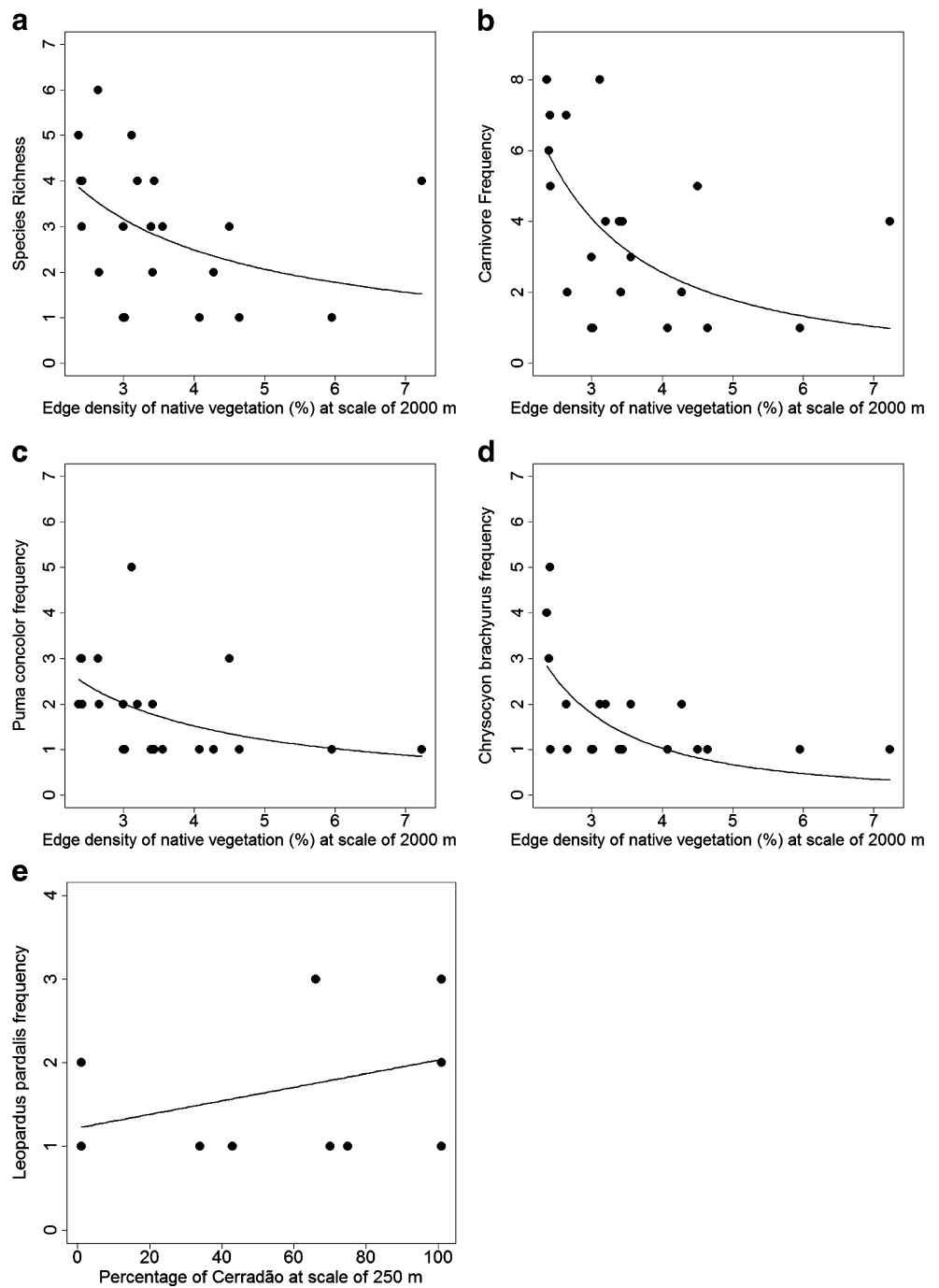
**Table 3** Carnivorous mammal species recorded at Northeast region of São Paulo State

*CD* *cerradão* or sclerophyllous forest, *SS* *cerrado sensu stricto* or typical savanna, *SF* semideciduous forest, *EP* eucalyptus plantation

<sup>a</sup> Species that were analyzed as response variable

Species	Family	Land use/landcover class				Total records
		CD	SS	SF	EP	
<i>Puma concolor</i> <sup>a</sup>	Felidae	7	2	1	8	18
<i>Leopardus pardalis</i> <sup>a</sup>	Felidae	9	2	0	2	13
<i>Puma yagouaroundi</i>	Felidae	0	0	0	1	1
<i>Leopardus tigrinus</i>	Felidae	0	1	0	0	1
<i>Chrysocyon brachyurus</i> <sup>a</sup>	Canidae	7	1	0	6	14
<i>Cerdocyon thous</i>	Canidae	2	0	0	0	2
<i>Eira Barbara</i>	Mustelidae	1	1	0	2	4
<i>Conepatus semistriatus</i>	Mephitidae	3	1	0	0	4
<i>Nasua nasua</i>	Procyonidae	1	1	0	0	2

**Fig. 3** Best fitted models ( $\Delta AIC_c=0$ ) for species richness (**a** RICH); carnivore frequency (**b** TOTFREQ); frequency of *Puma concolor* (**c** PUMA); frequency of *Chrysocyon brachyurus* (**d** CHRYS) and frequency of *Leopardus pardalis* (**e** LEOP)



Multiple scale perspective

Two response variables (RICH and PUMA) were well explained for more than one model, and for those models, we summed the wAICc. We consider this sum of wAICc as the total support to explain a variable of interest. On both cases, the variables were best explained by multiple scales, and the edge density of native vegetation at coarse scale (2,000 m) showed

the highest relative contribution, although edge density of *cerradão* at fine scale (<250 m) also appears among the most relevant models. Other three response variables (TOTFREQ, CHRYS and LEOP) were best explained by single but varying scales, where LEOP responded to the percentage of remaining *cerradão* at fine scale, and TOTFREQ and CHRYS responded mainly to the edge density of native vegetation at coarse scale (2,000 m).

**Table 4** Best set of models to explain the mammal's distribution on a heterogeneous landscape at the Northeast region of São Paulo state

Dependent variable	Curve shape	Selected models	<i>a</i>	<i>b</i>	$\Delta AICc$	wAICc	sum(wAICc)
RICH	Power	$a*ED2000NAT^{b+\epsilon}$	7.93	-0.84	0	0.32	
		$a*ED0250CD^{b+\epsilon}$	3.19	-0.17	1.81	0.13	0.45
TOTFREQ	Power	$a*ED2000NAT^{b+\epsilon}$	24.08	-1.61	0	0.73	0.73
PUMA	Power	$a*ED2000NAT^{b+\epsilon}$	5.91	-0.98	0	0.41	
		$a*ED0250CD^{b+\epsilon}$	2.06	-0.25	1.87	0.16	0.57
CHRY5	Power	$a*ED2000NAT^{b+\epsilon}$	14.78	-1.92	0	0.82	0.82
LEOP	Linear	$a+PL0250CD*b+\epsilon$	1.22	0.01	0	0.58	0.58

Refer to Table 2 to model abbreviations and see text for response variable details. Models with  $\Delta AICc < 2$  are equally plausible to explain the response variables. Akaike's information criterion weight is indicated by wAICc, and the total support for selected models for a response variable are noted as sum(wAICc)

*RICH* richness, *TOTFREQ* carnivore frequency, *PUMA* *Puma concolor* frequency, *CHRY5* *Chrysocyon brachyurus* frequency, *LEOP* *Leopardus pardalis* frequency, *ED* edge density, *PL* percentage of landscape cover

## Discussion

Recent studies have shown that agricultural as well as other man-altered landscape matrices are not necessarily a barrier to wildlife (McAlpine et al. 2006; Baldissera et al. 2008; Marsden and Symes 2008; Uezu et al. 2008). Our study shows that in a region bordered by cities and surrounded by intensive agriculture farms, where agribusiness is an intensive activity, large and medium carnivores can be found. However, probably this is only possible because of the presence of extensive patches of native ecosystems which are protected as natural reserves and private properties spatially arranged in a peculiar way. The importance of natural vegetation areas surrounding agroecosystems in the maintenance of the native fauna, as well as the spatial arrangement of fragments as corridors amongst native and man-altered habitats, has also been emphasized in recent studies (McAlpine et al. 2006; Baldissera et al. 2008; Marsden and Symes 2008).

In a previous study in the same area and using part of the data analyzed here, Lyra-Jorge et al. (2008) could not demonstrate the differential use of habitats by these same carnivorous species. Although those authors had noticed habitat preferences by some species, their analyses based exclusively on information about landcover types were not able to detect such preferences. On the other side, our findings suggest that multi-scaled landscape approach allows to predict the species distribution over the study region and to attest the different responses of each species to landscape features and/or scales.

Different set of models were selected to explain our response variables. Edge density best explained the number of records of two species (PUMA and CHRY5), whereas the percentage of *cerradão* at fine scale best explained LEOP. These responses agree with each species behavior. *P. concolor* and *C. brachyurus* are generalist species, with

low sensitivity to landscape change or disturbance (Devictor et al. 2008). Several studies (Lyra-Jorge et al. 2008; Coelho et al. 2008; Goulart et al. 2009) registered these species on sites or regions with low habitat quality. On the other hand, *Leopardus pardalis* is a feline with cryptic behaviour and needs large high quality areas and continuous habitat (Biatti et al. 2006). Its diet includes mainly small mammals and marsupials preys, species that in general avoid edge areas (Wang 2002). Still, the positive linear relationship between frequency of *L. pardalis* and the amount of *cerradão* emphasizes the relative importance of this type of habitat on the persistence of that species.

Although *P. concolor* and *C. brachyurus* are generalist species and relatively adapted to survive in altered areas, a negative relationship between the number of records and edge density came out (Table 4; Fig. 3) suggesting certain harmful effects of edge conditions on those species.

Several studies on fragmented landscapes have also registered lower effect of habitat fragmentation on generalist species (Umetsu et al. 2008; Uezu et al. 2008). This may occur mainly in highly fragmented regions with little amount of native habitats. On those situations, the effect of edge density could be small because the species that remains under worst conditions must be adapted to highly impacted ecosystems (Biatti et al. 2006).

Our results allow us to classify the target species into two major groups, based on their relationships with landscape features: (1) species highly sensitive to habitat loss, which can be best explained by the amount of natural habitats and (2) generalist species, which can be related to resource availability in edge conditions.

The scales on which species responded (fine or coarse) reflect the way they exploit local landscape resources. *P. concolor* and *C. brachyurus* are very vagile, and this justifies why large-scale landscapes (2,000 m on our case) best explained their records. On the other hand, *L. pardalis*,



which has movement capability five fold less than *P. concolor* or *C. brachyurus* (Aragona and Setz 2001), was best explained by fine-scale features (250 m). We highlight that the movement ability of a species can influence its persistence in the landscape because it is related to food search, resting places finding and escaping from humans.

In conclusion, this study shows the importance of including landscape spatial parameters when considering the use of habitats by fauna. Since large and medium carnivores are usually territorial animals, the understanding of how species interact with different landscape structures at different scales can drive both conservation and restoration programmes. Although the amount of remaining habitat plays an important role for highly sensitive species (like *L. pardalis*), our results suggest that the density of edges may prevail over habitat quantity in favour of generalist species frequency. Finally, our results emphasize the importance of considering multi-species (or multi-taxa) as target when planning landscape management actions, and highlight the importance of multiple-scale perspective for understanding the ecological patterns and processes relationship in the natural systems (Fortin and Dale 2005; Boscolo and Metzger 2009).

**Acknowledgments** The authors are thankful to Dr. Carlos Alberto Vettorazzi for his suggestions on a previous phase of this study and to Neotropical Grassland Conservancy and CNPQ for financial support. We are also very thankful to Patrick James, Danilo Boscolo and Tadeu Siqueira for their contributions in a later version of the paper. MCR thanks to Jean Paul Metzger's and Marie-Josée Fortin's research groups for all valuable discussions on landscape ecology and biodiversity conservation fields.

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