UNIVERSIDADE ESTADUAL DE CAMPINAS
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MARIANA NAGY BALDY DOS REIS

OCCUPANCY AND LANDSCAPE USE OF MEDIUM AND LARGE MAMMALS IN A LARGE ATLANTIC FOREST REMNANT

OCUPAÇÃO E USO DA PAISAGEM POR MAMÍFEROS DE MÉDIO E GRANDE PORTE EM UM GRANDE REMANESCENTE DE MATA ATLÂNTICA

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ORIENTADOR: Eleonore Zulnara Freire Setz
CO-ORIENTADOR: Adriano Garcia Chiarello

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ABSTRACT

Medium and large mammals exert important ecological functions on ecosystem maintenance and balance. However, several human impacts are global threats to mammals. Therefore, in order to effectively conserve this group and its ecological functions, it is necessary to establish its relation with landscape characteristics and with different protection status. We aimed to determine the main factors driving the occupancy and landscape use of two key groups of medium and large mammals (frugivores and predators), as well as to evaluate the influence of different protection status in conserving mammal ecological functions. We surveyed 45 sampling sites within one large Atlantic Forest remnant and applied a detection/non-detection sampling method using camera trap, scat sampling, and call survey data to estimate mammal occupancy and measure the degree of their ecological functions. Anthropogenic factors, such as road density and distance to a more protected area, were the main determinants of the occupancy and habitat use of frugivores and felids. Moreover, areas with higher protection status showed more mammal ecological functions than less protected areas, even those being protected. These results indicate that key mammal groups are sensitive to anthropogenic pressures even in conserved and protected areas, and highlight the importance of maintaining and creating high protection areas to effectively conserve mammals and their ecological functions.

RESUMO

Médios e grandes mamíferos exercem importantes funções ecológicas para a manutenção e equilíbrio dos ecossistemas. No entanto, diversos impactos humanos tem ameaçado globalmente a mastofauna. Portanto, para que a conservação desse grupo e suas funções ecológicas seja efetiva, é necessário estabelecer qual a sua relação com as características da paisagem e as diferentes categorias de proteção da área. Dessa forma, buscamos definir os principais fatores que influenciam o uso da paisagem e a ocupação de dois grupos-chave de médios e grandes mamíferos (frugívoros e predadores), bem como avaliar a influência de diferentes categorias de proteção na efetividade em se conservar funções ecológicas de mamíferos. Amostramos 45 sítios distribuídos em um remanescente grande de Mata Atlântica utilizando armadilhamento fotográfico, coleta de fezes e testes de *playback* e aplicamos um método de detecção/não-detecção para estimar a ocupação dos mamíferos e o grau de suas funções ecológicas. Fatores antrópicos, como densidade de estradas e distância da área de maior grau de proteção foram os principais determinantes da ocupação de frugívoros e do uso do habitat por felídeos. Ainda, áreas com maior grau de proteção apresentaram mais funções ecológicas de mamíferos do que áreas com menor grau, essas ainda que protegidas. Esses resultados indicam a sensibilidade de grupos-chave de mamíferos à pressões antrópicas mesmo em áreas mais conservadas e protegidas, e reiteram a importância de se ter áreas de alto grau de proteção para a conservação efetiva de mamíferos e suas funções ecológicas.

SUMÁRIO

1. INTRODUÇÃO

Médios e grandes mamíferos exercem diversas funções ecológicas importantes para a manutenção e equilíbrio dos ecossistemas. Frugívoros são componentes importante das florestas tropicais, pois influenciam a diversidade, estrutura e regeneração das plantas, seja por dispersão ou predação de sementes (Galetti et al. 2006; Wright 2000). Predadores são outro componente fundamental, pois regulam as cascatas tróficas, alterando as populações de presas, que como consequência, influencia a abundância, composição, sucessão, dispersão e diversidade das plantas (Crooks & Soulé 1999; Terborgh et al. 2001; Estes et al. 2011). Dessa forma, a perda desses grupos-chave pode trazer severas consequências ao ambiente, incluindo desde a redução da sobrevivência, recrutamento e germinação das plantas, até alteração no tamanho de sementes, ou ainda, impactos mais profundos, como mudanças nos regimes e estados alternativos de ecossistemas, a possíveis perdas de serviços ecossistêmicos (Estes et al. 2011; Wotton & Kelly 2011; Chapman & Chapman 1995; Galetti et al. 2013).

Impactos humanos tem ameaçado globalmente a fauna, e médios e grandes mamíferos são especialmente susceptíveis, dado à grande valorização de sua carne, suas grandes áreas de vida, e seus requisitos alimentares (Redford 1992; Chiarello 1999). As maiores ameaças desse grupo são a redução e fragmentação de habitat, a caça e muitas vezes conflitos diretos com o ser humano (Noss et al. 1996; Chiarello 1999; Michalski & Peres 2005; Murphy & Macdonald 2011; Magioli et al. 2015). Tais pressões antrópicas são reduzidas em áreas de proteção (ex. Unidades de Conservação - UCs) (Bruner et al. 2001; Peres & Palacios 2007; Andam et al. 2008), que conservam maiores densidades e possuem maiores ocupação de mamíferos de médio e grande porte (Stoner et al. 2007; capítulo 1, 2 e 3).

Recursos destinados à conservação, no entanto, são escassos, e portanto são necessárias medidas para se avaliar o que conservar, qual a melhor forma de se conservar, e em quais locais estabelecer Unidades de Conservação (Primack & Rogrigues 2001). Assim, um entendimento detalhado da relação entre espécies e seus ambientes é necessário para a elaboração de planos de manejo (Cabeza et al. 2004; Catullo et al. 2008; Kanagaraj et al. 2011; Spencer et al. 2011; Jorge et al. 2013). Ao mesmo tempo, são necessárias medidas para se avaliar se o esforço direcionado à conservação está sendo de fato efetivo e entender qual melhor estratégia de conservação (por exemplo, enquadramento da Unidade de Conservação) gera maior efetividade.

Dessa forma, aqui buscamos definir os principais fatores que influenciam o uso da paisagem e a ocupação de dois grupos-chave de médios e grandes mamíferos (frugívoros e predadores), bem como avaliar se diferentes categorias de proteção possuem diferentes efetividades em se conservar funções ecológicas de mamíferos.

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Capítulo 1: Using occupancy models to assess landscape structure influences on Neotropical frugivores in a multiple scale perspective

Mariana B. Nagy-Reis[1], César A. Estevo[1a], Eleonore Z. F. Setz[1b], Milton C. Ribeiro[2], Adriano G. Chiarello[3], James D. Nichols[4]

[1] Mammal Ecology and Behavior lab (LAMA), Department of Animal Biology, Universidade Estadual de Campinas (UNICAMP), Bertrand Russel, 1505, mailbox: 6109, Campinas, SP, 13083-970, Brazil. [a] Email: cesar_estevo@hotmail.com; [b] E-mail: setz@unicamp.br.

[2] Spatial Ecology and Conservation lab (LEEC), Department of Ecology, Universidade Estadual de São Paulo (UNESP), Av. 24A, 1515, Rio Claro, SP, 13506-900, Brazil. E-mail: mcr@rc.unesp.br.

[3] Department of Biology, Universidade de São Paulo (USP), Av. Bandeirante, 3900, Ribeirão Preto, SP, 14040-901, Brazil. E-mail: bradypus@ffclrp.usp.br.

[4] USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD, 20708, USA. E-mail: jnichols@usgs.gov.

Corresponding author: Mariana B. Nagy-Reis, Department of Animal Biology, Universidade Estadual de Campinas, UNICAMP, Biology Institute, Bertrand Russel, 1505, mailbox: 6109, Campinas, SP, 13083-970, Brazil.

E-mail: mariana.nbreis@gmail.com; Phone number: 55(11)98709-4109

Abstract

Frugivores are key components of Neotropical forests, regulating plant community, forest structure, and plant diversity; however, they are highly threatened by human impacts. To efficiently conserve this group, maintain their ecological functions, and plan management actions or establish future protected areas, we need to gather information about their status and relationship with the landscape using methods that incorporate imperfect detection. Here, we apply a detection/non-detection sampling method using camera trap and call survey data to estimate the occupancy of frugivores in a large Atlantic Forest remnant, and we evaluate the effect of landscape variables on their occupancy at multiple scales. Human accessibility and the distance to the reserve were the two main predictors of occupancy of three important frugivorous game species (paca – *Cuniculus paca*; deer – *Mazama* sp.; and collared peccary – *Pecari tajacu*). Environmental variables and geomorphometry were weaker determinants of frugivore occupancy, but there was some evidence that hydrographic density and intermediate and advanced forest succession have a positive effect on the occupancy of some frugivores. We showed that naïve occupancy can greatly underestimate species' rates of occupancy and that weather, season, and habitat-related variables are important influences on detection probability. We also demonstrated the importance of incorporating habitat heterogeneity and a multi-taxa and multi-scale approach when assessing population status and planning wildlife management actions.

Keywords: Site occupancy, camera trap, playback method, primates, ungulates, ground-dwelling birds.

1. Introduction

Since financial resources for conservation are limited, it is important to decide what to conserve as well as where and how to conserve them, optimizing the time and money invested (Primack & Rogrigues 2001). Frugivores can be considered a target group for conservation efforts because they are key components in forests, influencing plant diversity, structure and regeneration through seed dispersal and/or predation (Galetti et al. 2006; Wright 2000). This group constitutes a large portion of animal biomass in Tropical forests (Eisenberg & Thorington 1973; Terborgh, 1986), which is supported by the abundant fleshy fruit production in these ecosystems (Jordano, 2000). Interdependence between frugivores and plants is strong, with 70 to 94% of tropical trees adapted to seed dispersion by vertebrates (zoochoric) (Hamann and Curio, 1999; Jordano, 2000). Consequently, the loss of frugivores can have severe consequences for plant communities, including decreases in survival, recruitment, germination and the size of the seeds (Wotton & Kelly 2011; Chapman & Chapman 1995; Galetti et al. 2013), the loss of mechanisms that regulate tree demography (Keuroghlian & Eaton 2009), and an increase in local plant extinction (Galetti & Dirzo 2013).

Frugivores are highly sensitive to fragmentation and habitat loss due to home range and food requirements (Chiarello 1999). Illegal and unsustainable hunting – for food, ornaments or medicinal purposes – also decrease frugivore abundance and change patterns of seed dispersal and predation (Wright 2000). Selective logging and palm-heart or fruit harvesting can also impact frugivore populations (Moegenburg & Levey 2003; Kirika et al. 2008) as these activities decrease food availability, especially during periods of fruit scarcity (Galetti & Aleixo 1998, Keuroghlian & Eaton 2009).

A major question when planning wildlife management is the spatial relationship between environment and species (Cabeza et al. 2004; Spencer et al. 2011). When such relationships are not understood, areas designated for conservation may not provide suitable habitat for the target species and conservation gaps might be created (e.g Catullo et al. 2008; Kanagaraj et al. 2011). However, species distribution and occurrence studies often rely on data that do not permit sound inferences (e.g., presence-only data from various sources), or they use inference methods that do not deal adequately with sampling processes (e.g., use of presence/absence data in ways that do not incorporate imperfect detection). Such approaches are likely to have omission errors (false absence) (Rondinini et al. 2006; MacKenzie 2005), which can bias parameter estimation (Gu & Swihart 2004). On the other hand, occupancy models allow estimation of the proportion of sites being occupied and the influence of environmental variables on occupancy while accounting for detection probability and eliminating the issue of false absences in the data (MacKenzie et al. 2006).

We determined the occupancy of frugivores in a large Atlantic Forest remnant in Brazil and investigated the relationship between landscape characteristics at multiple scales and site occupancy rates, assessing the influence of protected area proximity, elevation, terrain slope, forest cover, hydrographic and road density. This information will be useful for planning management actions towards the conservation of this key component group in Neotropical forests as well as helping to evaluate the efficiency of reserves for frugivore conservation.

2. Methods

2.1. Study Site

Serra do Japi (coordinates 47°03'40"W to 46°52'20"W and 23°22'30"S to 23°11'35"S; Fig. 1) is located in southeastern Brazil. It represents one of the few large remnants of Atlantic Forest, a global hotspot for biodiversity conservation (Myers et al. 2000). Nowadays the Atlantic Forest is highly fragmented. More than 80% of the remnants are small (< 50 ha), highly isolated (average fragment distances 1,440 m) and under negative edge influences (73% of remnants are 250 m from any forest edge) (Ribeiro et al. 2009). The study site is a Natural Heritage Area (35,000 ha) considered part of the UNESCO's Atlantic Forest Biosphere Reserve (SMPMA 2008). Located within this area is the Biological Municipal Reserve (REBIO - 2,071 ha) surrounded by a Buffer Zone (11,946 ha) (Fig. 1). The REBIO presents the highest protection status in the area, where the only permitted activities are research and education. The area is characterized by semideciduous mesophile forest with mountainous terrain and a seasonal climate (Morellato 1992). The mean temperature is 19.7 ^{o}C, and the mean annual rainfall is 1,422 mm. A dry and cold season extends from April to September and a wet and warm season from October to March (Morellato 1992).

2.2. Selected species

We selected seven frugivores for our study: paca (*Cuniculus paca*); collared peccary (*Pecari tajacu*); deer (red-brocket deer: *Mazama americana*, and gray-brocket deer: *M. gouazoubira*); dusk-legged guan (*Penelope obscura*); gray-fronted dove (*Leptotila rufaxilla*); black-fronted titi monkey (*Callicebus nigrifrons*); and buffy-tufted marmoset (*Callithrix aurita*). Although not extrictly frugivores, fruits are the primarily item in the diet of these species (Dubost & Henry 2006, Bodmer 1991a, Chalukian 1997, Ballarini et al. 2013, Caselli & Setz 2011, Côrrea et al. 2000). We chose these species not only because they represent the main frugivores in Atlantic Forest remnants, but also because they perform slightly different ecological functions due to differences in body size, habits and seed dispersal and/or predation potential (Table 1).

2.3. Data collection

From April 2013 to March 2014, we surveyed 45 sampling sites distributed in a regular grid and spaced 1.5 km apart (176.6 ha sampling area per site). We tested sampling independence by performing a Moran's *I* autocorrelation test (Legendre & Legendre 1998) for each species (based on the number of detection records and geographic position of each site), using R 2.13.0 software (R Development Core Team 2011) and the *ape* package (Paradis et al. 2015). The species detections showed no evidence of spatial autocorrelation ($E(I)=-0.02$, $I\leq0$, $P>0.05$ for all species), except for *C. paca* ($I=0.04$, $P<0.001$). However, the home range of *C. paca* is extremely small (Table 1) and therefore it is unlikely that the same individual was recorded at more than one site, and any spatial autocorrelation is most likely due to spatial similarities in the habitat.

We recorded data on *C. paca*, *P. tajacu*, *Mazama* sp., *P. obscura*, and *L. rufaxilla* with passive infrared camera traps (Bushnell Trophy Cam), which is a valid method to sample these ground-dwelling animals (O'Brien & Kinnaird 2008, O'Connell et al. 2011). We fixed the cameras at about 20 cm above ground and programmed them to run continuously for approx. 70 days during each season (dry and wet; total of approx. 140 days sampled per site; N=5,198 trap days). All cameras were installed with a minimum distance of approx. 50 m from roads or trails and the sites were never located close to public or highly used roads.

We surveyed *C. nigrifrons* and *C. aurita* with three repeated playback tests at each site during each season (total of six visits per site; N=270 tests), a frequently used method to sample primates (e.g. Dacier at al. 2011, Gray et al. 2010, Peck et al. 2011). Because *C. nigrifrons* are more vocally active in the morning (Caselli 2008), all surveys were conducted between 7:00 and 13:00 h. The playback tests consisted of playing a call recording of each species (one at a time, with a 10-min. interval) through a speaker (Anchor Minivox Lite Portable, maximum amplitude of 109 db and frequency from 100 to 15,000 Hz). We recorded the presence of titi monkeys or marmosets at a site if we heard any vocalization (before or after the test) or saw at least one individual at the site.

2.4. Variables

2.4.1. Covariates used to model occupancy

At each sampling site, we determined elevation, terrain slope, percentage of high-quality forest cover, hydrographic density, road density and distance to reserve border. We obtained elevation (mean=1,025±134 m.a.s.l.) and terrain slope (25±11°) from digital elevation models (DEM) available from Topodata Geomorphic database of Brazil (INPE 2014). We mapped the land use of the study site using high resolution satellite image interpretation at a 1:5,000 scale and extensive field verification by a botanist. The land use categories were: initial, medium, and advanced forest succession cover; forestry (i.e. eucaliptus and pinus plantations); pasture; agriculture; and urban area (including rural instalations and residences). The covariate high-quality forest cover was considered the percentage of intermediate and advanced forest succession and was calculated using Geographical Resources Analysis Support System (GRASS) (Neteler et al. 2013). Hydrography and roads were mapped at a 1:5,000 scale with Quantum Gis software

(Álvarez 2013), using data from high resolution satellite images and cartographic maps (Secretariat of Economy and Planning - São Paulo State Government, at 1:10,000). We also estimated road and hydrographic densities using the Kernel density function in ArcGIS software (ESRI 2009). We measured the distance from each site to the nearest Biological Municipal Reserve (REBIO) border, giving negative distances to sites within the REBIO and positive distances otherwise. Then, we multiplied these distances by the protection status weight of the subarea in which each site was located (REBIO = 1; REBIO's Buffer Zone = 2; and within the Natural Heritage Area but outside these two subareas = 3). We were not able to incorporate the covariate 'weighted distance to reserve border' in the marmoset models (since the β coefficients did not converge), so we used only the area protection status weight for this species. We normalized all covariates and used only low correlated covariates ($r<0.50$, based on a Spearman's correlation matrix) in the final model sets.

We adopted a multi-spatial scale approach (Boscolo and Metzger 2010; Lyra-Jorge et al. 2010), testing the influence of the covariates on frugivore occupancy. The scales were defined as concentric circles (buffers) of 200, 500 and 1,000 m radius around each sampling site, and we calculated each site covariate for each scale. For pacas, dusk-legged guans and gray-fronted doves, we tested one buffer at approximately the home range scale (200 m = 12.6 ha sampled area) and two at landscape scales (500 m = 78.5 ha, and 1,000 m = 314.4 ha). For deer, black-fronted titi monkeys and buffy-tufted marmosets, we tested one home range scale (500 m) and one landscape scale (1,000 m). For collared peccaries, we tested only at the home range scale (1,000 m) as well as a smaller scale (500 m) because we could not establish a landscape buffer (i.e. > 1,000 m) and still retain minimal buffer overlap.

We expected that high-quality forest cover, hydrographic density, and human-related variables would be the main predictors of frugivore occupancy. Specifically, we predicted a positive association between occupancy and both quality habitat and hydrographic density, assuming these covariates to be associated with more fruiting trees. We predicted that occupancy would be negatively related to road density and the weighted distance to a protected area, as both roads and distance to protection might be related to higher hunting pressure. To a lesser degree, we predicted that slope and elevation would have a negative influence on occupancy as higher slopes might impose locomotion constraints and higher elevations might have lower plant richness and diversity (Lieberman et al. 1996).

2.4.2. Covariates used to model detection probability

We considered mean temperature, total precipitation, fruit availability, season (dry and wet) and percentage of high-quality forest cover as potential covariates for detection probability. Additionally, we included terrain slope (at the site) for the ground-dwelling species and the survey time of day for primates, predicting they would be negatively associated with detection. Fruit availability was measured as the monthly number of arboreal plant species producing fruits at the study site (from Morellato & Leitão-Filho 1992), and we expected that detection probability would increase in the wet season when fruits become more available. All climate variables were obtained from the Integrated Center of Agrometeorology Information (CIIAGRO 2014), and we hypothesized that weather variables and the season would be the main factors affecting detection probability as they can alter animal behavior. Furthermore, we predicted that the percentage of high-quality forest would be especially important for the detection of ground-dwelling birds, which might spend more time in the canopy than on the ground in sites with higher vegetation quality.

2.5. Occupancy and detection estimation

We used occupancy modeling (MacKenzie et al. 2002) – a likelihood-based method – to estimate the occupancy (ψ) of each frugivore and evaluate its influential factors, accounting for detection probability (p). The detection histories (H) of the ground-dwelling animals were constructed for each site over ten consecutive week-long sampling occasions during each season. We constructed primate detection histories (H) over three sampling occasions (one per playback test) during each season. For each site and sampling occasion, species detection was recorded as "1" while non-detection was recorded as "0". We treated the dry season as one primary sampling occasion and the wet season as another. We used multi-season models with three parameters, initial occupancy (dry season), colonization probability and extinction probability, with the latter two parameters corresponding to the time interval between dry and wet season. Given that we had only two seasons and a small sampling size, we were not able to investigate sources of variation in these two parameters, therefore, we held colonization and extinction constant in all analyses (i.e. gamma(.); eps(.); similarly to Licona et al. 2011).

We evaluated a suite of 22 *a priori* candidate models for each parameter (ψ and p) and estimated parameters using PRESENCE software (Hines 2006), performing a logistic regression analysis to determine the covariates that best explain occupancy and detection probability. First, we determined the scale that best represents each species' response to the habitat. We used a general model for *p* (that contained as many potential covariates as possible) and allowed initial occupancy (ψ) to vary (following MacKenzie 2006) by only the focal habitat covariate measured at the scales of the various buffer sizes (Online Appendix A, Table A1). We then developed another model set to investigate the variation in occupancy. We allowed ψ to be constant (ψ(.)) or to vary as a function of either a single covariate or a combination of two (additive effect). We used covariates at the best scale (from the previous step) and a general model for *p*. We also investigated which covariate(s) best explained the detection probability (*p*), using the top model(s) for ψ that were identified in the previous step. By using a general model for the parameters that were not investigated within a specific model set, we reduced the possibility that imposed constraints (on *p*, for example) would result in residual sampling variation being "attributed" to variation in occupancy. Because of the small data set for peccary (N=24 detection records), we were not able to use a general model for *p* when modeling ψ. Therefore, we modeled ψ using the two top-ranked covariates for *p* (the largest number of covariates the model could support).

We ranked candidate models using the Akaike Information Criterion ajusted for small sample size (AICc) (Burnham & Anderson 2002). We considered the covariate(s) from the top-ranked model(s) (ΔAICc<2) as the most likely determinant(s) of the species' occupancy or detection. When different spatial scales were equally plausible (ΔAICc<2), we chose to use the home range scale rather than the landscape scales in the final models. Additionally, we assessed the relative importance of each covariate by summing the Akaike weight (wAICc) of all the models in which that covariate was present and also examining 95% confidence intervals (CIs) to see whether they overlapped 0 or not

(Burnham & Anderson 2002). We applied model averaging (Burnham & Anderson 2002) in PRESENCE software (Hines 2006) to estimate the overall occupancy of each species at our study site during each season (dry and wet).

3. Results

3.1. Spatial scale and covariate selection

We excluded the percentage of high-quality forest cover at the 1,000 m scale, and slope at the 200 m and 500 m scales, because both variables correlated highly with elevation (at all buffer sizes; $p<0.05$, $r_s>0.50$) and road density at 500 m ($p<0.05$, $r_s>-0.50$), respectively. For most covariates and species, models with different scales were equally supported (Online Appendix A, Table A1). However, road density for paca (*Cuniculus paca*), the percentage of high-quality forest cover for guan (*Penelope obscura*), and hydrographic density for titi monkey (*Callicebus nigrifrons*) were best explained by landscape scales (ΔAICc between scales > 2).

3.2. Frugivore occupancy

We had 919 captures of our target ground-dwelling frugivores (N=5,198 trap days) and 214 records of primates (N=270 playback tests) (Table 2).

We had support for constant occupancy ($\psi(.)$) across sites for the arboreal and ground-dwelling/arboreal species (i.e. guan, dove, titi monkey, and marmoset; $\psi(.)$ model with AICc weights from 0.2 to 0.4; Online Appendix A, Table A2). Contrarily, the occupancy of the strictly ground-dwelling frugivores (i.e. paca, peccary, and deer) varied according to landscape features (Fig. 2; Online Appendix A, Table A2). At least one of the human-related covariates (road density and weighted distance to reserve border) was the main factor influencing the occupancy (negatively) of these ground-dwelling frugivorous mammals, emerging as the top-ranked model (Online Appendix A, Table A2) with high relative importance (Fig. 3). Most frugivores had higher occupancy closer to a more protected area (Fig. 3). Furthermore, distance from reserve was especially important for paca and relatively important for marmoset (Fig 3; Online Appendix A, Table A2). High-quality forest cover had a positive effect for most frugivores and was an important predictor of the occupancy of paca and, possibly, marmoset (Fig. 3; Online Appendix A, Table A2). Generally, the other analyzed variables had similar low relevance, since their model support did not differ substantially from that of the null models (Online Appendix A, Table A2). However, we had some evidence that hydrographic density could be a predictor of dove's and primate's occupancy; slope possibly had an effect on deer, and elevation on dove and titi monkey (only positive for the titis) (Fig. 3; Online Appendix A, Table A2).

3.3. Frugivore detection probability

The null model for detection probability (i.e. *p*(.)) was poorly supported for all frugivores (*p*(.) model with AICc weights from 0.00 to 0.08); weather, season, terrain slope and forest cover were the main predictors (Fig. 4; Online Appendix A, Table A3). The detection probability in the wet season was usually lower. Temperature greatly increased the detection of primates, and rainfall increased guan detection. In higher-quality habitats, peccaries, doves and titi monkeys were more readily detected, whereas guans were less easily detected. Terrain slope decreased paca detection but increased dove detection. The time of day during which titi monkeys were surveyed had a negative effect on their detection. Finally, the monthly fruit availability had overall low influence on detection.

4. Discussion

Our study is the first to estimate the occupancy of Neotropical frugivores and investigate how geomorphometry, environmental and anthropogenic factors might affect them at multiple spatial scales. Expanding our survey over other Atlantic Forest sites, including smaller forest remnants, and over a greater number of seasons would enable to estimate some vital rates for frugivores such as local extinction and colonization probabilities. Frugivores regulate plant communities (Galetti et al. 2006; Wright 2000), and most populations are decreasing and/or are threatened. For example, buffy-tufted marmoset (*Callithrix aurita*) is considered 'Vulnerable', red-brocket deer (*Mazama americana*) is 'Data deficient', and black-fronted titi monkey (*Callicebus nigrifrons*) is 'Near Threatened' (IUCN 2015). This scenario is especially concerning in human-dominated biomes such as the Atlantic Forest, a global biodiversity hotspot (Myers et al. 2000). Neverthless, several species are still poorly studied, including all eight species analysed here (IUCN 2015). There is a clear need to assess the status of frugivores and understand more about them to properly direct conservation efforts.

The low support for constant occupancy throughout our study area indicates that for some frugivores, their distribution is heterogenic even in continuous forest remnants. Similarly, previous studies demonstrated that the presence, abundance, density and biomass of some mammals can be restricted within continuous areas of Atlantic Forest (Galetti et. al. 2009, Jorge et al. 2013, Norris et al. 2011a, Norris et al. 2011b). Incorporating habitat covariates in models that estimate species occupancy may produce more accurate estimates (Linkie et al. 2007). However, previous studies with small mammals (Lindenmayer 2000, Umetsu et al. 2008), carnivores (Lyra-Jorge et al. 2010) and birds (Graf et al. 2005, Boscolo & Metzger 2009, Lawler & Edwards Jr. 2002) have shown the importance of a multi-scale approach when investigating species-habitat relationships. Likewise, we showed that variations in the scale at which the environment is measured can also influence estimates of animal occupancy, as some variables were better predictors of occupancy at one scale than at others. Therefore, taking into account habitat heterogeneity through a multi-spatial scale approach to population status assessment is essential in order to obtain estimates for wildlife management.

Our first prediction regarding frugivore occupancy was that intermediate and advanced forest succession patches and hydrographic density would have a positive effect, as they are usually related to a higher number of zoochoric trees (Tabarelli & Peres 2002) and water availability. This hypothesis was supported for most frugivores; both variables positively affected occupancy. Furthermore, the percentage of high-quality forest cover was a strong predictor of paca (*C. paca*) occupancy, and, contrary to previous literature (Norris et al. 2011b), we found some evidence that it might also be important for buffy-tufted marmosets (*C. aurita*). Hydrographic density might also positively affect gray-fronted doves (*Leptotila rufaxilla*), black-fronted titi monkeys (*Callicebus nigrifrons*) and buffy-tufted marmosets (*C. aurita*). A study based on presence-only data predicted that altitude limited the probability of suitable habitats for *C. aurita*, with populations present only bellow 1,000 m.a.s.l. in Atlantic Forest sites (Norris et al. 2011b). However, we recorded *C. aurita* groups up to 1,262 m.a.s.l., and their probability of occupancy did not decrease with elevation. This finding highlights the difficulties in drawing inferences about species-habitat relationships from presence-only data (see Yackulic et al. 2013). Despite the mountainous terrain of our study site, geomorphometry (slope and elevation) had overall low support for their effect on frugivore occupancy. Contrarily, human-related variables were important for several frugivores, having a negative influence on the occupancy of most species, particularly ground-dwelling mammals. Many frugivores, including pacas, peccaries and deer, are considered important game species and are sensitive to hunting (Peres & Palacios 2007, Redford 1992), selective logging and harvesting (Moegenburg & Levey 2003; Kirika et al. 2008). All these negative pressures are most likely to occur in areas more accessible to humans or with low (or inefficient) protection status (Bruner et al., 2001; Peres & Palacios, 2007). Although our entire study area is under some protection, paca and buffy-tufted marmoset occupancies decreased as the distance increased between sites and the most protected area (reserve). Similar to ungulates in the Amazon (*Mazama gouazoubira*, *M. americana*, and *Tayassu pecari*; Licona et al. 2011), the occupancy of large game species in Atlantic Forest (i.e. *P. tajacu* and *Mazama* sp.) was predicted by human accessibility (here measured by road density). Even when incorporating covariates at a finer-scale (as suggested by Licona et al. 2011), the only habitat-related variable affecting occupancy was slope (for deer, and to a low degree). Therefore, factors related to human presence or disturbance might be a greater determinant of the distribution of important frugivorous game species than environmental variables or geomorphometry.

In accordance with recent studies (Licona et al. 2011, Linkie et al. 2007, Sarmento et al. 2011, De Wan et al. 2009), our research emphasizes the feasibility of methods that incorporate detection probability when assessing landscape influences on population distribution. Although camera traps and playback tests are considered efficient ways to survey ground-dwelling animals (O’Brien & Kinnard 2008, O’Connel et al.

2011) and primates (Dacier at al. 2011, Gray et al. 2010, Peck et al. 2011), respectively, incorporating detection probability resulted in a relative increase above naïve occupancy by up to 146%. Furthermore, the low support for models with constant detection emphasizes the importance of ecological and behavioral studies that account for variables in detection probability. Some research may incorporate only habitat-related covariates (Linkie et al. 2007, Sarmento et al. 2011) or weather (Pellet & Schmidt 2005), but our results show that season, weather and habitat variables can be equally good predictors for animal detection probability.

Weather can affect the behavior of many animals. For example, they can adjust activity, space use and microhabitat selection at different temperatures (Carrascal et al. 2011, Giotto et al. 2013, Gestich et al. 2014). Here, temperature, precipitation and the season were important for the detection probability of most species. However, habitat-related variables such as forest cover and slope were also good predictors of detection probability. We speculate that differences in detection according to such variables could be related to locomotion constraints imposed by terrain slope as well as to possible variation in density in habitats with different degrees of quality. Furthermore, ground-dwelling birds can use both the tree canopy and the forest ground to forage. Therefore, we assume that they can spend different amounts of time in each forest stratum, depending on habitat characteristics. Regardless of the underlying mechanisms, our results show the overall importance of not only accounting for detection probability in surveys, but also incorporating habitat covariates. Proximity to roads or trails is another site covariate that may affect the detection probability of some animals (Blake & Mosquera 2014, Di Bitetti et al. 2014, Linkie et al. 2007). However, as this might not be the case for our target species (Blake & Mosquera 2014, Di Bitetti et al. 2014) and our data set was small, we standardized the data collection (see method section) and did not incorporate this variable when modeling detection probability. We believe that attention should be drawn to roads and trails, whether by dealing with it in sampling design or incorporating this variable in models, particularly when studying species more likely to be detected on or off roads (e.g. Neotropical felids – Blake & Mosquera 2014, Di Bitetti et al. 2014).

4.1. Management recommendations

Due to the relevance of Neotropical frugivores in ecosystems and their sensitivity to threats, several actions are required for their conservation, including forest regeneration and restoration and the alleviation of anthropogenic pressures such as hunting, selective logging and harvesting (Chiarello 1999, Wright et al. 2000, Galetti & Aleixo 1998, Moegenburg & Levey 2003; Kirika et al. 2008). Here we highlight the main management recommendations arising from our study:

1) To better assess animal populations and objectively evaluate species conservation status, it is fundamental to use methods that deal with imperfect detection, avoiding underestimating animal occupancy rates. Occupancy models can also estimate parameters that are essential to monitor populations (i.e. local extinction and colonization probabilities) (MacKenzie et al. 2006). Here we established and tested a method that could be used in further long-term multi-species monitoring programs by expanding our survey over time and space. Furthermore, we determined some of the landscape characteristics that are important for managing Atlantic Forest frugivores and establishing future protected areas for the group (see Magioli et al. 2015 for some guidelines to

maintain functional diversity of Atlantic Forest mammals). These landscape features are: the cover of intermediate and advanced forest succession, areas with high protection status, and hydrographic and road densities.

2) Species of frugivores play different ecological roles due to differences in body size, habit and relationship to plant seeds. Here we demonstrated that some frugivores might not respond to a given habitat feature as intensely as others might, and that their response may also depend on the landscape scale at which they are observed. Considering several species when establishing the landscape features necessary to protect the fauna can conserve more ecological functions than could a single species study (Lambeck 1997). Therefore, a multi-taxa and multi-scale approach should be used when planning landscape and wildlife management.

3) The establishment of reserves or other protected areas can decrease habitat loss (Andam et al. 2008) and anthropogenic pressures (Bruner et al. 2001; Peres & Palacios 2007). Our results suggest that reserves can also improve the occupancy of some frugivores (as their occupancy is higher inside and closer to the reserve). For other species, human accessibility is the strongest predictor, and the species can occur regardless of distance to more protected areas. This finding demonstrates that in addition to reserves, areas with lower protection status might also provide suitable habitats for some frugivores as long as human accessibility is low. However, since hunting occurs illegally in the Atlantic Forest and can be higher around reserves (Bruner et al. 2001; Ewers & Rodrigues 2008), management actions such as environmental education and effective law enforcement are also needed to ensure frugivore conservation.

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Figures

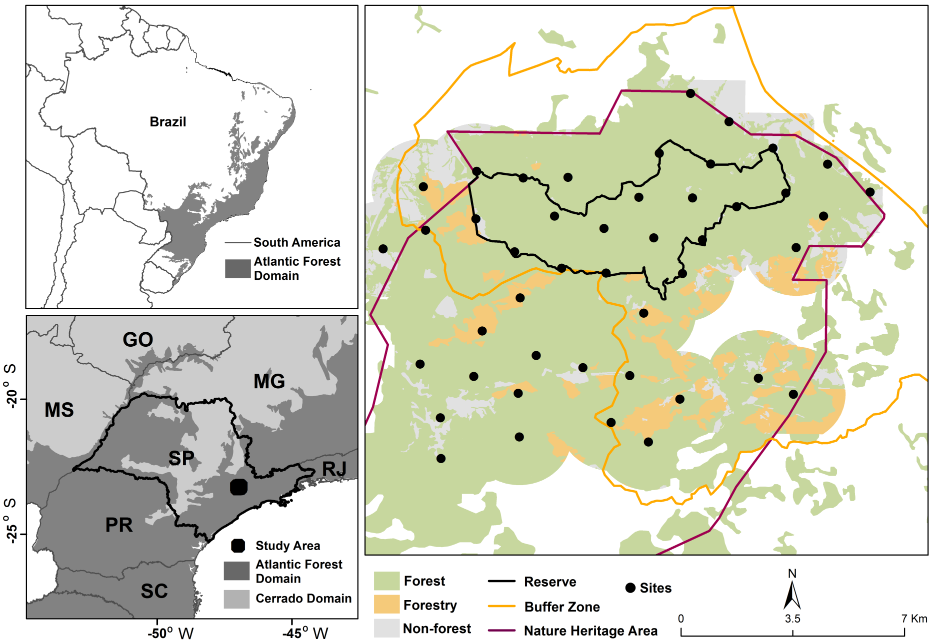

Fig. 1. Study area and sampling sites location at Serra do Japi (Brazil) where ground-dwelling mammals and birds were sampled using camera-traps and primates using playback tests.

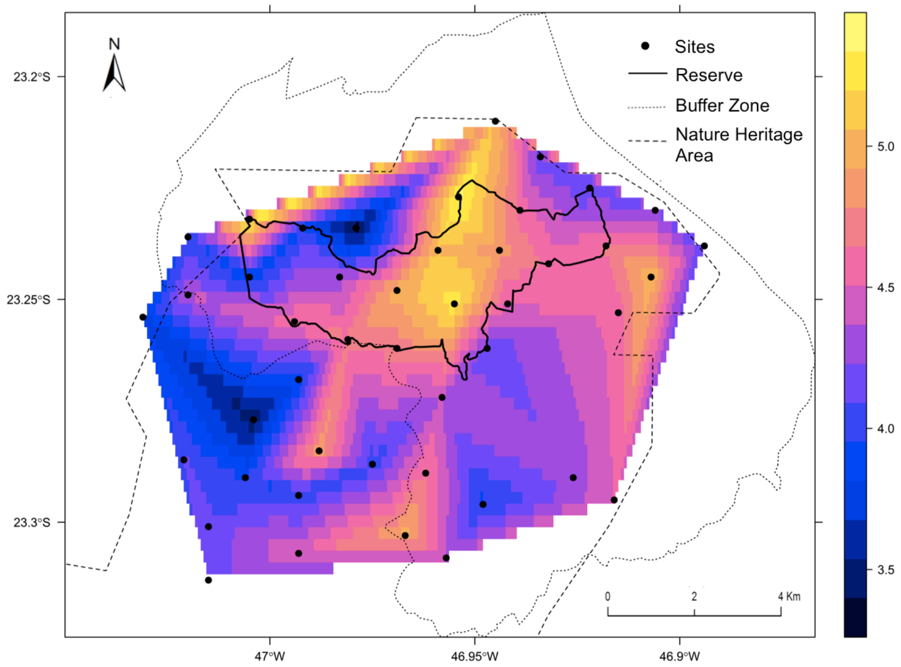

Fig. 2. Interpolated sum of site occupancies (average between seasons) of the seven frugivores at an Atlantic Forest site in Brazil: paca - *Cuniculus paca*, collared peccary - *Pecari tajacu*, deer - *Mazama* sp., dusk-legged guan - *Penelope obscura*, gray-fronted dove - *Leptotila rufaxilla*, black-fronted titi monkey - *Callicebus nigrifrons*, and buffy-tufted marmoset -*Callithrix aurita*.

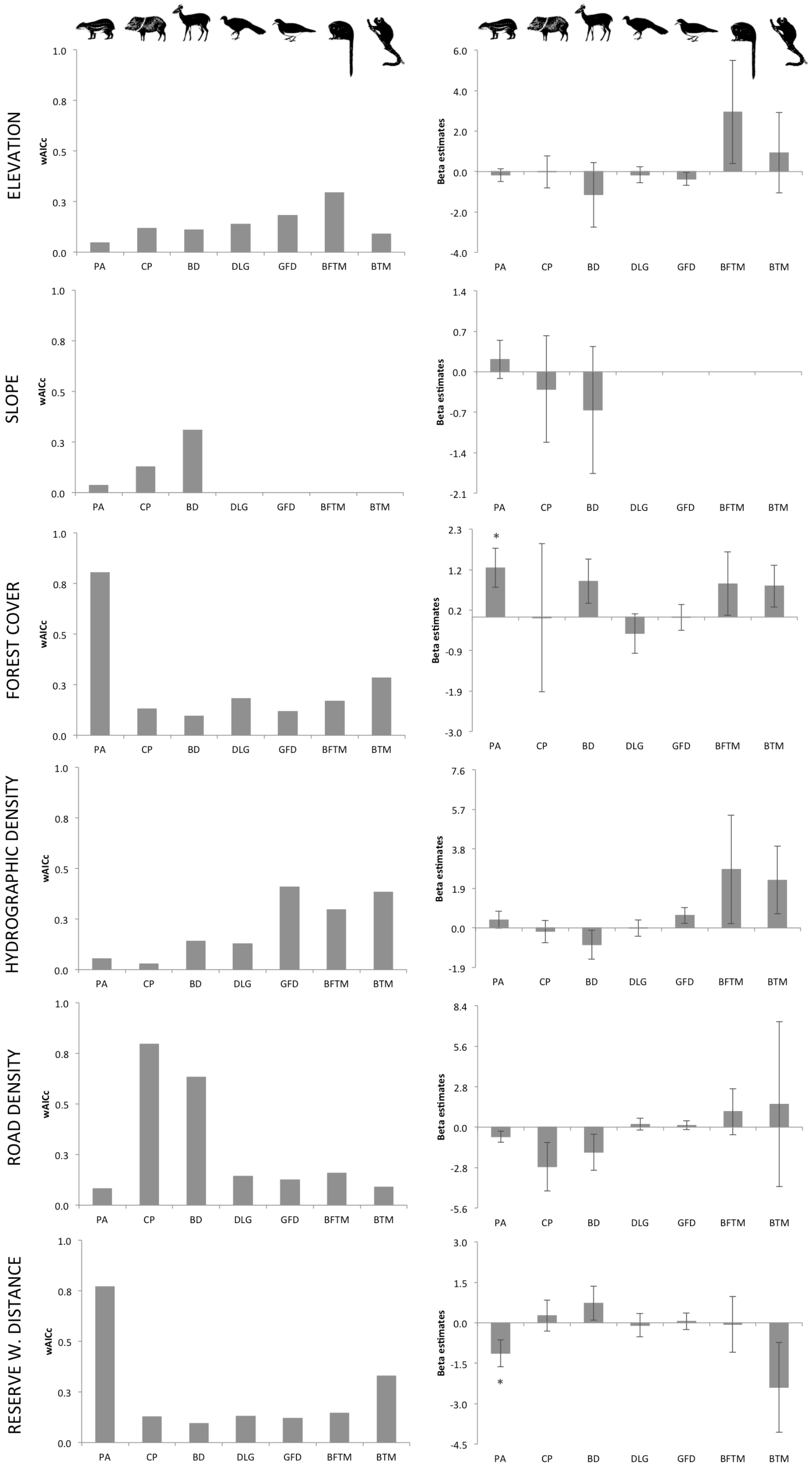
ELEVATION
SLOPE
FOREST COVER
HYDROGRAPHIC DENSITY
ROAD DENSITY
RESERVE W. DISTANCE
wAICc
Beta estimates
PA
CP
BD
DLG
GFD
BFTM
BTM
1.0
0.8
0.5
0.3
0.0
6.0
4.0
2.0
0.0
-2.0
-4.0
1.4
0.7
0.0
-0.7
-1.4
-2.1
2.3
1.2
0.2
-0.9
-1.9
-3.0
7.6
5.7
3.8
1.9
0.0
-1.9
8.4
5.6
2.8
0.0
-2.8
-5.6
3.0
1.5
0.0
-1.5
-3.0
-4.5
*
*

Fig. 3. Influence of geomorphometry, environmental, and anthropogenic covariates on frugivores occupancy in a large Atlantic Forest remnant, showing the sum of wAICc and the associated beta estimates with standard error. * indicates that 95% confidence interval does not include 0. PA=Paca (*Cuniculus paca*); CP=Collared peccary (*Pecari tajacu*); BD=Brocket deer (*Mazama* sp.); DLG=Dusk-legged guan (*Penelope obscura*); GFD=Gray-fronted dove (*Leptotila rufaxilla*); BFTM=Black-fronted titi monkey (*Callicebus nigrifrons*); and BTM=Buffy-tufted marmoset (*Callithrix aurita*).

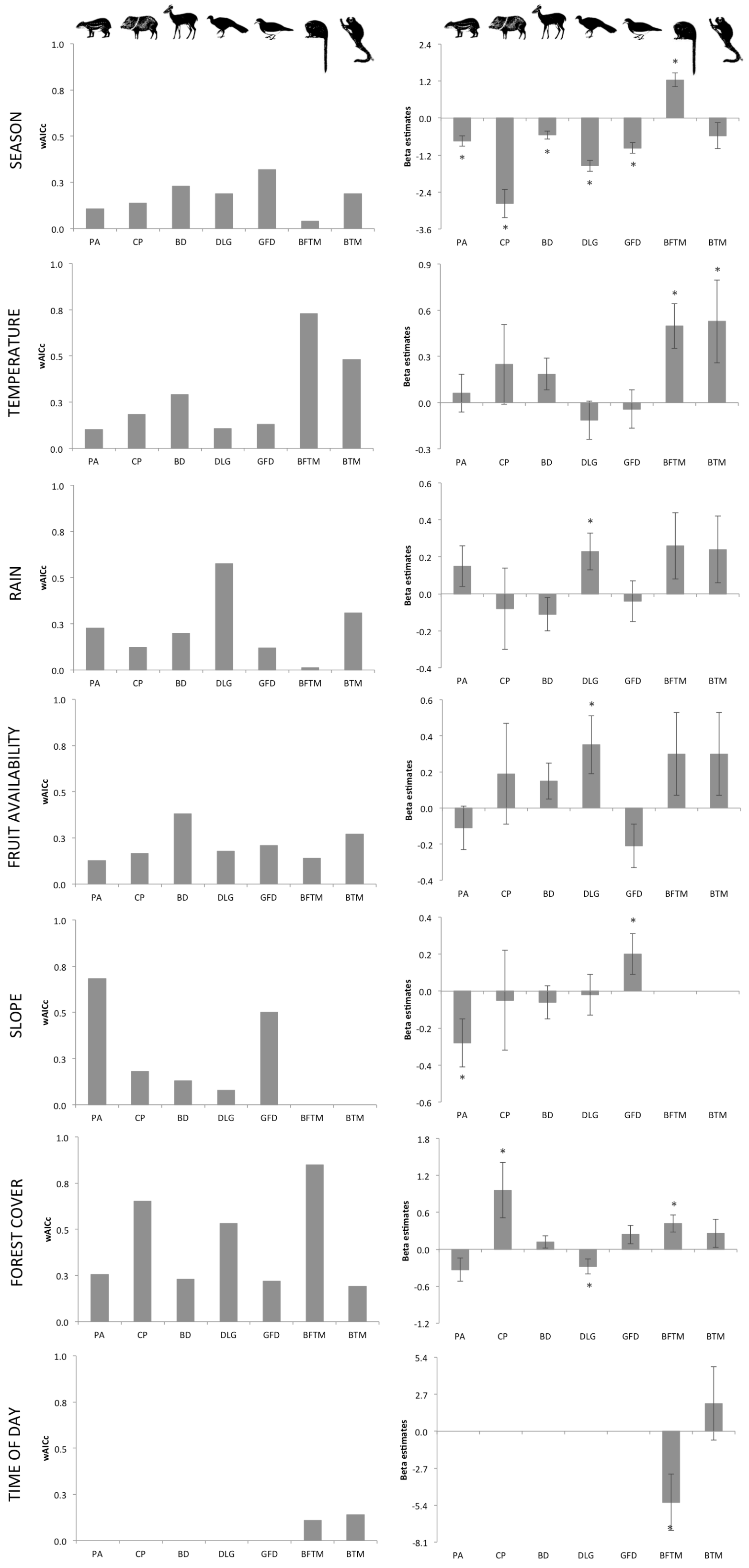
SEASON
TEMPERATURE
RAIN
FRUIT AVAILABILITY
SLOPE
FOREST COVER
TIME OF DAY
wAICc
Beta estimates
PA
CP
BD
DLG
GFD
BFTM
BTM
1.0
0.8
0.5
0.3
0.0
2.4
1.2
-1.2
-2.4
-3.6
0.9
0.6
0.3
-0.3
0.6
0.4
0.2
-0.2
-0.4
-0.6
1.8
-0.6
-1.2
5.4
2.7
-2.7
-5.4
-8.1
*

Fig. 4. Influence of each sample and site covariate on frugivores detection probability in a large Atlantic Forest remnant, showing the sum of wAICc and the associated beta estimates with standard error. * indicates that 95% confidence interval does not include 0. PA=Paca (*Cuniculus paca*); CP=Collared peccary (*Pecari tajacu*); BD=Brocket deer (*Mazama* sp.); DLG=Dusk-legged guan (*Penelope obscura*); GFD=Gray-fronted dove (*Leptotila rufaxilla*); BFTM=Black-fronted titi monkey (*Callicebus nigrifrons*); and BTM=Buffy-tufted marmoset (*Callithrix aurita*).

Tables

Table 1. Seven Neotropical frugivores, their body mass, habits (ground-dwelling – Gd or arboreal – Ar), degree of preference as game species, seed dispersal and/or predation potential and home range size.

Species	Body mass (kg)[1]	Habit	Game preference[2]	Seed[3]		Home range size (ha)[4]
				Disperser	Predator	
Paca	5-13[a]	Gd	++	++[a,b]	-	<4[a]
Collared peccary	17-35[a]	Gd	++	+[b,c]	++	10 to 305[b]
Brocket-deer[5]	11-48[a]	Gd	++	+[c]	++	<100[c]
Dusk-legged guan	1.8[b]	Gd/Ar	+	++[d]	-	11[d]
Gray-fronted dove	0.2[b]	Gd/Ar	-	+[e]	++	<10[e]
Black-fronted titi monkey	1.0-1.6[c]	Ar	-	++[f]	-	8 to 48[f]
Buffy-tufted marmoset	0.5[c]	Ar	-	++[g]	-	35[g]

Sources of the data: (1) a. Emmons & Feer 1997, b. Dunning Jr. 2007, c. Rowe 1996; (2) Redford 1992, Peres & Palacios 2007, Hill et al. 1997; (3) a. Dubost & Henry 2006, Pimentel & Tabarelli 2004; b. Keuroghlian & Eaton 2009; c. Bodmer 1991b; d. Strahl & Grajal 1991; e. Ballarini et al. 2013; f. Alvarez & Heymann 2012; g. Figueiredo & Longatti 1997; (4) a. Beck-King et al. 1999; b. Fragoso 1999, Keuroghlian et al. 2004; c. Duarte 1997, Maffei & Taber 2003; d. Guix & Ruiz 1997 (based on *P. superciliaris*); e. Boydstun & DeYoung 1988 (based *L. verreaux*); f. Caselli 2008, Neri 1997; g. Côrrea et al. 2000; (5) considering both *Mazama* sp. (*M. americana* and *M. gouazoubira*).

Table 2. Number of records (detections), number of sites with detections, naïve occupancy, estimated occupancy probability ($\hat{\psi}$), and relative increase above naïve occupancy when using estimates for frugivores in a seasonal large Atlantic Forest remnant.

	N detections	N sites w. detection	Naïve occup.		Occup. prob. $\hat{\psi}$[1]		Rel. increase above naïve occup. (%)[2]	
			S(1)	S(2)	S(1)	S(2)	S(1)	S(2)
Paca	199	25	0.38	0.49	0.41±0.24	0.53±0.13	9	8
Collared peccary	25	12	0.13	0.27	0.26±0.20	0.47±0.14	95	76
Brocket deer	322	43	0.80	0.76	0.87±0.13	0.77±0.02	9	2
Dusk-legged guan	166	39	0.60	0.69	0.70±0.03	0.84 ±0.00	17	22
Gray-fronted dove	191	29	0.36	0.51	0.37±0.08	0.56 ±0.01	4	10
Black-fronted titi monkey	175	44	0.91	0.93	0.97±0.03	0.93 ±0.02	6	0
Buffy-tufted marmoset	39	24	0.33	0.33	0.82±0.12	0.50 ±0.07	146	50

S(1) = dry season, S(2) = wet season. [1]Occupancy probability and standard deviation estimated by model averaging. [2]Percentage increase in estimated proportion of occupied sites when incorporating detection probability (*p*) [(occupancy probability/naïve occupancy)-1*100].

Online Appendix A

Table A1. Model selection analysis for occupancy (ψ) covariates (elevation, terrain slope, percentage of high-quality forest cover, hydrographic density and road density) measured at different scales (buffer sizes) for seven Neotropical frugivores at an Atlantic Forest site in Brazil.

Model	AICc	ΔAICc	wAICc	K	-2LLL
Elevation					
Paca					
ψ(.) p(global)	560.84	0	0.62	9	537.70
ψ(elev200) p(global)	563.89	3.05	0.14	10	537.42
ψ(elev500) p(global)	564.07	3.23	0.12	10	537.60
ψ(elev1000) p(global)	564.16	3.32	0.12	10	537.69
Collared peccary					
ψ(.) p(global)	204.74	0	0.60	5	193.2
ψ(elev1000) p(global)	206.69	1.95	0.23	6	192.48
ψ(elev500) p(global)	207.18	2.44	0.18	6	192.97
Brocket deer					
ψ(.) p(global)	881.20	0	0.70	9	858.06
ψ(elev1000) p(global)	884.24	3.04	0.15	10	857.77
ψ(elev500) p(global)	884.33	3.13	0.15	10	857.86
Dusk-legged guan					
ψ(.) p(global)	661.17	0	0.64	10	634.70
ψ(elev1000) p(global)	664.45	3.28	0.12	11	634.45
ψ(elev200) p(global)	664.53	3.36	0.12	11	634.53
ψ(elev500) p(global)	664.55	3.38	0.12	11	634.55
Gray-fronted dove					

ψ(.) *p*(global)	574.18	0	0.57	10	547.71
ψ(elev200) *p*(global)	576.48	2.30	0.18	11	546.48
ψ(elev500) *p*(global)	577.13	2.95	0.13	11	547.13
ψ(elev1000) *p*(global)	577.26	3.08	0.12	11	547.26
Black-fronted titi monkey					
ψ(.) *p*(global)	350.13	0	0.36	8	330.13
ψ(elev1000) *p*(global)	350.35	0.22	0.32	9	327.21
ψ(elev500) *p*(global)	350.43	0.30	0.31	9	327.29
Buffy-tufted marmoset					
ψ(.) *p*(global)	231.04	0	0.69	8	211.04
ψ(elev1000) *p*(global)	233.95	2.91	0.16	9	210.81
ψ(elev500) *p*(global)	234.12	3.08	0.15	9	210.98
Slope					
Paca					
ψ(.) *p*(global)	560.84	0	0.58	9	537.70
ψ(slope200) *p*(global)	563.32	2.48	0.17	10	536.85
ψ(slope1000) *p*(global)	563.74	2.90	0.14	10	537.27
ψ(slope500) *p*(global)	564.00	3.16	0.12	10	537.53
Collared peccary					
ψ(slope500) *p*(global)	203.76	0	0.45	6	189.55
ψ(slope1000) *p*(global)	204.71	0.95	0.28	6	190.5
ψ(.) *p*(global)	204.74	0.98	0.27	5	193.2
Brocket deer					
ψ(.) *p*(global)	881.20	0	0.50	9	858.06
ψ(slope500) *p*(global)	882.23	1.03	0.30	10	855.76
ψ(slope1000) *p*(global)	882.96	1.76	0.21	10	856.49
High-quality forest cover					

Paca					
ψ(forest200) *p*(global)	556.59	0	0.48	10	530.12
ψ(forest500) *p*(global)	557.39	0.80	0.32	10	530.92
ψ(forest1000) *p*(global)	558.94	2.35	0.15	10	532.47
ψ(.) *p*(global)	560.84	4.25	0.06	9	537.70
Collared peccary					
ψ(forest500) *p*(global)	201.49	0	0.61	6	187.28
ψ(forest1000) *p*(global)	203.08	1.59	0.27	6	188.87
ψ(.) *p*(global)	204.74	3.25	0.12	5	193.2
Brocket deer					
ψ(.) *p*(global)	881.20	0	0.61	9	858.06
ψ(forest500) *p*(global)	882.97	1.77	0.25	10	856.50
ψ(forest1000) *p*(global)	884.15	2.95	0.14	10	857.68
Dusk-legged guan					
ψ(.) *p*(global)	661.17	0	0.52	10	634.7
ψ(forest1000) *p*(global)	662.68	1.51	0.24	11	632.68
ψ(forest500) *p*(global)	663.87	2.70	0.13	11	633.87
ψ(forest200) *p*(global)	664.40	3.23	0.10	11	634.4
Gray-fronted dove					
ψ(.) *p*(global)	573.07	0	0.63	9	549.93
ψ(forest1000) *p*(global)	576.31	3.24	0.12	10	549.84
ψ(forest500) *p*(global)	576.33	3.26	0.12	10	549.86
ψ(forest200) *p*(global)	576.37	3.30	0.12	10	549.90
Black-fronted titi monkey					
ψ(.) *p*(global)	350.13	0	0.60	8	330.13
ψ(forest500) *p*(global)	352.20	2.07	0.21	9	329.06
ψ(forest1000) *p*(global)	352.49	2.36	0.18	9	329.35

Buffy-tufted marmoset					
ψ(.) *p*(global)	231.04	0	0.55	8	211.04
ψ(forest500) *p*(global)	232.09	1.05	0.32	9	208.95
ψ(forest1000) *p*(global)	233.95	2.91	0.13	9	210.81
Hydrographic density					
Paca					
ψ(.) *p*(global)	560.84	0	0.44	9	537.70
ψ(hydro200) *p*(global)	561.19	0.35	0.37	10	534.72
ψ(hydro500) *p*(global)	563.99	3.15	0.09	10	537.52
ψ(hydro1000) *p*(global)	564.01	3.17	0.09	10	537.54
Collared peccary					
ψ(.) *p*(global)	204.74	0	0.48	5	193.2
ψ(hydro1000) *p*(global)	205.61	0.87	0.31	6	191.4
ψ(hydro500) *p*(global)	206.39	1.65	0.21	6	192.18
Brocket deer					
ψ(.) *p*(global)	881.20	0	0.64	9	858.06
ψ(hydro500) *p*(global)	883.26	2.06	0.23	10	856.79
ψ(hydro1000) *p*(global)	884.28	3.08	0.14	10	857.81
Dusk-legged guan					
ψ(.) *p*(global)	661.17	0	0.66	10	634.70
ψ(hydro500) *p*(global)	664.67	3.50	0.11	11	634.67
ψ(hydro200) *p*(global)	664.69	3.52	0.11	11	634.69
ψ(hydro1000) *p*(global)	664.69	3.52	0.11	11	634.69
Gray-fronted dove					
ψ(.) *p*(global)	574.18	0	0.42	10	547.71
ψ(hydro200) *p*(global)	574.51	0.33	0.35	11	544.51
ψ(hydro500) *p*(global)	576.12	1.94	0.16	11	546.12

ψ(hydro1000) p(global)	577.59	3.41	0.08	11	547.59
Black-fronted titi monkey					
ψ(.) p(global)	350.13	0	0.46	8	330.13
ψ(hydro1000) p(global)	350.44	0.31	0.40	9	327.3
ψ(hydro500) p(global)	352.52	2.39	0.14	9	329.38
Buffy-tufted marmoset					
ψ(.) p(global)	231.04	0	0.47	8	211.04
ψ(hydro1000) p(global)	231.99	0.95	0.29	9	208.85
ψ(hydro500) p(global)	232.48	1.44	0.23	9	209.34
Road density					
Paca					
ψ(.) p(global)	560.84	0	0.38	9	537.70
ψ(roads500) p(global)	560.97	0.13	0.35	10	534.50
ψ(roads1000) p(global)	562.75	1.91	0.14	10	536.28
ψ(roads200) p(global)	563.03	2.19	0.13	10	536.56
Collared peccary					
ψ(roads1000) p(global)	197.09	0	0.83	6	182.88
ψ(roads500) p(global)	200.51	3.42	0.15	6	186.3
ψ(.) p(global)	204.74	7.65	0.02	5	193.2
Brocket deer					
ψ(roads500) p(global)	878.48	0	0.50	10	852.01
ψ(roads1000) p(global)	879.04	0.56	0.38	10	852.57
ψ(.) p(global)	881.20	2.72	0.13	9	858.06
Dusk-legged guan					
ψ(.) p(global)	661.17	0	0.64	10	634.70
ψ(roads200) p(global)	664.44	3.27	0.13	11	634.44
ψ(roads1000) p(global)	664.56	3.39	0.12	11	634.56

ψ(roads500) *p*(global)	664.69	3.52	0.11	11	634.69
Gray-fronted dove					
ψ(.) *p*(global)	574.18	0	0.62	10	547.71
ψ(roads1000) *p*(global)	577.00	2.82	0.15	11	547.00
ψ(roads200) *p*(global)	577.53	3.35	0.12	11	547.53
ψ(roads500) *p*(global)	577.67	3.49	0.11	11	547.67
Black-fronted titi monkey					
ψ(.) *p*(global)	350.13	0	0.58	8	330.13
ψ(roads1000) *p*(global)	351.64	1.51	0.27	9	328.5
ψ(roads500) *p*(global)	352.95	2.82	0.14	9	329.81
Buffy-tufted marmoset					
ψ(.) *p*(global)	231.04	0	0.68	8	211.04
ψ(roads1000) *p*(global)	233.89	2.85	0.16	9	210.75
ψ(roads500) *p*(global)	234.04	3.00	0.15	9	210.9

[1] *p*(global) = season + temperature + rain + fruit + slope; [2] *p*(global) = temperature + percentage of high-quality forest cover at 500 m buffer size; [3] *p*(global) = season + temperature + rain + fruit + slope + percentage of high-quality forest cover at 200 m buffer size; [4] *p*(global) = temperature + rain + fruit + time of day surveyed.

Table A2. Model selection analysis (cumulative wAICc>0.80) and occupancy (ψ) covariate coefficients (elevation, terrain slope, percentage of high-quality forest cover, hydrographic density, road density and weighted distance to reserve border) for seven Neotropical frugivores at an Atlantic Forest site in Brazil.

					Beta estimates					
Model	ΔAICc	wAICc	K	-2LLL	Elevation	Slope	Forest cover	Hydrography	Roads	Reserve w.dist.
Paca										
ψ(reserve+forest200) *p*(global)^1	0	0.63	11	522.80	-	-	1.29* (±0.54)	-	-	-1.13* (±0.50)
ψ(forest200) p(global)	3.79	0.09	10	530.12	-	-	1.15* (±0.51)	-	-	-
ψ(reserve+roads500) *p*(global)	5.53	0.04	11	528.33	-	-	-	-	-0.66 (±0.38)	-0.96* (±0.45)
ψ(forest200+hydro200) *p*(global)	6.27	0.03	11	529.07	-	-	1.05* (±0.52)	0.39 (±0.41)	-	-
Collared peccary										
ψ(roads1000) *p*(global)^2	0	0.41	7	178.47	-	-	-	-	-2.74 (±1.67)	-
ψ(roads1000+reserve) *p*(global)	2.74	0.10	8	178.24	-	-	-	-	-2.87 (±1.73)	0.27 (±0.58)
ψ(roads1000+forest500) *p*(global)	2.86	0.10	8	178.36	-	-	-1.13 (±1.94)	-	-2.75 (±1.65)	-
ψ(roads1000+slope1000) *p*(global)	2.87	0.10	8	178.37	-	-0.30 (±0.92)	-	-	-2.84 (±1.67)	-
ψ(roads1000+elev1000) *p*(global)	2.97	0.09	8	178.47	-0.02 (±0.79)	-	-	-	-2.75 (±1.69)	-
Brocket deer										
ψ(roads1000) *p*(global)^1	0	0.27	10	852.57	-	-	-	-	-1.73 (±1.25)	-
ψ(roads1000+slope1000) *p*(global)	0.40	0.22	11	849.44	-	-1.38 (±1.10)	-	-	-1.97 (±1.49)	-
ψ(.) *p*(global)	2.16	0.09	9	858.06	-	-	-	-	-	-
ψ(roads1000+hydro500) *p*(global)	2.18	0.09	11	851.22	-	-	-	-0.81 (±0.69)	-1.58 (±1.06)	-
ψ(roads1000+elev500) *p*(global)	2.60	0.07	11	851.64	-1.15 (±1.60)	-	-	-	-4.06 (±4.04)	-

ψ(reserve) *p*(global)	3.72	0.04	10	856.29	-	-	-	-	-	0.73 (±0.63)
ψ(slope1000) *p*(global)	3.92	0.04	10	856.49	-	-0.66 (±0.58)	-	-	-	-
Dusk-legged guan										
ψ(.) *p*(global)[3]	0	0.43	10	634.70	-	-	-	-	-	-
ψ(forest500) *p*(global)	2.70	0.11	11	633.87	-	-	-0.43 (±0.52)	-	-	-
ψ(roads200) *p*(global)	3.27	0.08	11	634.44	-	-	-	-	0.20 (±0.41)	-
ψ(elev200) *p*(global)	3.36	0.08	11	634.53	-0.16 (±0.39)	-	-	-	-	-
ψ(reserve) *p*(global)	3.48	0.08	11	634.65	-	-	-	-	-	-0.09 (±0.43)
Gray-fronted dove										
ψ(.) *p*(global)[3]	0	0.28	10	547.71	-	-	-	-	-	-
ψ(hydro200) *p*(global)	0.33	0.24	11	544.51	-	-	-	0.60 (±0.38)	-	-
ψ(elev200) *p*(global)	2.30	0.09	11	546.48	-0.36 (±0.33)	-	-	-	-	-
ψ(roads200) *p*(global)	3.35	0.05	11	547.53	-	-	-	-	0.13 (±0.31)	-
ψ(reserve) *p*(global)	3.49	0.05	11	547.67	-	-	-	-	-	0.06 (±0.31)
ψ(hydro200+elev200) *p*(global)	3.50	0.05	12	543.93	-0.26 (±0.35)	-	-	0.57 (±0.39)	-	-
ψ(forest200) *p*(global)	3.53	0.05	11	547.71	-	-	-0.01 (±0.34)	-	-	-
Black-fronted titi monkey										
ψ(.) *p*(global)[4]	0	0.21	8	330.13	-	-	-	-	-	-
ψ(elev500) *p*(global)	0.30	0.18	9	327.29	2.94 (±2.54)	-	-	-	-	-
ψ(hydro1000) *p*(global)	0.31	0.18	9	327.30	-	-	-	2.82 (±2.61)	-	-
ψ(forest500) *p*(global)	2.36	0.06	9	329.35	-	-	0.87 (±0.83)	-	-	-
ψ(roads500) *p*(global)	2.82	0.05	9	329.81	-	-	-	-	1.07 (±1.60)	-
ψ(reserve) *p*(global)	3.13	0.04	9	330.12	-	-	-	-	-	-0.06 (±1.04)
ψ(hydro1000+reserve) *p*(global)	3.14	0.04	10	326.80	-	-	-	3.56 (±3.29)	-	-1.19 (±1.74)

ψ(elev500+roads500) *p*(global)	3.18	0.04	10	326.84	4.00 (±4.78)	-	-	-	1.18 (±2.18)	-
Buffy-tufted marmoset										
ψ(.) *p*(global)[4]	0	0.21	8	211.04	-	-	-	-	-	-
ψ(hydro500+reserve) *p*(global)	0.51	0.16	10	205.08	-	-	-	2.30 (±1.62)	-	-2.39 (±1.67)
ψ(forest500) *p*(global)	1.05	0.12	9	208.95	-	-	0.81 (±0.55)	-	-	-
ψ(hydro500) *p*(global)	1.44	0.10	9	209.34	-	-	-	0.99 (±1.04)	-	-
ψ(reserve) *p*(global)	1.71	0.09	9	209.61	-	-	-	-	-	-2.31 (±5.52)
ψ(hydro500+forest500) *p*(global)	1.94	0.08	10	206.51	-	-	1.00 (±0.80)	1.38 (±1.52)	-	-
ψ(reserve+forest500) *p*(global)	2.61	0.06	10	207.18	-	-	1.19 (±0.88)	-	-	-1.39 (±1.37)

* 95% confidence interval does not include 0.

[1] p(global) = season + temperature + rain + fruit + slope; [2] p(global) = temperature + percentage of high-quality forest cover at 500 m buffer size; [3] p(global) = season + temperature + rain + fruit + slope + percentage of high-quality forest cover at 200 m buffer size; [4] p(global) = temperature + rain + fruit + time of day surveyed.

Table A3. Model selection analysis (cumulative wAICc>0.80) and detection probability (p) covariate coefficients (temperature, rain, fruit, wet season, percentage of high-quality forest cover, terrain slope, and time of day surveyed) for seven Neotropical frugivores at an Atlantic Forest site in Brazil.

					Beta estimates						
Model	ΔAICc	wAICc	K	-2LLL	Temperature	Rain	Fruit	Season	Forest cover	Slope	Time of day
Paca											
ψ(top) p(slope)[1]	0	0.20	7	528.20	-	-	-	-	-	-0.28* (±0.13)	-
ψ(top) p(slope+forest500)	0.19	0.18	8	525.42	-	-	-	-	-0.33 (±0.19)	-0.34* (±0.13)	-
ψ(top) p(slope+rain)	0.94	0.13	8	526.17	-	0.15 (±0.11)	-	-	-	-0.29* (±0.13)	-
ψ(top) p(.)	1.92	0.08	6	532.94	-	-	-	-	-	-	-
ψ(top) p(slope+fruit)	2.18	0.07	8	527.41	-	-	-0.11 (±0.12)	-	-	-0.30* (±0.13)	-

ψ(top) *p*(slope+temp)	2.76	0.05	8	527.99	0.06 (±0.12)	-	-	-	-	-0.28* (±0.13)	-
ψ(top) *p*(slope+season)	2.83	0.05	8	528.06	-	-	-	-0.74* (±0.17)	-	-0.28* (±0.13)	-
ψ(top) *p*(rain)	2.88	0.05	7	531.08	-	0.14 (±0.11)	-	-	-	-	-
Collared peccary											
ψ(top) *p*(forest500)[2]	0	0.26	6	179.41	-	-	-	-	0.96* (±0.45)	-	-
ψ(top) *p*(forest500+temp)	1.88	0.10	7	178.47	0.24 (±0.25)	-	-	-	0.99* (±0.44)	-	-
ψ(top) *p*(forest500+fruit)	2.34	0.08	7	178.93	-	-	0.19 (±0.28)	-	0.95* (±0.45)	-	-
ψ(top) *p*(.)	2.48	0.08	5	184.56	-	-	-	-	-	-	-
ψ(top) *p*(forest500+rain)	2.68	0.07	7	179.27	-	-0.08 (±0.22)	-	-	0.97* (±0.45)	-	-
ψ(top) *p*(forest500+season)	2.70	0.07	7	179.29	-	-	-	-2.77* (±0.46)	0.96* (±0.45)	-	-
ψ(top) *p*(forest500+slope)	2.79	0.07	7	179.38	-	-	-	-	0.93 (±0.48)	-0.05 (±0.27)	-
ψ(top) *p*(slope)	3.47	0.05	6	182.88	-	-	-	-	-	-0.33 (±0.26)	-
ψ(top) *p*(fruit)	4.41	0.03	6	183.82	-	-	0.24 (±0.28)	-	-	-	-
Brocket deer											
ψ(top) *p*(season)[2]	0	0.13	7	851.60	-	-	-	-0.55* (±0.13)	-	-	-
ψ(top) *p*(temp)	0.59	0.10	7	852.62	0.18 (±0.10)	-	-	-	-	-	-
ψ(top) *p*(.)	1.01	0.08	7	854.02	-	-	-	-	-	-	-
ψ(top) *p*(fruit)	1.15	0.07	8	849.82	-	-	0.15 (±0.10)	-	-	-	-
ψ(top) *p*(season+rain)	1.26	0.07	6	854.81	-	-0.11 (±0.09)	-	-0.53* (±0.13)	-	-	-
ψ(top) *p*(season+forest500)	1.34	0.07	7	852.14	-	-	-	-0.56* (±0.13)	0.12 (±0.10)	-	-
ψ(top) *p*(forest500)	2.12	0.04	8	851.55	-	-	-	-	0.13 (±0.10)	-	-
ψ(top) *p*(temp+forest500)	2.12	0.05	8	850.09	0.17 (±0.10)	-	-	-	0.12 (±0.10)	-	-
ψ(top) *p*(temp+rain)	2.14	0.04	7	853.08	0.19 (±0.10)	-0.1 (±0.09)	-	-	-	-	-
ψ(top) *p*(fruit+forest500)	2.32	0.04	8	850.59	-	-	0.15 (±0.10)	-	0.13 (±0.10)	-	-
ψ(top) *p*(season+temp)	2.41	0.04	8	850.70	0.07 (±0.14)	-	-	-0.60* (±0.16)	-	-	-
ψ(top) *p*(season+slope)	2.45	0.04	8	850.89	-	-	-	-0.54* (±0.13)	-	-0.06 (±0.09)	-
ψ(top) *p*(temp+fruit)	2.65	0.03	8	851.32	0.13 (±0.11)	-	0.09 (±0.11)	-	-	-	-
Dusk-legged guan											
ψ(top) *p*(forest500+rain)[3]	0	0.30	6	641.26	-	0.22* (±0.10)	-	-	-0.28* (±0.12)	-	-

ψ(top) *p*(rain)	2.22	0.10	5	646.15	-	0.20* (±0.10)	-	-	-	-	-
ψ(top) *p*(forest500)	2.29	0.10	5	646.22	-	-	-	-	-0.25* (±0.12)	-	-
ψ(top) *p*(season+rain)	3.03	0.07	6	644.29	-	0.23* (±0.10)	-	-1.55* (±0.18)	-	-	-
ψ(top) *p*(season+fruit)	3.21	0.06	6	644.47	-	-	0.35* (±0.16)	-1.80* (±0.23)	-	-	-
ψ(top) *p*(forest500+fruit)	3.74	0.05	6	645.00	-	-	0.13 (±0.12)	-	-0.26* (±0.12)	-	-
ψ(top) *p*(temp+rain)	3.99	0.04	6	645.25	-0.11 (±0.12)	0.22* (±0.10)	-	-	-	-	-
ψ(top) *p*(.)	4.03	0.04	4	650.50							
ψ(top) *p*(rain+fruit)	4.31	0.04	6	645.57	-	0.20* (±0.10)	0..09 (±0.12)	-	-	-	-
Gray-fronted dove											
ψ(top) *p*(slope)^3	0.00	0.13	5	552.86	-	-	-	-	-	0.20 (±0.11)	-
ψ(top) *p*(slope+forest200)	0.06	0.12	6	550.25	-	-	-	-	0.24 (±0.15)	0.27* (±0.12)	-
ψ(top) *p*(slope+fruits)	0.34	0.11	6	550.53	-	-	-0.18 (±0.12)	-	-	0.18 (±0.11)	-
ψ(top) *p*(fruits)	0.46	0.10	5	553.32	-	-	-0.21 (±0.12)	-	-	-	-
ψ(top) *p*(.)	0.99	0.08	4	556.39	-	-	-	-	-	-	-
ψ(top) *p*(slope+season)	1.10	0.07	6	551.29	-	-	-	-0.32 (±0.25)	-	0.21 (±0.11)	-
ψ(top) *p*(season)	1.68	0.05	5	554.54	-	-	-	-0.97* (±0.17)	-	-	-
ψ(top) *p*(slope+temp)	2.51	0.04	6	552.70	-0.04 (±0.12)	-	-	-	-	0.20 (±0.11)	-
ψ(top) *p*(slope+rain)	2.55	0.04	6	552.74	-	-0.04 (±0.11)	-	-	-	0.20 (±0.11)	-
ψ(top) *p*(fruits+forest200)	2.63	0.03	6	552.82	-	-	-0.20 (±0.12)	-	0.10 (±0.15)	-	-
ψ(top) *p*(fruits+temp)	2.74	0.03	6	552.93	0.09 (±0.14)	-	-0.26 (±0.14)	-	-	-	-
Black-fronted titi monkey											
ψ(top) *p*(temp+forest500)^3	0	0.62	7	323.75	0.48* (±0.14)	-	-	-	0.42* (±0.14)	-	-
ψ(top) *p*(forest500+season)	3.33	0.12	7	327.20	-	-	-	1.24* (±0.22)	0.43* (±0.14)	-	-
ψ(top) *p*(forest500+time)	4.07	0.08	7	327.87	-	-	-	-	0.40* (±0.14)	-	-5.19* (±2.05)
Buffy-tufted marmoset											
ψ(top) *p*(temp)^3	0	0.14	8	206.34	0.51* (±0.26)	-	-	-	-	-	-
ψ(top) *p*(temp+rain)	0.61	0.10	7	208.92	0.52* (±0.26)	0.26 (±0.18)	-	-	-	-	-
ψ(top) *p*(season)	0.98	0.08	6	213.48	-	-	-	-0.57 (±0.42)	-	-	-
ψ(top) *p*(.)	1.37	0.07	7	211.02	-	-	-	-	-	-	-

ψ(top) p(temp+forest500)	1.62	0.06	7	209.41	0.48 (±0.25)	-	-	-	0.23 (±0.22)	-	-
ψ(top) p(temp+fruit)	1.72	0.06	8	207.81	0.47 (±0.26)	-	0.22 (±0.23)	-	-	-	-
ψ(top) p(temp+season)	1.89	0.05	7	210.91	0.38 (±0.29)	-	-	-0.92 (±0.50)	-	-	-
ψ(top) p(rain)	2.21	0.05	8	208.44	-	0.24 (±0.18)	-	-	-	-	-
ψ(top) p(fruit)	2.30	0.04	8	208.60	-	-	0.30 (±0.23)	-	-	-	-
ψ(top) p(temp+time)	2.34	0.04	8	208.00	0.50 (±0.26)	-	-	-	-	-	2.03 (±2.69)
ψ(top) p(season+rain)	2.69	0.04	8	208.21	-	0.18 (±0.19)	-	-0.68 (±0.44)	-	-	-
ψ(top) p(forest500)	2.70	0.04	8	209.04	-	-	-	-	0.26 (±0.23)	-	-
ψ(top) p(season+forest500)	2.71	0.04	8	208.36	-	-	-	-0.72 (±0.45)	0.23 (±0.23)	-	-

* 95% confidence interval does not include 0.

[1] ψ(top) = weighted distance to reserve border + percentage of high-quality forest cover at 200 m buffer; [2]ψ(top) = road density at 1,000 m buffer size; [3]ψ(top) = constant (ψ(.)).

Capítulo 2: Landscape Use and Co-occurrence Patterns of Neotropical Spotted Cats

Mariana B. Nagy-Reis[1], James D. Nichols[2], Adriano G. Chiarello[3], Milton C. Ribeiro[4], Eleonore Z. F. Setz[1a]

[1] Mammal Ecology and Behavior lab (LAMA), Department of Animal Biology, Universidade Estadual de Campinas (UNICAMP), Bertrand Russel, 1505, mailbox: 6109, Campinas, SP, 13083-970, Brazil. [a] Email: setz@unicamp.br.

[2] USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD, 20708, USA. E-mail: jnichols@usgs.gov.

[3] Department of Biology, Universidade de São Paulo (USP), Av. Bandeirante, 3900, Ribeirão Preto, SP, 14040-901, Brazil. E-mail: bradypus@ffclrp.usp.br.

Corresponding author: Mariana B. Nagy-Reis, Department of Animal Biology,

[4] Spatial Ecology and Conservation lab (LEEC), Department of Ecology, Universidade Estadual de São Paulo (UNESP), Av. 24A, 1515, Rio Claro, SP, 13506-900, Brazil. E-mail: mcr@rc.unesp.br.

Universidade Estadual de Campinas, UNICAMP, Biology Institute, Bertrand Russel, 1505, mailbox: 6109, Campinas, SP, 13083-970, Brazil.

E-mail: mariana.nbreis@gmail.com; Phone number: 55(11)98709-4109

Short-title: Habitat Use and Co-occurrence of Spotted Cats

Abstract

Small felids influence ecosystem dynamics through prey and plant population changes. Although most of these species are threatened, they are accorded one of the lowest research efforts of all felids, and we lack basic information about them. Since Neotropical felids occur in sympatry, assessing the role of interspecific interactions along with the relative importance of landscape characteristics is necessary to understand how this group uses the habitat. Here, we selected three morphologically and closely related species of small Neotropical cats to evaluate the role of interspecific interactions, distance to reserve border, geomorphometry, environmental, and anthropogenic landscape attributes on their habitat use. We collected data with camera trapping and scat sampling in a large Atlantic forest remnant (35,000 ha). We used occupancy modeling to investigate whether these species occur together more or less frequently than would be expected if they were independent, while dealing with imperfect detection and incorporating possible habitat preferences into the models. We did not find evidence that one species affects the occupancy of the other. We found that proximity to a high protection area was a more important driver of Neotropical spotted cats' occurrence than interspecific interactions or geomorphometry and environmental landscape characteristics. Although intraguild interference competition is usually an important determinant of carnivore distribution, our evidences suggest that the occurrence of small felids can be most strongly influenced by areas with high protection status, emphasizing the importance of maintaining and creating reserves and other areas with elevated protection for the proper management and conservation of the group.

Keywords: *Leopardus*, ocelot, margay, oncilla, tricology, sympatry, co-existence, occupancy modeling, felid.

1. Introduction

Predators influence ecosystem dynamics and can regulate the trophic cascade [1, 2]. They affect prey population and, as a result, alter plant abundance, composition, succession, dispersion, and diversity [2, 3]. Consequently, the loss of this key group can lead to regime shifts, alternative states of ecosystems, and possible losses of ecosystem services [2]. Given the role of carnivores on ecosystem functioning and their sensitivity to the environment, their persistence may be indicative of potential ecological integrity [4]. Therefore, they can serve as a useful tool for protected area design and conservation planning [5].

Among the carnivores, felids are at an extreme end because of their unanimous coherence to eating flesh [6]. Historically, felids have suffered several anthropogenic impacts, particularly trapping for fur and direct felid-human conflict [7, 8]. More recently, mammalian carnivores face local extinction due to habitat loss and fragmentation, exacerbated by their relatively large home ranges, low densities, and direct persecution by humans [4,9-11].

Given the current scenario, understanding how species relate spatially to the environment and to human disturbances is critical to the assignment of areas for conservation and the development of conservation strategies [11-15]. Besides landscape characteristics, interspecific interactions may also regulate the occurrence, distribution or permanence of species [16]. In carnivore assemblages, intraguild interference competition and killing are important determinants of species abundance and distribution and can lead to adaptive responses in use of space and activity patterns [6, 17, 18], enabling the coexistence of morphologically similar species [19].

Because of relatively recent divergence and constrains imposed by foraging and diet, felids present similar morphologies [20, 21]. Thus, they are a good model for understanding how closely related and morphologically similar species can coexist. However, though most felids are sympatric, with the largest assemblages occurring in the tropical regions of the Americas, little attention has been given to the coexistence of these species and its implications [7]. The Neotropical spotted cats are the main sympatric small felids in the Neotropical rainforests: *Leopardus pardalis* - ocelot, *L. wiedii* - margay, and *L. guttulus* - oncilla (formerly known as *L.tigrinus* [22]). However, they have been accorded one of the lowest research efforts of all felids, and basic information on their biology and ecology is urgently needed [6, 7].

Frequently, studies on species occurrence and distribution assume that all species present at a location are detected with certainty. However, accounting for imperfect detection is fundamental to avoid omission errors (false absence) [23, 24] or bias in parameter estimation [25]. Such omission errors may lead to incorrect inferences about species-habitat relationship or patterns of species co-occurrence [26]. A more recent adaptation to the occupancy models [27] allows such problems to be dealt with by incorporating non-detection as well as possible habitat preferences directly into the model set and evaluating co-occurrence patterns among pairs of species [26].

We investigated the role of geomorphometry, environmental and anthropogenic landscape attributes at multiple scales and interspecific interactions in the habitat use of Neotropical spotted cats in a large Atlantic forest remnant. Using a likelihood-based framework, we estimated the probability of occurrence and co-occurrence while accounting explicitly for imperfect detectability and habitat preferences. We developed specific models based on different hypotheses about effects of competition and habitat on the occurrence patterns of Neotropical spotted cats. Our hypothesis is that if landscape characteristics are important factors determining how spotted cats use the habitat, we would expect anthropogenic-related variables to be the main predictors, with a negative association between occupancy and road density and between occupancy and distance from reserve center, as both might be related to increased human pressures. To a lesser degree, we predicted that prey, hydrographic density, and forest cover would have a positive effect on their habitat use, since those variables represent important resources (food and water availability) and high-quality habitats. We also expected elevation to have a weak influence on how Neotropical spotted cats use the habitat, unless species were segregating in altitute due to the montaneous terrain in our study site; this phenomenon has been observed in other taxa (e.g. [26]). If competition is a major determinant of the habitat use of Neotropical spotted cats, we would expect their occupancy and/or detection probability to be lower when another spotted cat is present or detected; co-occurrence should be less than expected by chance, predicting avoidance, considering the commonness of interference intraguild competition and killing among carnivores [6, 17, 18] (see Fig. 1 for a schema of the hypotheses). We believe that this information will be useful for planning management actions towards the conservation of this key group in Neotropical forests and helpful in clarifying the role of interspecific interactions on the occurrence of small felids, which could benefit our understanding of how small felids occur in other ecosystems worldwide.

2. Methods

2.1. Study Site

Serra do Japi (southeast Brazil, coordinates 47°03'40"W to 46°52'20"W and 23°22'30"S to 23°11'35"S; Fig. 2) is one of the few large remnants of Atlantic Forest. The Atlantic Forest represents a global hotspot for biodiversity conservation [28], and currently it is highly fragmented (more than 80% of the remnants are < 50 ha in size), highly isolated (average distance between fragments is 1,440 m), and under negative edge influences (73% of remnants are 250 m from any forest edge) [29]. The study site is a Natural Heritage Area (35,000 ha) considered part of the UNESCO's Atlantic Forest Biosphere Reserve [30]. Located within this area is the Biological Municipal Reserve (REBIO - 2,071 ha) surrounded by a Buffer Zone (11,946 ha) (Fig. 2). The REBIO presents the highest protection status in the area, where the only permitted activities are research and education. The site is characterized by semideciduous mesophilic forest with mountainous terrain and a seasonal climate [31] The mean temperature is 19.7 ^{o}C and the mean annual rainfall is 1,422 mm, with a dry and cold season occurring from April to September and a wet and warm season from October to March [31].

2.2. Data collection

From April 2013 to September 2014, we conducted three campaigns (1- April 2013 to September 2013; 2- October 2013 to March 2014; 3- April 2014 to September 2014) to survey 45 sampling sites (spaced approx. 1.5 km apart) distributed in a regular grid across the forest remnant (Serra do Japi). Data collection of the three Neotropical spotted cats (*Leopardus pardalis*, *L. wiedii*, and *L. guttulus*) at each sampling site was concentrated in approx. 70 days within each campaign. We used camera trapping (passive infrared camera traps; Bushnell Trophy Cam; N=5,198 trap days) and scat sampling during the first and the second campaigns, and only scat sampling during the third campaign. All cameras were fixed about 20 cm above ground and installed with a minimum distance of approx. 50 m from roads or trails, and none of the sites were located close to roads that were highly used or open to the public. We visited each sampling site six times and collected all scats found along a 1-km segment in the dirt road closest to each site (always within 1km from the sites).

2.3. Identification of species using tricology and genetic

Because felids defecate conspicuously to signal their presence [32, 33] and groom frequently [34], samples of scats with hairs are particularly easy to obtain. After washing the scats with running water and drying them, we collected the guard hairs found in each sample to identify the species to which the hair belonged. We cleaned the guard hairs with ethyl alcohol and the cuticular impressions were obtained by pressing the hairs against a thin layer of nail varnish and leaving them to dry for three to five minutes on glass slides with the help of a bench vise (adapted from [35]). We photographed the cuticular impressions at 400x magnification and compared the pattern of the cuticles with our reference collection (obtained from hairs collected from museum specimens) and published guides [36, 37].

Hair sampling can lead to reliable detections of rare and cryptic animals [38], and the use of mammalian hair for identification of taxa, known as tricology, is an established low-cost method (e.g. [39-45]). This technique has also been proven to be as consistent as molecular methods for identification of some Neotropical felids [46]. To test the accuracy of our identification through tricology, we conducted molecular analysis for 74% of the samples (N=49). We used mini-barcoding for molecular identification, comparing two markers from mitochondrial DNA [ATP6 (126 bp) and cytochrome oxidase I gene (COI) (187 bp)], applying the primers developed by [47]. The obtained sequences were compared with reference sequences from tissue samples of each species. We achieved confirmation for 100% of the samples, giving us confidence in our identification and confirming the reliability of the method.

2.4. Covariates used to model occupancy

For each site, we determined the elevation, percentage of high-quality forest cover, hydrographic density, road density, weighted distance to reserve border (i.e. proximity to highly protected area weighted by the protection status where the site was located), and prey index. We obtained elevation from digital elevation models (DEM) available from Topodata Geomorphic database of Brazil [48]. We mapped the vegetation cover of the study site using high resolution satellite image interpretation at a 1:5,000 scale, and validaded the cover map by extensive field verification by a botanist. We used the percentage of intermediate and advanced forest succession as an indicator of high-quality forest cover, which was calculated using Geographical Resources Analysis Support System (GRASS) [49]. Hydrography and roads were mapped at a 1:5,000 scale with Quantum Gis software [50], using data from high resolution satellite images and cartographic maps (Secretariat of Economy and Planning - São Paulo State Government, at 1:10,000). We also estimated road and hydrographic densities using the Kernel density function in ArcGIS software [51]. We measured the distance from each site to the nearest Biological Municipal Reserve (REBIO) border (in meters), giving negative distances to sites within the REBIO and positive distances otherwise. Then we multiplied these distances by the protection status weight of the subarea in which each site was located (REBIO = 1; REBIO’s Buffer Zone = 2; and within the Natural Heritage Area but outside these two subareas = 3), obtaining a distance from the reserve border weighted by the protection status of the area where the site was located (‘weighted distance to reserve border’, which ranged from -1,252 to 19,944). We were not able to incorporate the covariate ‘weighted distance to reserve border’ in the ocelot models (since the β coefficients did not converge), so we used only the distance to reserve border for this species. Given the height at which the cameras were positioned and the number of records, in separated analyses we estimated the occupancy of the main potential prey for each felid species using data from our camera traps ($N_{\text{small mammals}}=77$; $N_{\text{medium-sized mammals}}=897$; $N_{\text{ground-dwelling birds}}=1,936$). Although cameras are more commonly used to survey medium- and large-sized mammals, they can also be used to collect data on small mammals [52-57] and ground-dwelling birds [58-60]. They may provide a new and cost-effective technique for surveying terrestrial small mammals, particularly when presence data are the main requirement of the survey [61, 62]. The use of camera traps to collect data on small mammals to assess prey availability for carnivores was already performed [63], but here we went a step further and included imperfect detection on prey estimates (through occupancy modeling) instead of using the number of captures. We considered small mammals (<1kg; mainly small rodents and marsupials) and small birds (<0.2g; mainly passerines and doves) as the main prey for margay and oncilla, and small and medium-sized mammals (between 1 and 13kg; mainly opossums, Brazilian rabbit, paca, armadillo, and porcupine) as well as small and medium-sized birds (<0.5g; passerines, doves, and tinamous) for ocelot [64-70]. The prey index was obtained by summing the site occupancy of potential prey for each felid species. We normalized all covariates and used only covariates with low correlation ($r<0.50$, based on a Spearman's correlation matrix) in the final model sets.

We adopted a multi-spatial scale approach [10, 71] while testing the influence of the covariates on felid occupancy. The scales were defined as concentric circles (buffers) of 500 and 1,000 m radius around each sampling site (measures that retain minimal buffer overlap), and we calculated each site covariate for each scale.

2.5. Single-species occupancy models

We used single-season occupancy modeling [27] – with a likelihood-based approach – to estimate the occupancy (ψ) of each spotted cat species and evaluate its influential factors, accounting for detection probability (p). Because the size of the home ranges of ocelots, margays, and oncillas exceeds that of our sampling unit [72-75] we used occupancy as a measure of their habitat use [23,76]. The detection histories (H) were constructed for each site over fifteen sampling occasions (three sampling occasions of each method - camera trap and scat - for the first and the second campaigns and three sampling occasions of scat sampling for the third campaign). Each sampling occasion of scat sampling consisted of one visit at the site, while each occasion for camera trapping comprised of a consecutive 18-day camera trap survey. For each site and sampling occasion, species detection was recorded as "1" while non-detection was recorded as "0".

We evaluated candidate models and estimated parameters using PRESENCE software [77], performing a logistic regression analysis to determine the covariates that best explain occupancy. First, we determined the scale that best represents each species' response to the habitat. We used a general model for p (that consisted of as many potential covariates as possible) and allowed occupancy (ψ) to vary (following [78]) by only the focal habitat covariate measured at the scales of the various buffer sizes (Online Appendix A, Table A1). We then developed another model set to investigate the variation in occupancy. We allowed ψ to be constant ($\psi(.)$) or to vary as a function of either a single covariate or a combination of two (additive effect). We used covariates at the best scale (from the previous step) and a general model for *p*. The potential covariates used in the general model for *p* were: method used to survey each sampling occasion (scat sampling or camera trapping), season (dry 2013, wet 2013, or dry 2014), degree of soil coverage by plants or leaf litter on the roads where scats were sampled (0- no coverage; 1- low to medium coverage; and 2- high coverage), and percentage of high-quality forest cover at the 500 m buffer around each site. By using a general model for the parameters that were not investigated within a specific model set, we reduced the possibility that imposed constraints (on *p*, for example) would result in residual sampling variation being attributed to a variation in occupancy.

We ranked candidate models using the Akaike's Information Criterion adjusted for small sample size (AICc) [79] and excluded all models that did not converge. We considered the covariate(s) from the top-ranked model(s) (ΔAICc<2) as the most likely determinant(s) of the species' occupancy. When different spatial scales were equally plausible (ΔAICc<2), we chose to use the scale closer to the home range size of the spotted cats (1,000 m) in the final models. Additionally, we assessed the relative importance of each covariate by summing the Akaike weights (wAICc) of all the models in which that covariate was present [79]. We applied model averaging [79] to estimate the overall occupancy of each species at our study site.

2.6. Co-occurrence models

We investigated whether the presence of one species influences the occupancy and detection probability of another species by pair-wise comparisons for all species using two-species single-season occupancy models [26]. We used the ψBa/rBa parameterization in PRESENCE software [77], assuming that the dominant species was always the larger in the analyzed pair (ocelot in ocelot-margay and ocelot-oncilla pairs, and margay in the margay-oncilla pair; [80]). The parameters estimated for occupancy were: ψA (occupancy of dominant species), ψBA (occupancy of subordinate species when the dominant species is present), and ψBa (occupancy of subordinate species when the dominant species is absent). We modeled ψA, ψBA, and ψBa, incorporating the best covariate revealed in the single-species models for each species to account for possible differences in habitat preferences. We built models that assumed that the occupancy of the subordinate species was influenced by the dominant species ($\psi BA \neq \psi Ba$) or was independent of the dominant species ($\psi BA = \psi Ba$).

For detection probability, the parameters estimated were: rA (probability of dominant species being detected when the subordinate species is present), pA (probability of dominant species being detected when the subordinate species is absent), pB (probability of subordinate species being detected when the dominant species is not present), rBA (probability of subordinate species being detected when the dominant species is present and detected), rBa (probability of subordinate species being detected when the dominant species is present but not detected). We built models where the detection probability of the subordinate species was influenced by the presence ($pB \neq rBa$ and rBA) or detection ($rBa \neq rBA$) of the dominant species or was independent of the dominant species ($pB = rBa = rBA$), as well as models that assumed that the detection of the dominant species was influenced by the detection of the subordinate species ($r\mathrm{A} \neq p\mathrm{A}$) or independent ($r\mathrm{A} = p\mathrm{A}$).

We calculated the species interaction factor (SIF) for occupancy (phi; [81]) and detection probability (delta $= \frac{r\mathrm{A} \times r\mathrm{BA}}{r\mathrm{A} \times \left((r\mathrm{A} \times r\mathrm{BA}) + ((1 - r\mathrm{A}) \times r\mathrm{Ba})\right)}$; adapted from the formula for phi from [81]). We obtained the parameters' estimates by model averaging [79] the estimates of each species-pair model set. If two species occur or are detected independently, SIF=1. If SIF<1, species co-occur or are detected less frequently than would be expected if they were independent (i.e. avoidance). If SIF>1, species co-occur or are detected more frequently than expected (i.e. aggregation) [81].

We used the AICc to rank candidate models [79] after excluding models that did not converge. To infer about the co-occurence patterns, we considered the estimated parameters ($\psi\mathrm{A}$, $\psi\mathrm{BA}$, $\psi\mathrm{Ba}$, $r\mathrm{A}$, $p\mathrm{A}$, $p\mathrm{B}$, $r\mathrm{Ba}$, $r\mathrm{BA}$), the relation between them, the top-ranked model(s) ($\Delta\mathrm{AICc}<2$), and the SIF calculated for each species pair.

3. Results

3.1. Spatial scale and covariate selection

We excluded the prey index for ocelot because it was highly correlated with geomorphometry such as elevation and slope (at all buffer sizes) ($p<0.05$ and $r_s>0.80$). Models with different scales were equally supported for most covariates and species, with the exception of high-quality forest cover for ocelot, which was better explained by the 500 m scale (Online Appendix A, Table A1).

3.2. Single-species occupancy

We had 123 detections (N=5,198 trap days) of the three Neotropical spotted cats (Tab. 1). There was little evidence for the null model with constant occupancy ($\psi(.)$) across sites ($\psi(.)$ model with AICc weights ≤ 0.14) (Online Appendix A, Table A2) and the cats' occupancy varied according to landscape characteristics (Fig. 3). Margay and ocelot had higher occupancies closer to a more protected area (Fig. 3), and weighted distance to reserve border was the main factor influencing their occupancy, emerging as the top-ranked model (Online Appendix A, Table A2) with high relative importance (Fig. 4). All other analyzed covariates had overall low relevance (Fig. 4; Online Appendix A, Table A2).

3.3. Co-occurrence patterns

There was no evidence that one species affects the occupancy of the other (Table 2; Table 3). For all three pairs of species (ocelot-margay, ocelot-oncilla, and margay-oncilla), the models where the pair had a similar occupancy, and where the subordinate species had similar occupancy regardless of the dominant being at the site or not (i.e. $\psi\mathrm{A}=\psi\mathrm{BA}=\psi\mathrm{Ba}$), were ranked as the top models (Table 2). Furthermore, models where the covariate 'weighted distance from reserve border' was incorporated with ocelot and margay occupancy were always ranked better than the models without this covariate, reinforcing the importance of the reserve for both species (Table 2).

We also found no evidence that the presence of margay or oncilla has an effect on the detection probability of the more dominant species, the ocelot (i.e. $p\mathrm{A}\neq r\mathrm{A}$), or that the presence or detection of ocelot has an effect on the detection of margay (i.e. $p\mathrm{B}\neq r\mathrm{BA}=r\mathrm{Ba}$ or $p\mathrm{B}\neq r\mathrm{BA}\neq r\mathrm{Ba}$) (Table 3 and 4). However, we found evidence that the presence of margay and the presence and detection of ocelot increases the detection probability of oncilla (i.e. margay-oncilla: $p\mathrm{B}\neq r\mathrm{BA}=r\mathrm{Ba}$; ocelot-oncilla: $p\mathrm{B}\neq r\mathrm{BA}\neq r\mathrm{Ba}$; Tables 3 and 4).

4. Discussion

When investigating species' distribution and their use of habitat, assessing the relative importance of landscape attributes and the role of interspecific interactions is often difficult. Here, we used occupancy modeling [26, 27] to explicitly incorporate detection probability and habitat variables while examining co-occurrence patterns and landscape use by three sympatric and morphologically similar species of Neotropical cats. Predators can be considered a key group because they affect prey and plant population, influencing ecosystem dynamics [1-3]. However, most species of felids are threatened, or we lack basic information about them. All three Neotropical spotted cats analyzed here are suffering from population decrease, and two (*L. wiedii* and *L. guttulus*) are considered 'Near Threatened' or 'Vulnerable' [82]. We demonstrated that the proximity to a more protected area is the main factor influencing the habitat use of Neotropical spotted cats in a large Atlantic forest remnant, and we had low support for the hypothesis that interspecific interactions modulate how they use the landscape.

Our first prediction that among the landscape characteristics, the human-related variables would be more important predictors of landscape use by Neotropical spotted cats was in part corroborated. We had some evidence that road density, which is also a measure of human accessibility, may have a negative effect on some spotted cats (given its negative beta estimates for two out of the three species analyzed), particularly on ocelots; however, it did not have a strong effect and was not a major factor for them. On the other hand, the spotted cats, especially ocelots and margays, used more areas closer to the reserve – a more protected area – even though our entire study area is under some type of protection (Biological Reserve, Buffer Zone, or Natural Heritage). Although 'weighted distance to reserve' was not in the top model for oncilla, the influence of this covariate on its occupancy was also in the predicted direction (negative). In other Atlantic Forest sites (in Argentina), only the occupancy of ocelots and larger felids (pumas and jaguars) were higher in high protection areas, while the contrary was observed for margays and oncillas [83]. Here, we demonstrated that the protection status might be important for all Neotropical spotted cats. Anthropogenic impacts are a major cause of felid mortality in several regions of the globe, and it accounts for up to 70% of deaths in some populations [7, 84]. Roads and human accessibility are important determinants of the occupancy of sensitive species (e.g. game species - [85]); and road kills can be common among felids and other carnivores [86, 87]. Larger felids are frequently involved in conflicts with humans due to preying on domestic animals or livestock [8, 84, 88-90]. Felids can also be exposed to diseases carried by domestic carnivores and to poaching, which even at moderate levels over a relatively short period of time can lead to massive population decline [84, 91, 92]. The exploitation of populations by the fur trade is the main threat to Neotropical spotted cats [7, 93]. Although the Brazilian government banned the export of wildcat skins in 1967, and despite the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) was enacted in 1975 [84], illegal hunting of felids still occurs (e.g. [88]). Hunting and other human-related pressures are most likely to occur in areas with low (or inefficient) protection status, high accessibility, or close proximity to reserves [84, 94-96]. In highly protected populations, anthropogenic mortality is rare [84].

Prey availability can also influence the abundance, density, occupancy and habitat use of carnivores [63, 97-100]. Although the influence of the prey index was in the predicted direction (positive), this variable and the environmental (hydrographic density and high-quality forest cover) and elevation covariates had a weak effect on the spotted cats’ habitat use. The possible opportunistic feeding behavior of Neotropical small cats [69] could explain the lack of effect of prey on their habitat use. However, we also note that prey availability, measured as the sum of prey occupancy at each site, ranged slightly across sites (mean 1.31±0.12) and did not account for differences in density. Therefore, we cannot yet discard a possible effect of prey on spotted cats' habitat use.

Intraguild competition is an important determinant of carnivores abundance and distribution, as it leads to spatial or temporal segregation among species [6, 17, 101]. However, when examining species co-occurrence patterns, it is often difficult to distinguish the difference between habitat preferences and competitive exclusions. Furthermore, since species present at a location are not always detected with certainty, incorporating detection probability along with habitat preferences directly into the model set may avoid incorrect inferences about co-occurrence patterns [26]. For instance, our single-species models showed that incorporating detection probability can result in a relative increase of up to 476% above naïve occupancy, emphasizing the importance of ecological and behavioral studies on cryptic and elusive species to account for detection probability. Our study is the first to assess co-occurrence patterns of small cats while dealing with imperfect detection.

We found no evidence that the presence of ocelot, margay, and oncilla have a negative influence on how each other uses the habitat, thus competitive exclusion among them is unlikely, at least within a conserved and protected area. Nonetheless, because occupancy does not account for variations in density, it is still possible that the presence of one species affect the density of the other, as previously suggested [102]. We also encourage further researches to analyze the effects of larger felids (e.g. pumas and jaguars) on the habitat use of smaller cats, which unfortunately, we did not have data to investigate (only six detections of pumas and none of jaguar). Finally, since land use and human activity can alter occupancy patterns [103] and behavior [104] of carnivores, it would be of interest to explore whether interspecific relations and co-occurrence patterns among small felids are affected by human disturbances.

However, we did find evidence that one species affects the behavior of the other, as oncilla is more likely to be detected if margay is present or if ocelot is either present or detected. Felids are highly territorial and use scent marks such as urine and feces to mark their territories [32]. We sampled felids in part using their scats, and the fact that the detection probability of this method was over twice the detection probability of camera traps implies that detection of an individual relied heavily on the presence of its feces and, therefore, its territorial scent mark. Two things should be noted: first, since we collected the feces as they were detected, the area of most detections became unmarked. Second, scent marks are frequently overmarked either by the same animal or other individuals [32]. Therefore, we suggest that the presence of a spotted cat (and consequently, its feces) increased the detection of another spotted cat as it was attracted to either over mark the feces or use an area rendered unmarked through collection of the scats. However, to clarify the mechanisms underlying our findings, more detailed studies on the behavior of the Neotropical spotted cats are necessary. What we can suggest so far is that such behavioral mechanisms are potentially regulating how these small felids share their habitats, and consequently alleviating the competition among them.

In conclusion, our results suggest that human-related factors, such as distance to a highly protected area, are more important drivers of Neotropical spotted cats' habitat use than are interspecific interactions, environmental landscape attributes, geomorphometry or, potentially, prey availability. We suggest that the dietary overlap of the three species might be small enough to allow co-existence [64-70], or that another behavioral mechanism besides differences in habitat preference, such as time partitioning, may allow them to co-exist [83, 93, 105, 106].

4.1. Management recommendations

Given the importance and vulnerability of spotted cats in Neotropical forests, several actions are required for their conservation, including enhancing forest connectivity and gathering basic information on their ecology and behavior [4, 107]. Here we underline the main management recommendations resulting from our study:

1) The use of methods that incorporate detection probability is critical to the understanding of species' responses to habitat and interspecific interactions. We showed how the use of occupancy models that deal with imperfect detection result in a tremendous relative increase above naïve occupancy for rare, cryptic, and elusive animals such as small felids. Our research also emphasizes the feasibility of alternative methods for surveying felids, such as scat sampling combined with tricology, which has a higher detection probability than camera traps and supplies non-invasive material for studying diet and performing molecular analysis, providing essential information on population parameters and ecology [33, 108]. We also confirmed the reliability of tricology as a low cost alternative to molecular methods for identification of Neotropical felids, as long as meticulous procedure is adopted by a trained researcher.

2) We demonstrated that the most important factor for managing small felids can be the maintenance of high protection areas and the establishment of future conservation areas for the group. Protected areas can decrease habitat loss [109] and anthropogenic pressures

94, 95] as well as improve the occupancy of key groups (Nagy-Reis et al. present study). However, because poaching may still occurs illegally, effective law enforcement and other management actions such as environmental education are also important to ensure the conservation of small felids.

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Figures

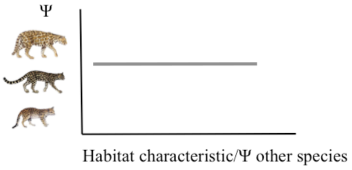
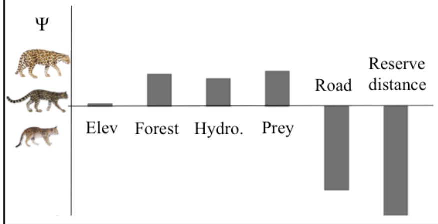
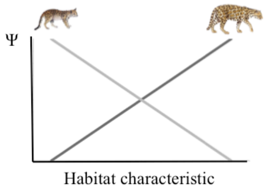
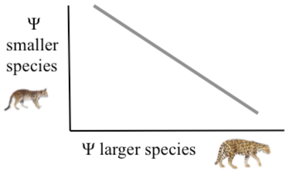
<table>
<tr><th>Hypothesis</th><th colspan="2">Expected</th><th>Scheme</th></tr>
<tr><td>Null hypothesis
Neotropical spotted cats occur regardless of habitat or interespecific interactions.</td><td colspan="2">Homogenous occurrence throughout the landscape and species co-occur as expected by chance.</td><td> </td></tr>
<tr><td rowspan="2">Hypothesis 1
Neotropical spotted cats occurrence depends on landscape attributes.</td><td rowspan="2">Heterogeneous occurrence throughout the landscape (according to habitat characteristics), indicating habitat preferences.</td><td>Species have similar habitat preferences.</td><td> </td></tr>
<tr><td>Species have different habitat preferences (segregation in space).</td><td> </td></tr>
<tr><td>Hypothesis 2
Neotropical spotted cats occurrence depends on interespecific interactions.</td><td colspan="2">Species co-occur less than expected by chance, indicating competition.</td><td> </td></tr>
</table>

Fig. 1. Study hypotheses for the occurrence of Neotropical spotted cats in a large Atlantic Forest remnant.

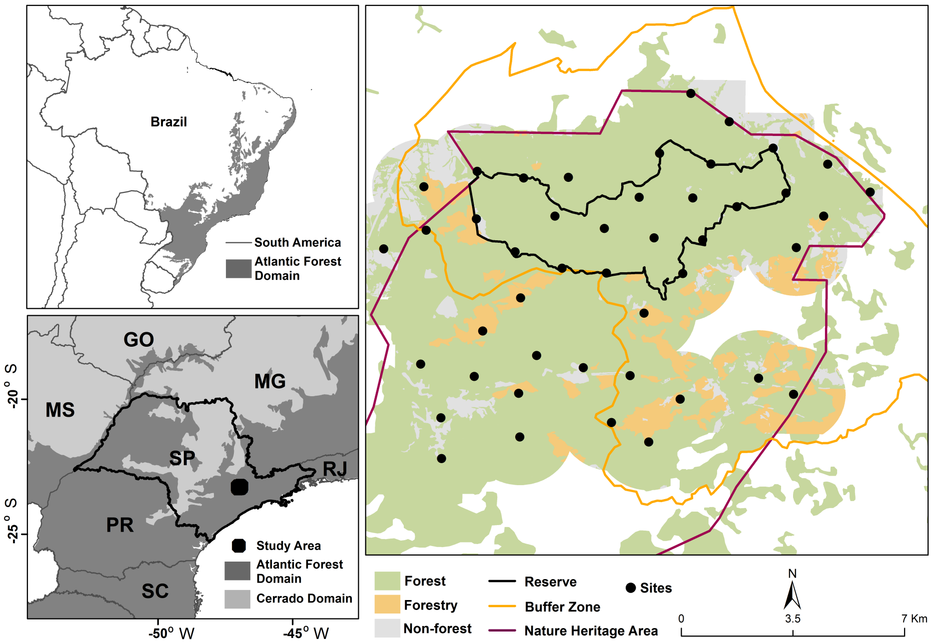


Fig. 2. Study area and the sampling sites' locations at Serra do Japi (Brazil) where Neotropical spotted cats were sampled using camera-trap and scat sampling.

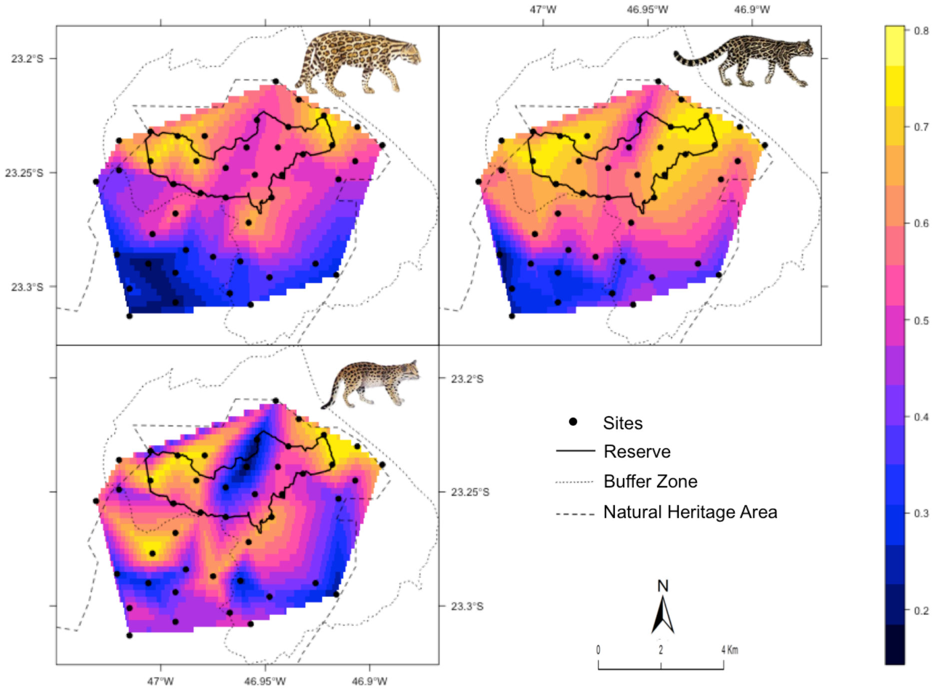


Fig. 3. Interpolated site occupancy of the three spotted cats at an Atlantic Forest site in Brazil: ocelot - *Leopardus pardalis* (top left), margay - *L. wiedii* (top right), oncilla - *L. guttulus* (bottom left).

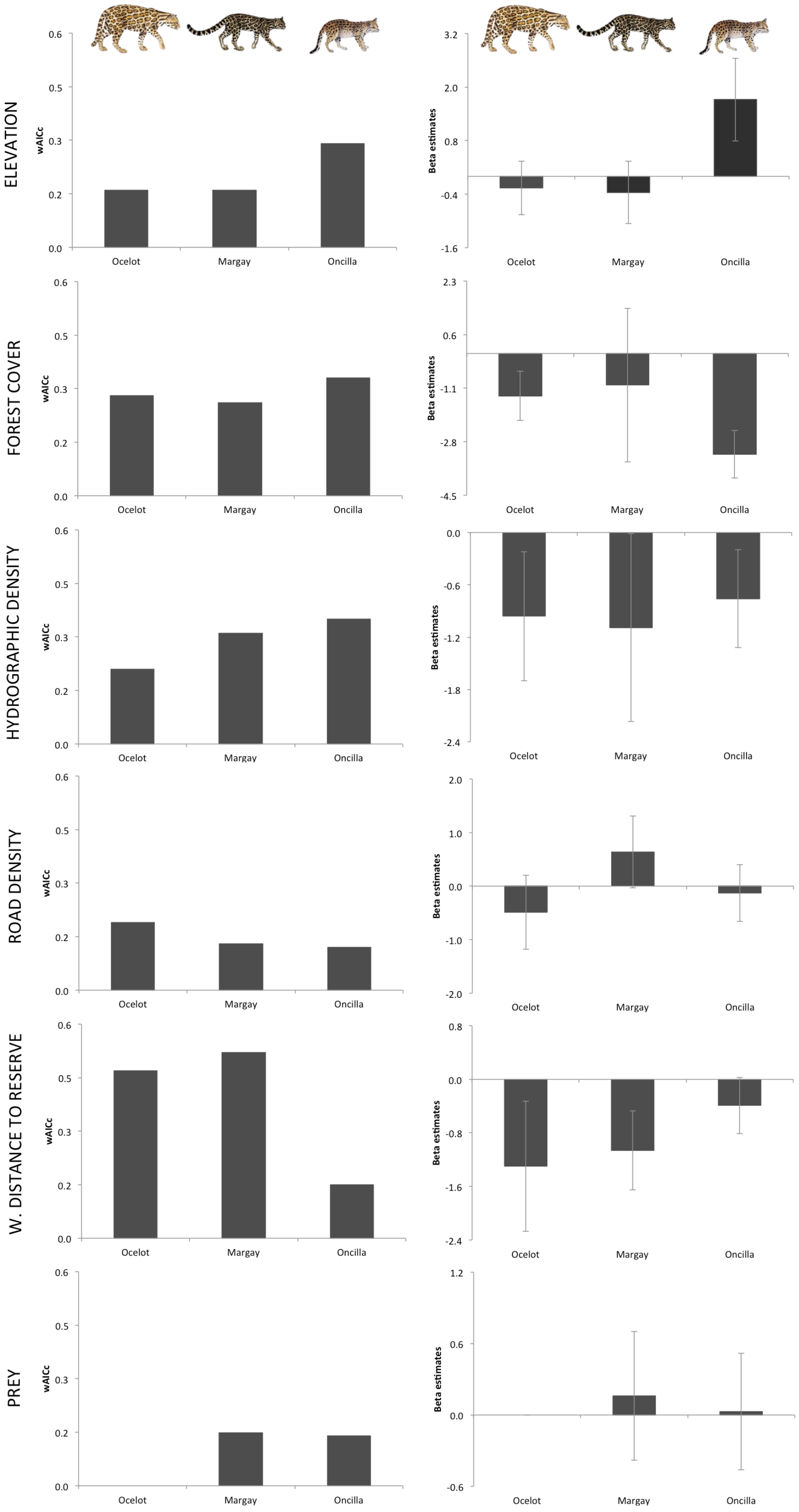

ELEVATION
FOREST COVER
HYDROGRAPHIC DENSITY
ROAD DENSITY
W. DISTANCE TO RESERVE
PREY
wAICc
Beta estimates
Ocelot
Margay
Oncilla
0.6
0.5
0.3
0.2
0.0
3.2
2.0
0.8
-0.4
-1.6
2.3
0.6
-1.1
-2.8
-4.5
0.0
-0.6
-1.2
-1.8
-2.4
2.0
1.0
0.0
-1.0
-2.0
0.8
0.0
-0.8
-1.6
-2.4
1.2
0.6
0.0
-0.6

Fig. 4. Influence of geomorphometry, environmental, and anthropogenic covariates on the occupancy of spotted cats in a large Atlantic Forest remnant, showing the sum of wAICc and the associated beta estimates with standard error estimated from the single-season single-species models.

Tables

Table 1. Number of records (detections) by each method (scat sampling and camera trap), number of sites with detections, naïve occupancy, estimated occupancy probability ($\hat{\psi}$) from multi-season single-species models, and relative increase above naïve occupancy when using estimates of the three Neotropical spotted cats in a large Atlantic Forest remnant.

	N detections		N sites w. detections	Naïve occup.	Detection probability (p)			Rel. increase above naïve occup. (%)
	Scats	Camera trap			Scats	Camera trap	Occup. prob. $\hat{\psi}$[1]	
Ocelot	10	16	9	0.13	0.07	0.09	0.48 (±0.15)	260
Margay	27	12	10	0.11	0.11	0.05	0.64 (±0.17)	476
Oncilla	29	29	16	0.22	0.21	0.09	0.64 (±0.13)	188

[1] Occupancy probability and standard deviation estimated by model averaging. [2] Percentage increase in estimated proportion of occupied sites when incorporating detection probability (p) [(occupancy probability/naïve occupancy)-1*100].

Table 2. Co-occurrence occupancy models used to evaluate the role of interspecific interactions on the habitat use of three sympatric Neotropical spotted cats in a large Atlantic Forest remnant.

Model	AICc	ΔAICc	wAICc	K	-2LLL
OCELOT VS. MARGAY					
ψA(reserve dist)=ψBA(reserve dist)=ψBa(reserve dist) p(global[1])	348.43	0	0.74	7	331.40

ψA(reserve dist),ψBA(reserve dist)=ψBa(reserve dist) *p*(global^{1})	350.77	2.34	0.23	8	330.77
ψA=ψBA=ψBa *p*(global^{1})	355.26	6.83	0.02	6	341.05
ψA,ψBA=ψBa *p*(global^{1})	357.01	8.58	0.01	7	339.98
ψA,ψBA,ψBa *p*(global^{1})	359.96	11.53	0.00	8	339.96
OCELOT VS. ONCILLA					
ψA(reserve dist)=ψBA=ψBa *p*(global^{2})	384.38	0	0.69	6	370.17
ψA(reserve dist),ψBA=ψBa *p*(global^{2})	387.18	2.80	0.17	7	370.15
ψA(reserve dist),ψBA,ψBa *p*(global^{2})	390.13	5.75	0.04	8	370.13
ψA=ψBA=ψBa *p*(global^{2})	389.43	5.05	0.06	5	377.89
ψA,ψBA=ψBa *p*(global^{2})	390.73	6.35	0.03	6	376.52
ψA,ψBA,ψBa *p*(global^{2})	391.99	7.61	0.02	7	374.96
MARGAY VS. ONCILLA					
ψA(reserve dist)=ψBA=ψBa *p*(global^{3})	448.01	0	0.46	3	441.42
ψA(reserve dist),ψBA=ψBa *p*(global^{3})	450.00	1.99	0.17	4	441.00
ψA=ψBA=ψBa *p*(global^{3})	449.95	1.94	0.17	2	445.66
ψA(reserve dist),ψBA,ψBa *p*(global^{3})	451.35	3.34	0.09	5	439.81
ψA,ψBA=ψBa *p*(global^{3})	451.81	3.80	0.07	3	445.22
ψA,ψBA,ψBa *p*(global^{3})	452.70	4.69	0.04	4	443.70

p(global^{1}) = *p*A,*r*A,*p*B,*r*BA,*r*Ba; *p*(global^{2}) = *p*A=*r*A,*p*B,*r*BA,*r*Ba; and *p*(global^{3}) = *p*A=*r*A=*p*B=*r*BA=*r*Ba.

Table 3. Occupancy (ψ), detection probability (*p* and *r*), and species interaction factor (SIF - phi and delta) estimated from co-occurrence occupancy models of three sympatric Neotropical spotted cats in a large Atlantic Forest remnant.

	ψA	ψBA	ψBa	*p*A	*p*B	*r*A	*r*BA	*r*Ba	Phi	Delta
Ocelot vs. Margay	0.59	0.63	0.63	0.10	0.08	0.05	0.08	0.08	1.00	1.00
Ocelot vs. Oncilla	0.66	0.77	0.77	0.04	0.04	0.06	0.38	0.10	1.00	3.26
Margay vs. Oncilla	0.62	0.68	0.63	0.07	0.07	0.09	0.18	0.12	1.03	1.38

ψA (occupancy of dominant species), ψBA (occupancy of subordinate species when the dominant species is present), ψBa (occupancy of subordinate species when the dominant species is absent), *r*A (probability of dominant species being detected when the subordinate species is present), *p*A (probability of dominant species being detected when the subordinate species is absent), *p*B (probability of subordinate species being detected when the dominant species is not present), *r*BA (probability of subordinate species being detected when the dominant species is present and detected), *r*Ba (probability of subordinate species being detected when the dominant species is present but not detected).

Table 4. Co-occurrence occupancy models used to evaluate the role of interspecific interactions on the detection probability of three sympatric Neotropical spotted cats in a large Atlantic Forest remnant.

	OCELOT VS. MARGAY				OCELOT VS. ONCILLA				MARGAY VS. ONCILLA			
Model	ΔAICc	wAICc	K	-2LLL	ΔAICc	wAICc	K	-2LLL	ΔAICc	wAICc	K	-2LLL
ψ(top) *p*A=*r*A=*p*B=*r*BA=*r*Ba	**0**	0.53	3	333.55	9.73	0.00	3	387.53	**0**	0.22	3	441.42
ψ(top) *p*A=*r*A,*p*B=*r*BA=*r*Ba	**1.66**	0.23	4	332.80	8.32	0.01	4	383.70	**1**	0.13	4	440.16
ψ(top) *p*A,*r*A,*p*B=*r*BA=*r*Ba	2.92	0.12	5	331.52	7.15	0.02	5	379.99	**1.29**	0.12	5	437.76
ψ(top) *p*A=*r*A,*p*B,*r*BA=*r*Ba	4.19	0.06	5	332.79	6.44	0.03	5	379.28	**0.34**	0.19	5	436.81
ψ(top) *p*A,*r*A,*p*B,*r*BA=*r*Ba	5.53	0.03	6	331.45	6.31	0.03	6	376.48	**1.37**	0.11	6	435.16
ψ(top) *p*A=*r*A,*p*B,*r*BA,*r*Ba	6.85	0.02	6	332.77	**0**	0.63	6	370.17	**0.70**	0.16	6	434.49
ψ(top) *p*A,*r*A,*p*B,*r*BA,*r*Ba	8.29	0.01	7	331.40	**1.56**	0.29	7	368.91	2.09	0.08	7	433.07

Ocelot vs. Margay ψ(top) = ψA(reserve dist)=ψBA(reserve dist)=ψBa(reserve dist); Ocelot vs. Oncilla ψ(top) = ψA(reserve dist),ψBA=ψBa; Margay vs. Oncilla ψ(top) = ψA=ψBA=ψBa.

Online Appendix A

Table A1. Model selection analysis for occupancy (ψ) covariates (elevation, terrain slope, percentage of high-quality forest cover, hydrographic density and road density) measured at different spatial scales (buffer sizes) for three Neotropical spotted cats at a large Atlantic Forest remnant in Brazil.

Model	AICc	ΔAICc	wAICc	K	-2LLL
ELEVATION					
Ocelot					
ψ(.) p(global)	154.78	0	0.64	5	143.24
ψ(elev500) p(global)	157.28	2.50	0.18	6	143.07
ψ(elev1000) p(global)	157.42	2.64	0.17	6	143.21
Margay					
ψ(.) p(global)	202.20	0	0.61	5	190.66
ψ(elev500) p(global)	204.30	2.10	0.21	6	190.09
ψ(elev1000) p(global)	204.71	2.51	0.17	6	190.5
Oncilla					
ψ(.) p(global)	252.75	0	0.62	5	241.21
ψ(elev500) p(global)	255.07	2.32	0.19	6	240.86
ψ(elev1000) p(global)	255.15	2.40	0.19	6	240.94
HIGH-QUALITY FOREST COVER					
Ocelot					
ψ(.) p(global)	154.78	0	0.45	5	143.24
ψ(forest500) p(global)	154.86	0.08	0.43	6	140.65
ψ(forest1000) p(global)	157.35	2.57	0.12	6	143.14

Margay					
ψ(.) *p*(global)	202.20	0	0.60	5	190.66
ψ(forest1000) *p*(global)	204.13	1.93	0.23	6	189.92
ψ(forest500) *p*(global)	204.65	2.45	0.18	6	190.44
Oncilla					
ψ(.) p(global)	252.75	0	0.58	5	241.21
ψ(forest500) p(global)	254.28	1.53	0.27	6	240.07
ψ(forest1000) p(global)	255.40	2.65	0.15	6	241.19
HYDROGRAPHIC DENSITY					
Ocelot					
ψ(.) *p*(global)	154.78	0	0.61	5	143.24
ψ(hydro1000) *p*(global)	157.01	2.23	0.20	6	142.80
ψ(hydro500) *p*(global)	157.11	2.33	0.19	6	142.90
Margay					
ψ(hydroo1000) *p*(global)	201.69	0	0.44	6	187.48
ψ(.) *p*(global)	202.20	0.51	0.34	5	190.66
ψ(hydro500) *p*(global)	203.12	1.43	0.22	6	188.91
Oncilla					
ψ(.) *p*(global)	252.75	0	0.39	5	241.21
ψ(hydro1000) *p*(global)	253.08	0.33	0.33	6	238.87
ψ(hydro500) *p*(global)	253.35	0.60	0.29	6	239.14
ROADS DENSITY					
Ocelot					
ψ(.) *p*(global)	154.78	0	0.51	5	143.24
ψ(roads500) *p*(global)	155.86	1.08	0.30	6	141.65
ψ(roads1000) *p*(global)	156.82	2.04	0.19	6	142.61

Margay					
ψ(.) *p*(global)	202.20	0	0.56	5	190.66
ψ(roads1000) *p*(global)	203.49	1.29	0.29	6	189.28
ψ(roads500) *p*(global)	204.82	2.62	0.15	6	190.61
Oncilla					
ψ(.) *p*(global)	252.75	0	0.63	5	241.21
ψ(roads500) *p*(global)	255.02	2.27	0.20	6	240.81
ψ(roads1000) *p*(global)	255.37	2.62	0.17	6	241.16

p(global) = method + soil coverage + percentage of high-quality forest cover at 500 m buffer size.

Table A2. Single-season single-species occupancy models (cumulative wAICc>0.80) used to evaluate the effect of weighted distance to reserve border, geomorphometry, environmental, and anthropogenic landscape attributes on the habitat use of sympatric Neotropical spotted cats at a large Atlantic Forest remnant in Brazil.

					Beta estimates					
Model	ΔAICc	wAICc	K	-2LLL	Elevation	Forest cover	Hydrography	Roads	Reserve distance	Prey
Ocelot										
ψ(dist reserve) *p*(global)	0	0.25	6	139.03	-	-	-	-	-1.30 (±0.97)	-
ψ(.) *p*(global)	1.54	0.12	5	143.24	-	-	-	-	-	-
ψ(forest500) *p*(global)	1.62	0.11	6	140.65	-	-1.35 (±0.78)	-	-	-	-
ψ(reserve dist+roads1000) *p*(global)	2.12	0.09	7	138.33	-	-	-	-0.49 (±0.69)	-1.46 (±1.39)	-
ψ(forest500+hydro1000) *p*(global)	2.14	0.09	7	138.35	-	-1.82	-0.96 (±0.74)	-	-	-

					(±0.92)				
ψ(reserve dist+elev1000) *p*(global)	2.64	0.07	7	138.85	-0.26 (±0.60)	-	-	-	-1.38 (±0.95)	-
ψ(reserve dist+hydro1000) *p*(global)	2.77	0.06	7	138.98	-	-	-0.13 (±0.57)	-	-1.27 (±0.99)	-
ψ(roads1000) *p*(global)	3.58	0.04	6	142.61	-	-	-	-0.41 (±0.54)	-	-
Margay										
ψ(reserve dist) *p*(global)	0	0.18	6	186.39	-	-	-	-	-1.06 (±0.59)	-
ψ(reserve dist+hydro1000) *p*(global)	1.09	0.10	7	184.66	-	-	-1.09 (±1.08)	-	-0.90 (±0.58)	-
ψ(hydro1000) *p*(global)	1.09	0.10	6	187.48	-	-	-1.41 (±1.12)	-	-	-
ψ(.) *p*(global)	1.60	0.08	5	190.66	-	-	-	-	-	-
ψ(reserve dist+roads1000) *p*(global)	1.63	0.08	7	185.20	-	-	-	0.64 (±0.67)	-1.06 (±0.60)	-
ψ(reserve dist+forest1000) *p*(global)	2.11	0.06	7	185.68	-	-1.00 (±2.44)	-	-	-1.19 (±0.88)	-
ψ(reserve dist+elev1000) *p*(global)	2.50	0.05	7	186.07	-0.36 (±0.70)	-	-	-	-1.26 (±0.78)	-
ψ(reserve dist+prey) *p*(global)	2.73	0.05	7	186.30	-	-	-	-	-0.98 (±0.62)	0.16 (±0.54)
ψ(prey) *p*(global)	2.69	0.05	6	189.08	-	-	-	-	-	0.73 (±0.69)
ψ(hydro1000+elev1000) *p*(global)	2.78	0.04	7	186.35	0.68 (±0.75)	-	-1.98 (±1.64)	-	-	-
ψ(roads1000) *p*(global)	2.89	0.04	6	189.28	-	-	-	0.78 (±1.09)	-	-
Oncilla										
ψ(forest500+elev1000) *p*(global)	0	0.15	7	235.60	1.72 (±0.93)	-3.20 (±0.75)	-	-	-	-
ψ(.) *p*(global)	0.12	0.14	5	241.21	-	-	-	-	-	-

ψ(hydro1000) *p*(global)	0.45	0.12	6	238.87	-	-	-0.76 (±0.56)	-	-	-
ψ(hydro1000+elev1000) *p*(global)	1.37	0.07	7	236.97	1.29 (±1.26)	-	-2.14 (±2.20)	-	-	-
ψ(forest500) *p*(global)	1.65	0.06	6	240.07	-	-1.06 (±0.97)	-	-	-	-
ψ(hydro1000+forest500) *p*(global)	1.79	0.06	7	237.39	-	-0.85 (±0.58)	-1.10 (±0.85)	-	-	-
ψ(dist reserve) *p*(global)	1.94	0.06	6	240.36	-	-	-	-	-0.39 (±0.42)	-
ψ(hydro1000+prey) *p*(global)	2.50	0.04	7	238.10	-	-	-1.05 (±0.73)	-	-	-0.45 (±0.51)
ψ(elev1000) *p*(global)	2.52	0.04	6	240.94	0.22 (±0.43)	-	-	-	-	-
ψ(roads1000) *p*(global)	2.74	0.04	6	241.16	-	-	-	-0.13 (±0.53)	-	-
ψ(prey) *p*(global)	2.79	0.04	6	241.21	-	-	-	-	-	0.03 (±0.49)

p(global) = method + soil coverage + percentage of high-quality forest cover at 500 m buffer size.

Protection status affect ecological functions of Neotropical mammal communities

Mariana B. Nagy-Reis[1], Milton C. Ribeiro[2], Adriano G. Chiarello[3], Eleonore Z. F. Setz[1a]

[1]Mammal Ecology and Behavior lab (LAMA), Department of Animal Biology, Universidade Estadual de Campinas (UNICAMP), Bertrand Russel, 1505, mailbox: 6109, Campinas, SP, 13083-970, Brazil. [a]Email: setz@unicamp.br.

[2]Spatial Ecology and Conservation lab (LEEC), Department of Ecology, Universidade Estadual de São Paulo (UNESP), Av. 24A, 1515, Rio Claro, SP, 13506-900, Brazil. E-mail: mcr@rc.unesp.br.

[3]Department of Biology, Universidade de São Paulo (USP), Av. Bandeirante, 3900, Ribeirão Preto, SP, 14040-901, Brazil. E-mail: bradypus@ffclrp.usp.br.

Corresponding author: Mariana B. Nagy-Reis, Department of Animal Biology, Universidade Estadual de Campinas, UNICAMP, Biology Institute, Bertrand Russel, 1505, mailbox: 6109, Campinas, SP, 13083-970, Brazil.

E-mail: mariana.nbreis@gmail.com; Phone number: 55(11)98709-4109

Abstract

Protected areas can decrease habitat loss and human-related pressures while improving the density and occupancy of key groups. However, different categories of protected area vary substantially in their degree of enforcement, which may ensure different levels of effectiveness. Here we investigated the effectiveness of different protection statuses in preserving the ecological functions of mammals in a large block of Atlantic Forest and its surroundings, proposing a way to measure protection effectiveness through the degree of potential ecological function integrity regionally, while incorporating detection probability. We applied a detection/non-detection sampling method using camera trap data to estimate the occupancy of five mammal functional types: a) carnivore/predator (ocelot - *Leopardus pardalis*); b) insectivore (nine-banded armadillo - *Dasypus novemcinctus*); c) large-seed disperser (paca - *Cuniculus paca*); d) omnivore (tayra - *Eira barbara*); and e) seed predator (collared-peccary - *Pecari tajacu*). We compared the occupancy of each mammal functional type and overall potential ecological function integrity (measured by the summed occupancies) across three areas that differed in protection status within the same forest remnant: a) high protection (Municipal Reserve); b) medium protection (Buffer Zone); and c) low protection (Natural Heritage Area). The strictly protected area (Municipal Reserve) and its Buffer Zone had more mammal ecological functions than the area with fewer restrictions on land-use and no on-site enforcement (Natural Heritage Area). Moreover, the occupancy of the most sensitive functional types, such as carnivore and large-seed disperser, heavily relied on higher protection areas, which could impact the overall ecosystem functioning and ecological services of areas with lower protection statuses. Our study shows that areas designated

for conservation through different degrees of protection can present different levels of effectiveness in retaining ecological functions and ecosystem services, suggesting that management strategies and degree of enforcement should be carefully planned when assigning areas for conservation.

1. Introduction

Protected areas can decrease habitat loss and human-related pressures (Bruner et al. 2001; Peres & Palacios 2007; Andam et al. 2008), improve the density and occupancy of key ecological groups (Stoner et al. 2007; Nagy-Reis et al. submitted a and b), and provide several ecological and cultural services, such as carbon storage, watershed protection, biodiversity maintenance, and recreation and spiritual fulfillment (DeFries et al. 2007). However, different protection categories vary substantially in the degree of enforcement (Phillips 2004), and the effectiveness of the protected area depends on several related aspects such as the density of guards and the degree of border demarcation (Bruner et al. 2011). Therefore, areas assigned with different protection statuses may ensure different levels of effectiveness. In practice, however, little attempt has been made to quantify how the protection category influences the effectiveness of the protected area (Stoner et al. 2007), and how this influence the maintenance of varying ecological functions at regional level.

Different measures of effectiveness, such as deforestation rate (Andam et al. 2008; Nagendra 2008), species diversity (Rodrigues et al. 2004), density (Stoner et al. 2007) and occurrence (Brooks et al. 2004), have been used to investigate the role of protected areas or to designate areas for conservation. However, species occurrence data is frequently obtained from presence-only data or methods that do not deal with imperfect detection. Such data usually contains omission errors, which affects the comprehensiveness, representativeness, and efficiency of areas selected for conservation (Rondinini et al. 2006).

The occurrence of groups that impact ecosystem functioning and are also sensitive to the environment can indicate potential ecological integrity (Noss et al. 1996), which can be useful for quantifying the effectiveness of protected areas. Large- and medium-sized mammals can influence ecosystem dynamics by performing several important ecological functions: predators can alter prey populations, regulating the trophic cascade (Terborgh et al. 2001; Estes et al. 2011); herbivores, seed dispersers, and seed predators can modify the diversity, regeneration, structure, and distribution of plants (Wright 2003; Galetti et al. 2006). Mammals are also strongly sensitive to anthropogenic pressures such as hunting and habitat alteration (Chiarello 1999; Michalski & Peres 2005; Peres & Palacios 2007; Galetti et al. 2009; Licona et al. 2011; Nagy-Reis submitted a and b). Therefore, measuring the degree of maintenance of ecological function of mammal communities to assess protected area effectiveness may provide more information about ecological processes than simpler approaches. However, measuring ecological functions may require a fine-scale analysis. Nonetheless, despite limitations, spatial data on species are essential in conservation planning and cannot be replaced by broad-scale surrogates (Brooks et al. 2004).

Here we investigated the effectiveness of different protection statuses in preserving ecological functions of mammals in a large block of Atlantic Forest and its surroundings, proposing a way to measure protection effectiveness through the degree of potential ecological function integrity while incorporating detection probability. We tested whether areas with higher protection status have more ecological functions than areas with lower protection status, and we examined the influence of three protection statuses (a- high protection - Municipal Reserve; b- medium protection - Buffer Zone; c- low protection - Natural Heritage Area) on the occupancy of different mammal functional types (a- carnivore; b- insectivore; c- omnivore; d- seed disperser; and e- seed predator) (see Fig. 1 for hypotheses schema).

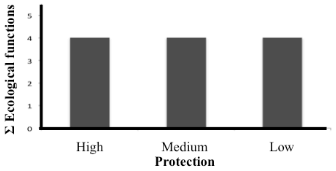
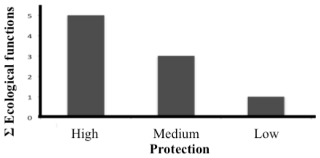
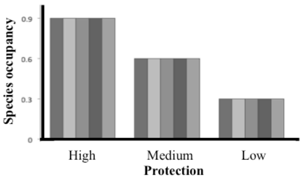
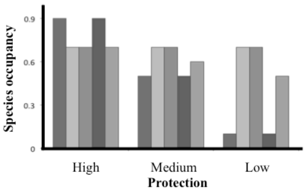
<table>
<tr><td>Hypothesis</td><td colspan="2">Expected</td></tr>
<tr><td>Null hypothesis
Area protection status does not influence the ecological functions.</td><td colspan="2">Similar ecological functions across different protection statuses.
 </td></tr>
<tr><td rowspan="2">Alternative hypothesis
Area protection status influences the ecological functions.</td><td rowspan="2">Distinctive ecological functions across different protection statuses.
 </td><td>Species with different ecological functions have similar responses to protection status.
 </td></tr>
<tr><td>Species with different ecological functions have distinctive responses to protection status.
 </td></tr>
</table>

Fig. 1. Study hypotheses for the influence of protection status on the ecological functions of mammals.

2. Methods

2.1. Study Area

Serra do Japi (southeast Brazil, coordinates 47°03'40"W to 46°52'20"W and 23°22'30"S to 23°11'35"S; Fig. 2) is one of the few large remnant blocks of Atlantic Forest, a global hotspot for biodiversity conservation (Myers et al. 2000). The Atlantic Forest suffers severe anthropogenic pressures and is highly fragmented (over 80% of the remnants are < 50 ha in size), highly isolated (average fragment distances 1,440 m), and under negative edge influences (73% of remnants are 250 m from any forest edge) (Ribeiro et al. 2009). The study area is an ideal scenario in which to investigate the degree of ecological function maintenance in areas under different protection statuses, because within the same remnant there are three areas in different protection statuses and, therefore, under different degree of enforcement. The forest block is composed of a Natural Heritage Area (35,000 ha) and a Biological Municipal Reserve (REBIO; 2,071 ha) surrounded by a Buffer Zone (11,946 ha) (SMPMA 2008 - see Fig. 2). The REBIO (equivalent to IUCN Protected Area Category Ia - Strict Nature Reserve; Phillips 2004) presents the highest protection status in the region, where the only permitted activities are research and education. The Buffer Zone represents the second most protected category, where there are private lands, but all activities are regulated. Finally, the Natural Heritage Area (equivalent to IUCN Protected Area Category V - Protected Landscape; Phillips 2004) is the least protected category, where there are private lands, and restrictions on land-use apply only to activities that potentially alter the characteristics of the area. The study area is characterized by semideciduous mesophile forest with mountainous terrain and a seasonal climate (Morellato 1992). The mean temperature is 19.7^{o} C and the mean annual rainfall is 1,422 mm, with a dry and cold season from April to September and a wet and warm season from October to March (Morellato 1992).

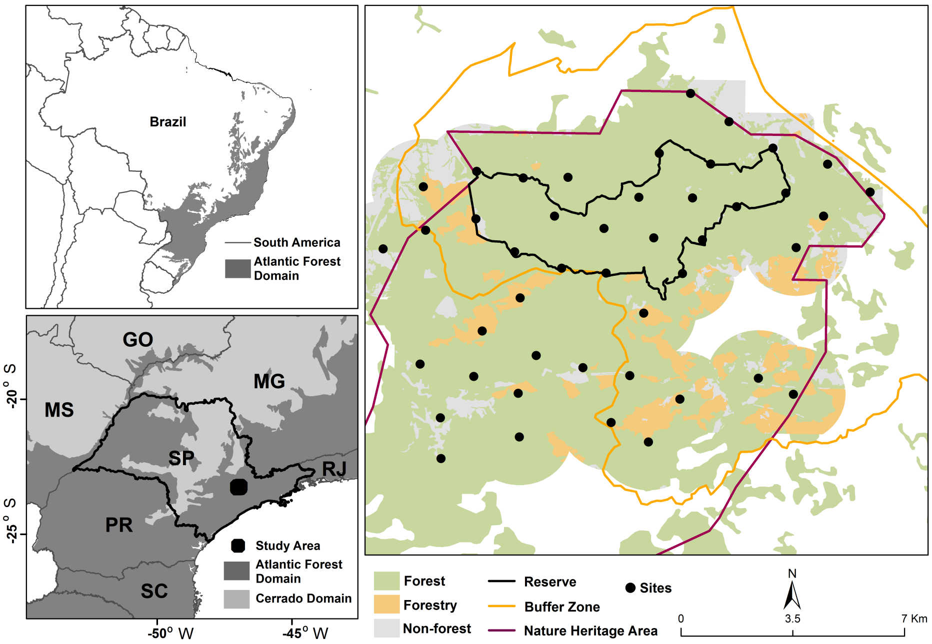


Fig. 2. Study area and sampling sites location at Serra do Japi (Brazil) where the degree of ecological functions of medium- and large-sized mammals was measured with occupancy modeling for three protection status (a- high protection - Biological Reserve; b- medium protection - Buffer Zone; and c- low protection - Natural Heritage Area).

2.2. Selected functional types

From the pool of species present at our study site (Online Appendix, Tab. 1), we selected five medium- and large-sized terrestrial mammals that presented unique ecological functions or were the main species to perform each ecological function (and additionally, that we had enough data; Fig 3).

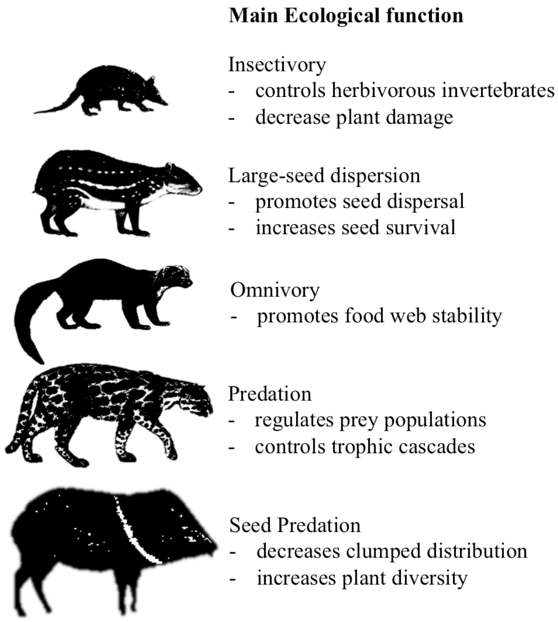


Fig 3. Mammal functional type classification and derived ecological functions. From the top to the bottom: nine-banded armadillo (*Dasypus novemcinctus*), paca (*Cuniculus paca*), tayra (*Eira barbara*), ocelot (*Leopardus pardalis*), collared peccary (*Pecari tajacu*).

2.3. Data collection

We collected data with passive infrared camera traps (Bushnell Trophy Cam) for all species and with scat sampling combined with the camera trapping for ocelot. The sampling sites (N=45) were distributed in a regular grid and spaced approx. 1.5 km apart. The cameras were fixed about 20 cm above the ground and programmed to run continuously during approx. 70 days in each season (dry and wet) from April 2013 to March 2014 (N=5,198 trap days).

We conducted six visits to each sampling site (three in each season, from April 2013 to September 2014) and collected all felid scat found along a 1-km segment of the dirt road closest to each sampling site (always within 1km from the sampling sites). We identified ocelot feces through tricology—the use of mammalian hair for identification of taxa—which is a widely-used method (e.g. Chernova 2001; Day 1966; De Marinis & Asprea 2006; Hilton & Kutscha 1978; Kennedy 1982; Meng & Wyss 1997; Mukherjee et al. 1994). This method has been proven to be as consistent as molecular methods for identification of ocelots (Miotto et al. 2007). We washed the scats with running water, dried them, and collected the guard hairs. Then, we cleaned the guard hairs with ethyl alcohol and obtained the cuticular impressions by pressing the hairs against a thin layer of nail varnish; we let them dry for three to five minutes on glass slides with the help of a bench vise (adapted from Quadros & Monteiro-Filho 2006). We photographed the cuticular impressions at 400x magnification and compared the pattern of the cuticles with our reference collection (obtained from hairs collected from museum specimens) and published guides (Quadros & Monteiro-Filho 2010; Vanstreels et al. 2010). In order to guarantee the accuracy of our identification, we conducted molecular analysis for all ocelot samples (N=8) and obtained confirmation for 100% of the samples, confirming the reliability of the method. We used mini-barcoding, comparing the obtained sequences of two markers from mitochondrial DNA—ATP6 (126 bp) and cytochrome oxidase I gene (COI) (187 bp); applying the primers developed by Chaves et al. 2012—with reference sequences from tissue samples of each species.

2.4. Data analysis

2.4.1.Occupancy modeling

We estimated the site occupancy of each mammal functional type (carnivore, insectivore, omnivore, seed disperser, and seed predator) and summed them to measure potential ecological function integrity at each sampling site. Occupancy modeling is a method that estimates the probability of occupancy (ψ) while accounting for detection probability (*p*) (MacKenzie et al. 2002). We constructed the detection histories (H) of the collared-peccary, nine-banded armadillo, paca, and tayra for each sampling site over ten consecutive week-long sampling occasions during each season. For ocelot, we constructed the detection history (H) over six sampling occasions during each season: the first three sampling occasions of each season consisted of three repeated visits for scat sampling, and the following three occasions comprised three consecutive 18-day camera trap surveys. For each sampling site and sampling occasion, we recorded species detection as "1" and non-detection as "0". We treated the dry season 2013 as one season and the wet season 2013 as another. We treated the dry season of 2014 as a third season for ocelot. We used multi-season models with three parameters: initial occupancy (dry season), colonization probability and extinction probability; the latter two parameters correspond to the time interval between seasons. Given our small sampling size, we were not able to investigate sources of variation in these two parameters and, therefore, we used constant extinction and colonization (i.e. eps(.) and gamma(.)).

Incorporating variables into occupancy and dealing with detection probability lead to more precise site occupancy estimates (MacKenzie et al. 2002; Linkie et al. 2007). Therefore, we modeled site occupancy and detection probability as functions of a set of environmental, geographic, and anthropogenic variables, performing a logistic regression analysis in PRESENCE software (Hines 2006). For occupancy, we used elevation, terrain slope (except for ocelot, since slope may not restrict the locomotion of the species), percentage of high-quality forest cover (see below), hydrographic density, road density and weighted distance to reserve border. For detection probability, we used mean temperature, total precipitation, season (climate variables) and fruit availability (only for frugivorous species), and percentage of high-quality forest cover (habitat variables). For ocelot, we also used method-related variables for detection probability, such as the method adopted to survey each sampling occasion (scat sampling or camera trapping) and the degree of soil coverage by plants or leaf litter on the roads where scats were sampled (0– no coverage; 1– low to medium coverage; 2– high coverage).

We obtained elevation and terrain slope from digital elevation models (DEM) available from Topodata Geomorphic database of Brazil (INPE 2014).We mapped the vegetation cover of the study area using high resolution satellite image interpretation on a 1:5,000 scale and extensive field verification by a botanist. We calculated high-quality forest cover (the percentage of intermediate and advanced forest succession) using Geographical Resources Analysis Support System (GRASS) (Neteler et al. 2013). Hydrography and roads were mapped on a 1:5,000 scale using Quantum Gis software (Álvarez 2013) and data from high resolution satellite images and cartographic maps (1:10,000 scale; Secretariat of Economy and Planning - São Paulo State Government). We estimated road and hydrographic densities within a radius of 200, 500 and 1,000m around the 45 sampling sites using the Kernel density function in ArcGIS software (ESRI 2009). We measured the distance from each sampling site to the nearest Biological Municipal Reserve (REBIO) border, giving negative distances to sites within the REBIO and positive distances otherwise. Then, we multiplied these distances by the protection status weight of the subarea in which each sampling site was located (REBIO = 1; REBIO’s Buffer Zone = 2; and within the Natural Heritage Area but outside these two subareas = 3), obtaining a distance from the reserve border weighted by the protection status of the area where the sampling site was located ('weighted distance to reserve border'). Fruit availability was measured as the monthly number of arboreal plant species producing fruits at the study area (from Morellato & Leitão-Filho 1992). All climate variables were obtained from the Integrated Center of Agrometeorology Information (CIIAGRO 2014). We adopted a multi-spatial scale approach (Boscolo and Metzger 2010; Lyra-Jorge et al. 2010), and after testing different scales for each species (200-, 500- and 1,000-m radius concentric circles around each sampling site), we used in the final models the covariates at the scale that best explained each species occupancy. When different spatial scales were equally plausible (ΔAICc<2), we chose the scale closest the species home range to use in the final models. We normalized all covariates and used only those with low correlation ($r<0.60$, based on a Spearman's correlation matrix) in the final model sets.

We used a general model for p (that contained as many potential covariates as possible) and allowed occupancy (ψ) to be constant ($\psi(.)$) or to vary as a function of either a single covariate or a combination of two (additive effect, following MacKenzie 2006). By using a general model for the parameters that were not investigated within a specific model set, we reduced the possibility that imposed constraints (on p, for example) would result in residual sampling variation being attributed to variation in occupancy.

2.4.2. Monte Carlo simulation

To investigate if different protection statuses hold different mammal functional types, we first produced estimates of the occupancy of each functional type (a- carnivore; b- insectivore; c- omnivore; d- seed disperser; and e- seed predator) per sampling site.

We excluded all models from the previous step that did not converge, ranked candidate models using the Akaike Information Criterion (AIC), and applied model averaging (Burnham & Anderson 2002) to estimate the site occupancy of each mammal functional type in each sampling site using PRESENCE (Hines 2006). We averaged the site occupancy of all seasons to obtain a final estimation for each sampling site. Then we calculated the absolute difference between the mean site occupancy of each mammal functional type at each protection status (a- high protection - Biological Reserve; b- medium protection - Buffer Zone; and c- low protection - Natural Heritage Area) and compared this difference to the distribution of differences expected under the null hypothesis (mammal functional types are similar across protection statuses). The distribution of the differences expected under null hypothesis was generated by 1,000 simulations (Monte Carlo simulation; Manly 1997) to calculate the associated two-tailed p-value. We performed the same analysis to test if higher protection statuses indeed have higher overall potential ecological function integrity, calculating the absolute difference between the summed site occupancy of all mammal functional types at each of the three protection statuses and comparing this difference with the distribution of differences expected under the null hypothesis (the site overall potential ecological function integrity is similar across different protection statuses). We performed this analysis in R 3.1.1 software (R Development Core Team 2014).

3. Results

The three protection statuses (high protection - Biological Reserve, medium protection - Buffer Zone, and low protection - Natural Heritage Area) held different levels of occupancy of each of the five mammal functional types (carnivore, insectivore, omnivore, seed disperser, and seed predator) (Fig. 4; Tab. 1). The most sensitive mammal functional types, i.e. carnivore and seed disperser, were the most affected by the protection status, occupying the high protection status at twice the rate of the low protection status (Fig. 4; Tab. 1).

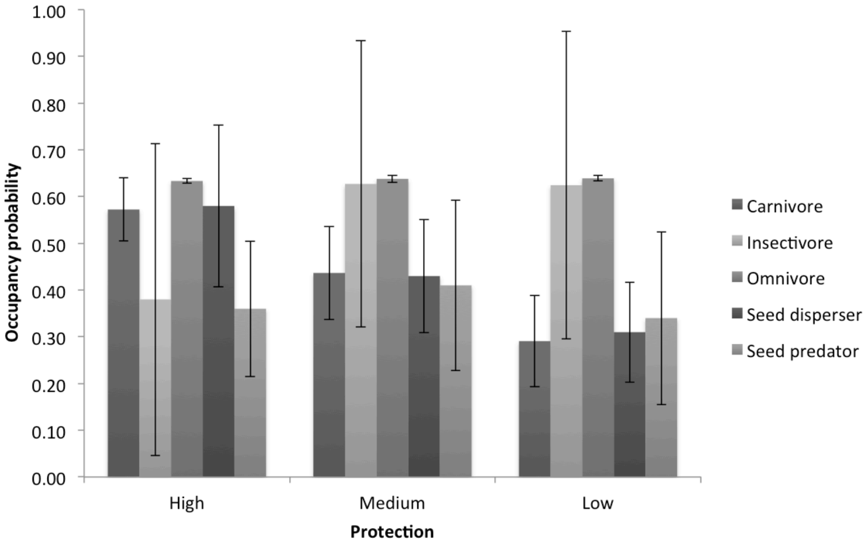


Fig. 4. Estimated occupancy probability ($\hat{\psi}$) and standard deviation (SD) for each ecological function in three different protection statuses (a- high protection - Biological Reserve; b- medium protection - Buffer Zone; and c- low protection - Natural Heritage Area) in a large Atlantic Forest remnant in Brazil.

Tab. 1. Observed and simulated (expected under the null hypothesis) differences in the occupancy probability (%) of each mammal functional type between each pair of protection statuses (a- high protection - Biological Reserve; b- medium protection - Buffer Zone; and c- low protection - Natural Heritage Area) in a large Atlantic Forest remnant in Brazil. Significant results (p<0.05) in bold.

	Protection		
	High vs. Medium	High vs. Low	Medium vs. Low

	Obs. diff.	Sim. diff.	Obs. diff.	Sim. diff.	Obs. diff.	Sim. diff.
Carnivore	**14**	**3**	**27**	**4**	**13**	**4**
Insectivore	**25**	**10**	23	10	1	11
Omnivore	**1**	**0**	**1**	**0**	0	0
Seed disperser	**14**	**5**	**25**	**5**	**11**	**4**
Seed predator	4	5	2	5	6	5

The overall potential ecological function integrity (summed site occupancy of all mammal functional types) was similar between the high protection status (Biological Reserve mean 2.53 ± 0.39 SD) and the medium protection status (Buffer Zone mean 2.54 ± 0.38 SD; observed difference: 0.01, difference expected under the null hypothesis - simulated difference: 0.1, p=0.93). The low protection status (Natural Heritage Area mean 2.21 ± 0.37 SD) had similar overall potential ecological function integrity than the medium protection status (observed difference: 0.3, difference expected under the null hypothesis - simulated difference: 0.1, p=0.07), but lower than the high protection status (observed difference: 0.3, difference expected under the null hypothesis - simulated difference: 0.1, p=0.04, in accordance with our prediction).

At least 75% of the sampling sites within any of the three protection statuses had three mammal functional types or more; however, only 8% of the sampling sites at the low protection status had all five mammal functional types, compared to as much as 36% of sites located at the other two protection statuses (Tab. 2).

Tab. 2. Percentage of sampling sites within each protection status (a- high protection - Biological Reserve; b- medium protection - Buffer Zone; and c- low protection - Natural Heritage Area) with occupancy higher than 30% ($\hat{\psi}$ >0.3) for each mammal functional type and percentage of sampling sites with more than three, four, or all five mammal functional types with site occupancies higher than 30% ($\hat{\psi}>0.3$) in a large block of Atlantic Forest remnant in Brazil.

	High	Medium	Low
Carnivore	100	91	50
Insectivore	41	82	75
Omnivore	100	100	100
Seed disperser	86	82	42
Seed predator	50	64	42
>3	91	100	75
>4	59	73	25
>5	27	36	8

4. Discussion

Depending on the protection status, protected areas vary substantially in their degree of enforcement and other management characteristics (Phillips 2004), which could reflect differences in conservation effectiveness (Bruner et al. 2011). However, little attempt had previously been made to test and quantify this. In this study, through sampling a large block of Atlantic Forest with three different protection statuses and using occupancy modeling (MacKenzie et al. 2002) to explicitly incorporate habitat variables and detection probability while examining occupancy patterns of mammals, we have shown that the effectiveness in preserving ecological functions of mammals can vary according to the protection status of the area.

High protection areas can benefit key groups, improving their density and occupancy while reducing anthropogenic mortality (Stoner et al. 2007; Loveridge et al. 2011; Chap. 1 and 2). In our study, the strictly protected area and its buffer zone had higher potential ecological function integrity and a broader extent with all five mammal functional types presenting high occupancies. Changes in abundance, rather than outright extinction, can also cause loss of function (Kremen 2005). When a species is extremely diminished, it may no longer exert its key functional roles structuring the ecosystem (phenomenon known as “ecological extinction”; Kremen 2005). Therefore, measuring population parameters instead of only investigating presence/absence of species is needed to properly access proxies of multiple ecological processes. Given the relationship between abundance and occupancy (Royle et al. 2005; MacKenzie et al. 2006), low occupancies (e.g. < 30%) could indicate that such populations may be too reduced to properly exert their ecological functions. In this sense, the fact that only 8% of the sampling sites within the low protection status have all five ecological functions with site occupancies higher than 30% is especially concerning. Species’ functional characteristics strongly influence ecosystem properties and community structure (Hooper et al. 2005). Functional richness, for instance, can increase ecosystem properties through complementarity and facilitation processes (Hooper et al. 2005), because species from different trophic levels, and therefore, with different functional types, provide distinct ecosystem services (Dobson et al. 2006). For this reason, our evidences point that even in large protected areas there can be ecossystem processes and services being lost due to a low protection status.

The occupancy of two key groups (carnivore and large-seed disperser) heavily relied on higher-protection areas. Predators are essential components of the ecosystem, as they affect prey and plant populations, regulating the trophic cascade (Crooks & Soulé 1999; Terborgh et al. 2001; Estes et al. 2011). Large-seed dispersers are another key component because, besides influencing overall plant diversity, structure and regeneration, they are also able to disperse seeds that can not be dispersed by smaller and more abundant frugivores (Wright 2000; Galetti et al. 2006; Galetti et al. 2013). Due to high anthropogenic impacts, in most Atlantic Forest fragments, for example, a few if not only one species of each of these two groups is present. In such cases where few species perform a specific function (i.e. ecosystem function classified as brittle), ecosystem functions and services then decline rapidly as the abundance of such species is reduced (Dobson et al. 2006). Consequently, the lack of these two functional types can cause severe impacts on ecosystem functioning and ecological services. Usually, this mechanism is triggered by habitat degradation (reduction in habitat quality and quantity; Dobson et al. 2006). Our results suggest that this can also happen in areas that are protected but do not have a strong enforcement or management to guarantee ecological integrity.

We proposed a way to measure protection effectiveness through the degree of potential ecological function integrity while incorporating animal detection probability using occupancy modeling (MacKenzie et al. 2002), and we showed the feasibility of this method, which could be a useful management tool in further long-term multi-species monitoring programs once replicated over a longer timeframe and larger areas. Spatial data on species are essential in conservation planning (Brooks et al. 2004), and presence-absence data provide researchers and wildlife managers with relevant information on species distribution (MacKenzie 2005). However, regardless of the level of analytic complexity, if detection probability is not accounted for, the biological and sampling processes will not be distinguished in the results (MacKenzie 2005). Therefore, when species occurrence is measured without considering imperfect detection, thus leading to "false absences" (i.e. species is at a site but is undetected), erroneous management decisions are taken (MacKenzie 2005). Furthermore, occupancy models can also estimate vital rates such as local extinction and colonization probabilities (MacKenzie et al. 2006). Therefore, expanding our survey over time would allow an evaluation of whether different protection statuses maintain different ecological functions through time and how the populations are faring under each type of protection status. This is particularly important because while functional ecology is a good indicator of potential ecological integrity, the real value of the protected area is its ability to support viable long-term populations of species (Primack 1993).

In conclusion, our study shows that areas designated for conservation through different management strategies and degrees of enforcement can present different levels of effectiveness in retaining mammal ecological functions. We clearly need larger-scale studies to evaluate how area protection status affects ecological functions at a broader scale. However, we believe that our findings are likely applicable to other areas and other ecosystems across the globe, and that this study is a first step towards a better understanding of the role of different protection categories in conservation effectiveness. We also showed that creating and maintaining more strictly protected areas is essential to conserve biodiversity and ecosystems, as these protection statuses retain higher ecological function integrity. We also demonstrated that using a multiple ecological functions approach is essential to measure proxies of multiple ecological processes, once different functional types can respond differently to the protection status. We suggest as a next step to identify and test what specific management actions contribute the most for the maintenance of ecological functioning of protected areas.

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Online Appendix

Tab. 1. Medium- and large-sized mammals surveyed with camera traps at a large Atlantic Forest remnant (Serra do Japi) inBrazil.

Family	Species	Common name	N records*
	ARTIODACTYLA		
Bovidae	*Bos primigenius*	Cattle	20
Cervidae	*Mazama* sp.	Deer	322
Equidae	*Equus ferus caballus*	Horse	1
Tayassudae	*Pecari tajacu*	Collared peccary	25
	CARNIVORA		
Canidae	*Canis familiaris*	Domestic dog	35
	Cerdocyon thous	Crab-eating fox	2
Mustelidae	*Eira barbara*	Tayra	43
Procyonidae	*Nasua nasua*	South American coati	290
	Procyon cancrivorus	Crab-eating raccoon	10
Felidae	*Felis silvestris catus*	Domestic cat	1
	Leopardus pardalis	Ocelot	17
	Leopardus guttulus	Oncilla	29
	Leopardus wiedii	Margay	12
	Puma concolor	Puma	3
	Puma yaguarondi	Jaguarundi	9
	DIDELPHIMORPHIA		
Didelphidae	*Didelphis* sp.	Opossum	385
	LAGOMORPHA		

Leporidae	*Lepus europaeus*	European hare	4
	Sylvilagus brasiliensis	Brazilian rabbit	123
	PRIMATES		
Callitrichidae	*Callithrix aurita*	Buffy-tufted marmoset	1
Pitheciidae	*Callicebus nigrifrons*	Black-fronted titi monkey	**
	RODENTIA		
Cuniculidae	*Cuniculus paca*	Paca	199
Erethizontidae	*Coendou prehensilis*	Prehensile-tailed porcupine	1
Hydrochaeridae	*Hydrochaeris hydrochaeris*	Capybara	11
	XENARTHRA		
Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	48
	Euphractus sexcintus	Six-banded armadillo	13
	Cabassous sp.	Naked-tailed armadillo	1
Myrmecophagidae	*Tamandua tetradactyla*	Southern anteater	2

*Number of photos with 60-minute interval; **Visual records only.

3. CONCLUSÕES GERAIS

Esse trabalho investigou o papel de variáveis ambientais, geográficas e antrópicas sobre a ocorrência e uso de hábitat dos mamíferos de médio e grande porte Neotropicais de forma a lidar explicitamente com problemas associados à detecção imperfeita. Consistentemente demonstramos que fatores antrópicos, como a densidade de estradas e a distância da área de proteção mais restritiva (reserva biológica) são os principais fatores influenciando a ocupação e o uso do habitat dos grupos-chave (frugívoros e carnívoros). Ainda, mostramos como o número de funções ecológicas desempenhadas por mamíferos em áreas de maior proteção (reserva biológica e áreas de amortecimento) é maior do que em áreas de menor grau de proteção (área natural tombada). Nossa área de estudo (Serra do Japi), que é o segundo maior bloco de Mata Atlântica do estado de São Paulo, pode ser considerada uma área bem conservada, e toda sua extensão está sob alguma categoria de proteção (reserva biológica, zona de amortecimento e área natural tombada). No entanto, vimos a clara importância de áreas com maior proteção e de uso mais restritivo para a conservação dos mamíferos. Tais resultados reforçam a importância de se estabelecer e manter Unidades de Conservação para a proteção da mastofauna e suas funções ecológicas. Mas, mais do que isso, apontam a importância de se estabelecer e manter áreas de proteção de enquadramentos mais restritivos para que essa conservação seja efetiva.

3.1. Importância da Serra do Japi e futuras direções

A Serra do Japi é uma das últimas grandes áreas de Mata Atlântica contínua (Morelatto 1992) e uma das poucas áreas que recebeu alto grau de indicação pelo Biota Fapesp para criação/ampliação de Unidade de Conservação de Proteção Integral

(Rodrigues et al. 2008). Além de ser uma área importante para a preservar as populações locais, sua proximidade com as matas preservadas das serranias do litoral e do complexo Cantareira/Mantiqueira fornece um possível corredor de fauna (SMPMA 2008). Ainda, é uma importante fonte de preservação e restauração das espécies presentes em remanescentes menores e mais isolados do interior (SMPMA 2008), o que ajuda a persistência genética e demográfica das populações a longo prazo. No entanto, dada a sua localização entre o eixo São Paulo-Jundiaí-Campinas, encontra-se em uma região altamente urbanizada, sofrendo especialmente com o crescimento imobiliário, descarte de lixo e atividades de caça e pesca (SMPMA 2008).

Estudos florísticos na região indicam a necessidade de ampliação da Unidade de Conservação e de enquadramentos mais restritivos para a efetiva proteção da flora (Cardoso-Leite et al. 2005). Nosso trabalho, agora trazendo dados para a fauna, reitera essa necessidade de ampliação da Reserva Biológica Municipal da Serra do Japi ou a criação de uma nova Unidade de Conservação nos seus arredores para assegurar integridade ecológica na área. Outra importante medida seria a geração de um sistema de proteção envolvendo os proprietários e moradores presentes na região, oferecendo oficinas de educação ambiental e programas de compensação à comunidade local, além da expansão da patrulha pela guarda municipal, fatores fundamentais para se ter uma conservação efetiva (Bruner et al. 2001).

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Profa. Dra. Rachel Meneguello
Presidente
Comissão Central de Pós-Graduação

Declaração

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Assinatura : Mariana
Nome do(a) autor(a): **Mariana Nagy Baldy dos Reis**
RG n.° 32876107-2

Assinatura : Eleonore
Nome do(a) orientador(a): **Eleonore Zulmara Freire Setz**
RG n.° 4374445

UNICAMP
COORDENADORIA DE PÓS-GRADUAÇÃO
INSTITUTO DE BIOLOGIA
Universidade Estadual de Campinas
Caixa Postal 6109. 13083-970, Campinas, SP, Brasil
Fone (19) 3521-6378. email: cpgib@unicamp.br
IB

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Assinatura: ______________________________
Nome do(a) aluno(a): Mariana Nagy Baldy dos Reis

Assinatura: ______________________________
Nome do(a) orientador(a): Eleonore Zulnara Freire Setz

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