

# Relative importance of anthropogenic landscape characteristics for Neotropical frugivores at multiple scales

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## Keywords

occupancy; camera traps; call survey; multi-taxa; protected areas; anthropogenic landscape; frugivores; Atlantic Forest.

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## Abstract

Frugivores are key components of Neotropical forests, regulating plant communities, forest structure, and plant diversity; however, they are highly threatened by human impacts worldwide. To effectively conserve this group, maintain their ecological functions, and plan management actions or establish future protected areas, we need to gather information about their relationship with the landscape attributes. Here, we used camera traps and call surveys (April 2013 to March 2014) to estimate the occupancy of seven frugivores (a rodent, two ungulates, two primates and two ground-dwelling birds) at 45 sampling sites distributed within a protected area of Atlantic Forest (35 000 ha) in south-east Brazil. We evaluated the relative effects of anthropogenic landscape variables, environmental attributes and geomorphometry on their occupancy at multiple scales. To achieve this, we measured landscape metrics at three spatial scales (200, 500 and 1000 m) around each sampling site and used multi-season occupancy modeling. Factors related to human presence or disturbance, such as human accessibility, proximity to the reserve, and forest cover, were the main predictors of occupancy by frugivorous game species (paca – *Cuniculus paca*; brocket deer – *Mazama* sp.; and collared peccary – *Pecari tajacu*). Strictly environmental and geomorphometric variables were weaker determinants of frugivore occupancy. Our results also suggest that weather, season and habitat-related variables can equally influence animal detection probability. Moreover, different species of frugivores responded differently to landscape attributes, and their response depended on the spatial landscape scale at which they perceive their habitat. This highlights the importance of a multi-taxa and multi-scale approach when assessing species-habitat relationships and planning wildlife management actions.

## Introduction

Given limited financial resources for conservation, important decisions must be made regarding what, where and how to conserve in order to optimize the time and money invested in conservation (Primack & Rodrigues, 2001). Frugivores can be considered a target group for conservation efforts because they are key components in tropical forests, influencing plant diversity, structure and regeneration through seed dispersal and/or predation (Wright *et al.*, 2000; Galetti *et al.*, 2013). This group constitutes a large portion of animal biomass in Tropical forests (Terborgh, 1986), which is supported by the abundant fleshy fruit production in these

ecosystems (Jordano, 2000). Frugivores and plants are strongly interdependent: up to 90% of tropical trees are adapted to seed dispersal by vertebrates (Jordano, 2000). Thus, the loss of frugivores can have severe consequences for plant communities, including decrease of seed survival, recruitment, germination and size (Chapman & Chapman, 1995; Galetti *et al.*, 2013); loss of mechanisms that regulate tree demography (Keuroghlian & Eaton, 2009); and increased local plant extinction (Galetti & Dirzo, 2013).

The food requirements and relatively large home ranges of medium and large-sized frugivores make them highly sensitive to fragmentation and habitat loss (Chiarello, 1999). Illegal and unsustainable hunting – for food, ornaments or

medicinal purposes – also decreases frugivore abundance and alters patterns of seed dispersal and predation (Wright *et al.*, 2000). Selective logging and palm-heart or fruit harvesting can likewise impact frugivore populations (Moegenburg & Levey, 2003; Kirika, Farwig & Böhning-gaese, 2008), as these activities decrease food availability, especially during periods of fruit scarcity (Keuroghlian & Eaton, 2009).

A major question when planning wildlife management is the spatial relationship between environment and species occurrence. When such relationships are not understood, areas designated for conservation may not provide suitable habitat for the target species and may create conservation gaps. 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), which can bias parameter estimation (Gu & Swihart, 2004). Occupancy models improve inference accuracy because they allow one to estimate 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 seven frugivores (a rodent, two ungulates, two primates and two ground-dwelling birds) at 45 sampling sites within a protected area of Atlantic Forest (35 000 ha) in Brazil, and we investigated the relationship between landscape characteristics and site occupancy rates at multiple scales. By studying a biologically diverse group of frugivores with varying preferences as game species (Table 1), we aimed to assess the relative importance of anthropogenic-related landscape attributes, compared to environmental and geomorphometric characteristics, for each species. We hypothesize that human- and disturbance-related factors would be more important than strictly environmental and geomorphometric characteristics in explaining species distribution. More precisely, we predicted that game species

in particular would present lower occupancies in areas with higher human access, and higher occupancies in areas closer to a more protected area or in more preserved sites (i.e. sites with higher forest quality). Little is known about many Neotropical frugivores, including all those studied here (IUCN, 2015). We therefore expected to complement existing information on important drivers of each species' occurrence, providing information that could be used for planning management actions directed at their conservation.

## Materials and methods

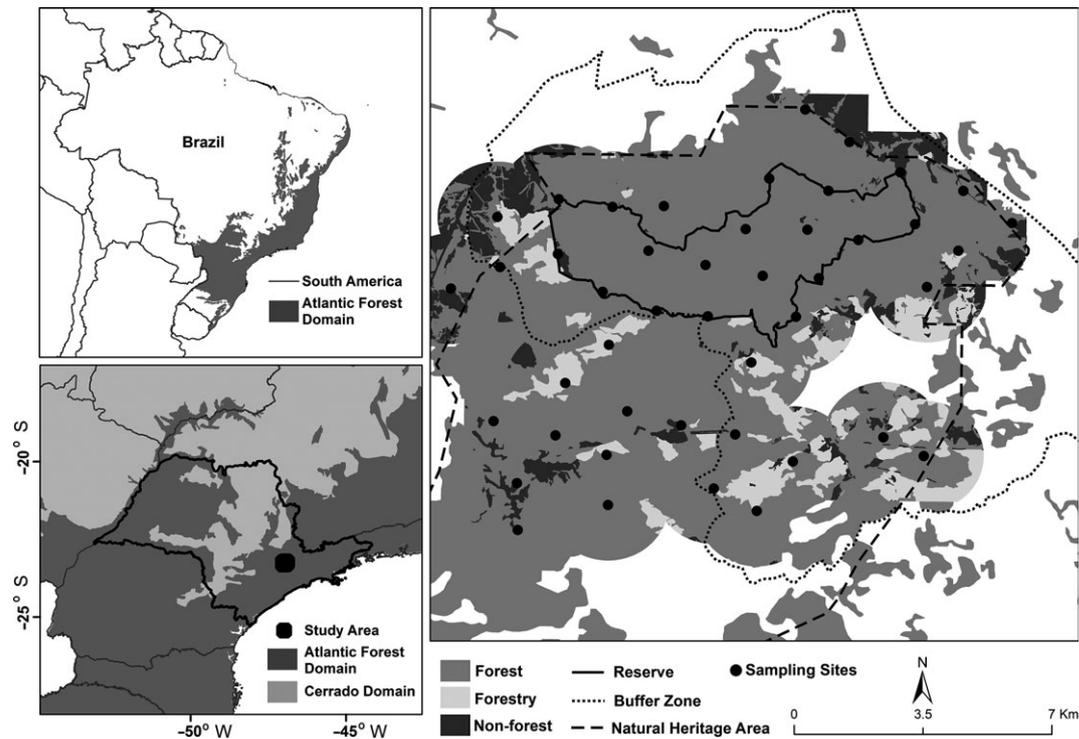
### Study area

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 between the metropolis of São Paulo and the highly urbanized cities of Jundiaí and Campinas, in southeastern Brazil. Serra do Japi represents one of the few large remnants of Atlantic Forest, a global hotspot for biodiversity conservation (Myers *et al.*, 2000). Today, the Atlantic Forest is highly fragmented with less than 16% of its original vegetation remaining (Ribeiro *et al.*, 2009). More than 80% of the remnants are small (<50 ha), highly isolated (average fragment distances 1440 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) that forms part of UNESCO's Atlantic Forest Biosphere Reserve (SMPMA, 2008). Located within this area is the Biological Municipal Reserve (REBIO – 2071 ha) surrounded by a buffer zone (11 946 ha; Fig. 1). The REBIO presents the highest protection status in the area, where guards actively patrol and the only permitted activities are research and education. The area is characterized by semideciduous mesophile forest, a mountainous terrain and a seasonal climate (Morellato, 1992). The mean temperature is 19.7°C, and the mean annual rainfall is 1422 mm. A dry and cold season extends from April to September, and a wet and warm season from October to March (Morellato, 1992).

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

Species	Body mass (kg) <sup>1</sup>	Habit	Game preference <sup>2</sup>	Seed <sup>3</sup>		Home range size (ha) <sup>4</sup>
				Disperser	Predator	
Paca	5–13 <sup>a</sup>	Gd	++	++ <sup>a,b</sup>	–	<4 <sup>a</sup>
Collared peccary	17–35 <sup>a</sup>	Gd	++	+ <sup>b,c</sup>	++	123–305 <sup>b</sup>
Brocket deer <sup>5</sup>	11–48 <sup>a</sup>	Gd	++	+ <sup>c</sup>	++	<100 <sup>c</sup>
Dusky-legged guan	1.8 <sup>b</sup>	Gd/Ar	+	++ <sup>d</sup>	–	11 <sup>d</sup>
Gray-fronted dove	0.2 <sup>b</sup>	Gd/Ar	–	+ <sup>e</sup>	++	<10 <sup>e</sup>
Black-fronted titi monkey	1.0–1.6 <sup>c</sup>	Ar	–	++ <sup>f</sup>	–	17–48 <sup>f</sup>
Buffy-tufted marmoset	0.5 <sup>c</sup>	Ar	–	++ <sup>g</sup>	–	35 <sup>g</sup>

Sources of the data: (1) a. Emmons & Feer, 1997; b. Dunning, 2007; c. Rowe, 1996;. (2) Redford, 1992; Peres & Palacios, 2007. (3) a. Dubost & Henry, 2006; Pimentel & Tabarelli, 2004; b. Keuroghlian & Eaton, 2009; c. Bodmer, 1991b; d. Strahl & Grajal, 1991; e. Ballarín *et al.*, 2013; f. Alvarez & Heymann, 2012; g. Figueiredo & Longatti, 1997. (4) a. Beck-King, Van Helversen & Beck-King, 1999; b. Keuroghlian, Eaton & Longland, 2004; c. Duarte, 1997; Maffei & Taber, 2003; d. Guix & Ruiz, 1997 (based on *Penelope superciliosus*); e. Boydston & DeYoung, 1988 (based on *Leptotila verreauxi*); f. Caselli, 2008; Nagy-Reis & Setz, 2017; g. Corrêa *et al.*, 2000. (5) considering *Mazama americana* and *Mazama gouazoubira*.



**Figure 1** Study area where ground-dwelling mammals and birds were sampled using camera-traps and primates using playback tests. On the right, the location of sampling sites (45) at Serra do Japi (southeastern Brazil), with mapped vegetation in grayscales. Adapted from Nagy-Reis *et al.*, 2017.

### Selected frugivore species

We selected seven frugivores for our study: paca *Cuniculus paca*; collared peccary *Pecari tajacu*; brocket deer (red-brocket deer *Mazama americana* and gray-brocket deer *Mazama gouazoubira*); dusky-legged guan *Penelope obscura*; gray-fronted dove *Leptotila rufaxilla*; black-fronted titi monkey *Callicebus nigrifrons*; and buffy-tufted marmoset *Callithrix aurita*. Although not strictly frugivores, these species' diets consist primarily of fruits (Bodmer, 1991a; Chalukian, 1997; Corrêa, Coutinho & Ferrari, 2000; Dubost & Henry, 2006; Ballarini, Frizzas & Marini, 2013; Nagy-Reis & Setz, 2017). 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 and differ in biology, ecology and preferability as game species (Table 1).

### Data collection

We surveyed 45 uniformly distributed sampling sites across the forest remnant (Fig. 1). The distance between sampling sites was *c.* 1.5 km (177 ha sampling area per sampling site; units viewed as circles of 0.75 km radius). This distance between the sampling sites provided a good coverage of our study area, and it conforms to the TEAM guidelines in the TEAM Terrestrial Vertebrate (camera trap) Monitoring

Protocol Implementation Manual (TEAM Network, 2011). Furthermore, we found no evidence for spatial autocorrelation in our data while using this spacing (see Supporting Information Table S1). We conducted two campaigns to collect data at each sampling site: 1- April 2013 to September 2013 (dry season); and 2- October 2013 to March 2014 (wet season). A different group of 15 sampling sites was surveyed every 2 months within each campaign. All sites were sampled during each campaign.

We recorded data on *C. paca*, *P. tajacu*, *Mazama* spp., *P. obscura*, and *L. rufaxilla* with passive infrared camera traps (Bushnell Trophy Cam;  $N = 5198$  trap days), which is a validated method for sampling these ground-dwelling animals (O'Connell, Nichols & Karanth, 2011). All cameras were installed off roads and trails.

We surveyed *C. nigrifrons* and *C. aurita* with six repeated playback tests at each sampling site (three per campaign/season;  $N = 270$  tests), an adequate method for sampling primates (Gestich *et al.*, 2016). All surveys were conducted during the hours when *C. nigrifrons* was most vocally active (7:00–13:00 h; Caselli, 2008). 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 primates at a sampling site if we heard or saw any individual at the location.

## Landscape variables

We mapped the land use, hydrography, and roads of the study area with Quantum GIS software (Álvarez, 2013), using high-resolution satellite image interpretation at a 1:5000 scale, cartographic maps at a 1:10 000 scale (Secretariat of Economy and Planning, São Paulo State Government), and extensive field verification by a botanist (see Acknowledgments). We considered the following land use categories: forests at initial, intermediate, and advanced succession; forestry (i.e. *Eucalyptus* spp. and *Pinus* spp. plantations); pasture; agriculture; and urban area (including rural installations and residences).

Because observed responses of organisms to the environment may depend on the scale at which the environment is perceived (and thus measured), we adopted a multi-spatial scale approach (Boscolo & Metzger, 2009). The scales were defined as concentric circles (buffers) of 200-, 500- and 1000-m radius around each sampling site. Landscape metrics were calculated for each scale. We standardized all covariates and used only weakly correlated covariates in the final model sets (see Supporting Information Table S2).

## Covariates used to model occupancy

In the buffer surrounding each sampling site, we obtained values for the following covariates: mean elevation, mean slope, percentage of high-quality forest cover (see below), road density, and hydrographic density. We obtained elevation and terrain slope from digital elevation models (DEM) available from the Topodata Geomorphic database of Brazil (INPE, 2014). We considered the percentages of intermediate and advanced forest succession as indicative of high-quality forest cover, and these percentages were calculated in the Geographical Resources Analysis Support System (GRASS; Neteler *et al.*, 2012). Road and hydrographic densities were obtained using the Kernel density function in ArcGIS software (ESRI, 2009). Furthermore, we determined the proximity of each sampling site to the strictly protected area, REBIO (Biological Municipal Reserve); these proximity values were then weighted by the protection status where the sampling site was located (hereafter 'weighted distance to reserve border'). First, we measured the distance from each sampling site to the nearest border of the REBIO, giving negative distances to sites within the REBIO and positive distances otherwise (i.e. the center of the reserve received the smallest value). Then, we multiplied these distances by the protection status weight of the area in which each sampling site was located (REBIO = 1; REBIO's buffer zone = 2; within the Natural Heritage Area but outside REBIO and its buffer zone = 3; outside these three areas = 4). We were not able to incorporate this covariate in the marmoset models because the  $\beta$  coefficients did not converge; therefore, we used only the area protection status weight for this species.

We expected that anthropogenic variables would be the main predictors of frugivore occupancy, especially for game species. Specifically, we hypothesized that occupancy would

be negatively related to road density and the weighted distance to reserve border, as both are associated with high anthropogenic impacts (e.g. hunting). We also hypothesized that occupancy would be positively related to the percentage of high-quality forest cover, as it represents a less disturbed environment. To a minor degree, we predicted that hydrographic density would have a positive effect on occupancy, based on the assumption that this covariate is associated with water availability. Finally, we predicted that slope and elevation would have a negative effect on occupancy, as higher slopes may constrain locomotion, and higher elevations may have lower plant richness and diversity (Lieberman *et al.*, 1996). Because we lack basic information on the species analyzed (IUCN, 2015), we assumed that all species would have a similar response (i.e. same predicted direction, either positive or negative), but with different strengths. For instance, we expected that the main game species (*C. paca*, *P. tajacu*, *Mazama* spp.) would exhibit the strongest response to anthropogenic characteristics.

## Covariates used to model detection probability

We considered mean temperature, total precipitation, overall monthly fruit availability, season (dry and wet), and percentage of high-quality forest cover as potential covariates for detection probability. For the ground-dwelling species, we also included terrain slope (at the site), and for primates, the time of the day that the surveys were conducted as we predicted these variables would be negatively associated with detection. Monthly fruit availability was considered as the number of arboreal plant species bearing fruits, per month within the study area (derived from a 5-year phenological study at Serra do Japi; Morellato & Leitão-Filho, 1992); and we expected that detection probability would increase with higher temporal availability of fruit. 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 (e.g. Giotto *et al.*, 2013). Lastly, we predicted that the percentage of high-quality forest would increase the detection of most species, as it represents better quality habitats.

## Occupancy and detection estimation

We used multi-season occupancy modeling (MacKenzie *et al.*, 2003) to estimate the occupancy ( $\psi$ ) of each frugivore, and to evaluate the factors influencing occupancy, while accounting for detection probability ( $P$ ). We used models with four parameters: initial occupancy (dry season), detection probability, colonization probability, and extinction probability; the last two parameters corresponding to the time interval between dry and wet seasons. Given that we conducted this study over only two seasons and have a relatively small sample size, we were not able to investigate sources of variation in colonization and extinction. Therefore, we held colonization and extinction constant in all

analyses (i.e.  $\gamma(\cdot)$ ;  $\epsilon(\cdot)$ ; similar to Licona *et al.*, 2011).

We estimated parameters using PRESENCE software (Hines, 2006), using logistic regression models to determine the covariates that best explain occupancy and detection probability. We used a three-step approach: (1) Assess the appropriate spatial scale for each covariate; (2) Investigate sources of variation in  $\psi$ , while modeling  $P$  in the most general way possible (see Supporting Information Table S3 for details on general models for detectability), to determine the most influential covariates for occupancy, the parameter with biological meaning and our main focus; and (3) Investigate sources of variation in  $P$ , exploring the most influential covariates for detection probability. These steps are detailed below.

In the first step, we determined the scales that best represent each species' response to the landscape covariates. We used a general model for  $P$  (which contained as many potential covariates as possible; following MacKenzie, 2006) and allowed initial occupancy ( $\psi$ ) to vary by only the focal landscape covariate measured at the respective scales of the various buffer sizes (see Supporting Information Table S3). When different spatial scales were equally plausible ( $\Delta\text{AICc} < 2$ ), we chose to use the home range scale rather than the landscape scales in the next step. Secondly, we developed another model set to investigate the variation in occupancy using each covariate at its scale of strongest response for each species (from the previous step). We allowed  $\psi$  to be constant ( $\psi(\cdot)$ ) or to vary as a function of either a single covariate or a combination of two covariates (additive effect), and we used a general model for  $P$  (see Supporting Information Table S4). 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. Thirdly, we determined which covariate(s) best explained the detection probability ( $P$ ), allowing  $P$  to be constant or to vary as a function of either a single covariate or a combination of two (see Supporting Information Table S5). In this step, we used the same  $\psi$  as in the top-ranked model from the previous step.

In total, we evaluated a suite of 22 *a priori* candidate models for each parameter ( $\psi$  and  $P$ ). We built only those models that translated plausible biological hypotheses regarding the effects of variables on each species' occupancy ( $\psi$ ) and detection probability ( $P$ ), and we used balanced model sets (i.e. all covariates were present in the same number of models). We ranked candidate models using the Akaike Information Criterion adjusted for small sample size (AICc;  $N$  = number of sampling sites) (Burnham & Anderson, 2002). We considered the covariate(s) from the top-ranked model(s) ( $\Delta\text{AICc} < 2$ ) as the most likely determinant(s) of the species' occupancy or detection. Additionally, we assessed the relative importance of each covariate by summing the Akaike weights ( $w_i$ ) of all the models ( $i$ ) in which that covariate was present, and we examined the 95% confidence intervals (CIs) to see whether the  $\beta$  parameters

describing the relationships overlapped with 0 or not (Burnham & Anderson, 2002). We also calculated the evidence ratio in favor of our hypothesis that anthropogenic factors would be more important than strictly environmental and geomorphometric characteristics. For this, we summed the Akaike weights ( $w_i$ ) of models with the anthropogenic-related factors (road density, weighted distance to reserve border, and percentage of high-quality forest cover) and divided it by the Akaike weights ( $w_i$ ) of all models with strictly environmental and geomorphometric characteristics (elevation, slope, and hydrography density). We applied model averaging (Burnham & Anderson, 2002) in PRESENCE software (Hines, 2006) to estimate the occupancy of each species in each season at each sampling site. Then we calculated the average site occupancy across the two seasons for each species and summed these values to obtain an overall occupancy of frugivores at each sampling site. Finally we applied a bivariate interpolation function onto the pixels of our study area. This allowed us to estimate the occupancy between sampling sites even without having covariates for these areas. This procedure resulted in a map with frugivores' overall occupancy in our study area. We implemented this analysis in R software version 3.1.1 (R Development Core Team, 2014) using the 'akima' package (Akima *et al.*, 2013).

## Results

### Spatial scale

Models with the same covariate measured at different spatial scales (landscape vs. home range scales) were not always equally supported (see Supporting Information Table S3). For instance, models with hydrographic density for paca and gray-fronted dove, and models with forest quality for paca, where the covariates were measured at the home range scale (200 m) were substantially more supported than models with these covariates at the landscape scale (1000 m;  $\Delta\text{AICc} > 2$  between models). Models with hydrographic density for black-fronted titi monkey and road density for collared peccary and paca were more supported at the 1000-m scale than at finer scales. See Supporting Information Table S3 for the selected spatial scale of each covariate for each species.

### Frugivore occupancy

We had 919 captures of our target ground-dwelling frugivores ( $N = 5198$  trap days) and 214 records of primates ( $N = 270$  playback tests per species; Table 2). The summed site occupancies of the seven frugivores suggest a higher overall occurrence of the group in the center of the reserve (Fig. 2).

We found evidence that the occupancy of the strictly ground-dwelling frugivores – paca, collared peccary, and brocket deer, which are important game species – was influenced by human- and disturbance-related characteristics. At least one of the anthropogenic covariates (i.e. road density, weighted distance to reserve border and percentage of high-

**Table 2** Number of records (detections), number of sampling 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

Species	N detections	N sites w/detection	Naïve occup.		Occup. prob. $\hat{\psi}^1$		Rel. increase above naïve occup. (%) <sup>2</sup>	
			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
Dusky-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.

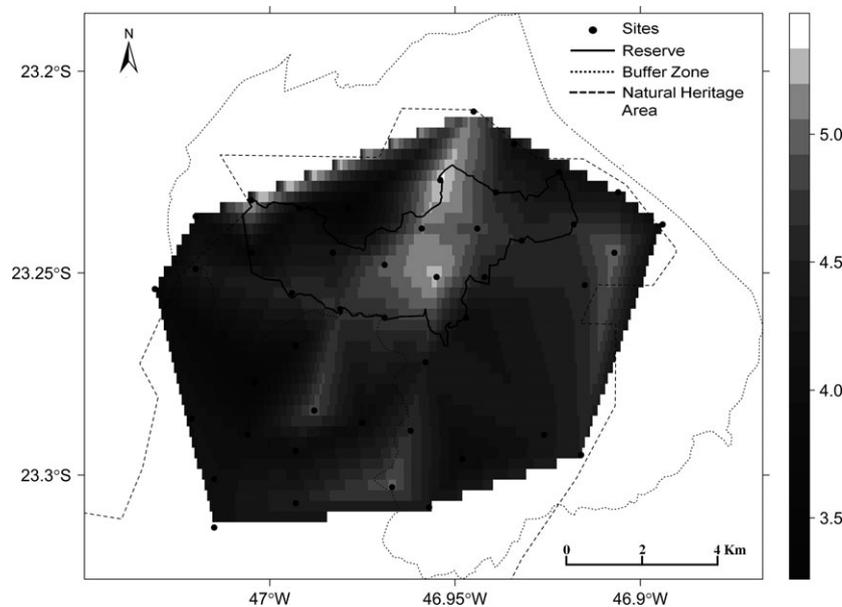
<sup>1</sup>Occupancy probability and standard deviation estimated by model averaging.

<sup>2</sup>Percentage increase in estimated proportion of occupied sites when incorporating detection probability ( $P$ ) [(estimated occupancy probability/naïve occupancy) − 1 × 100].

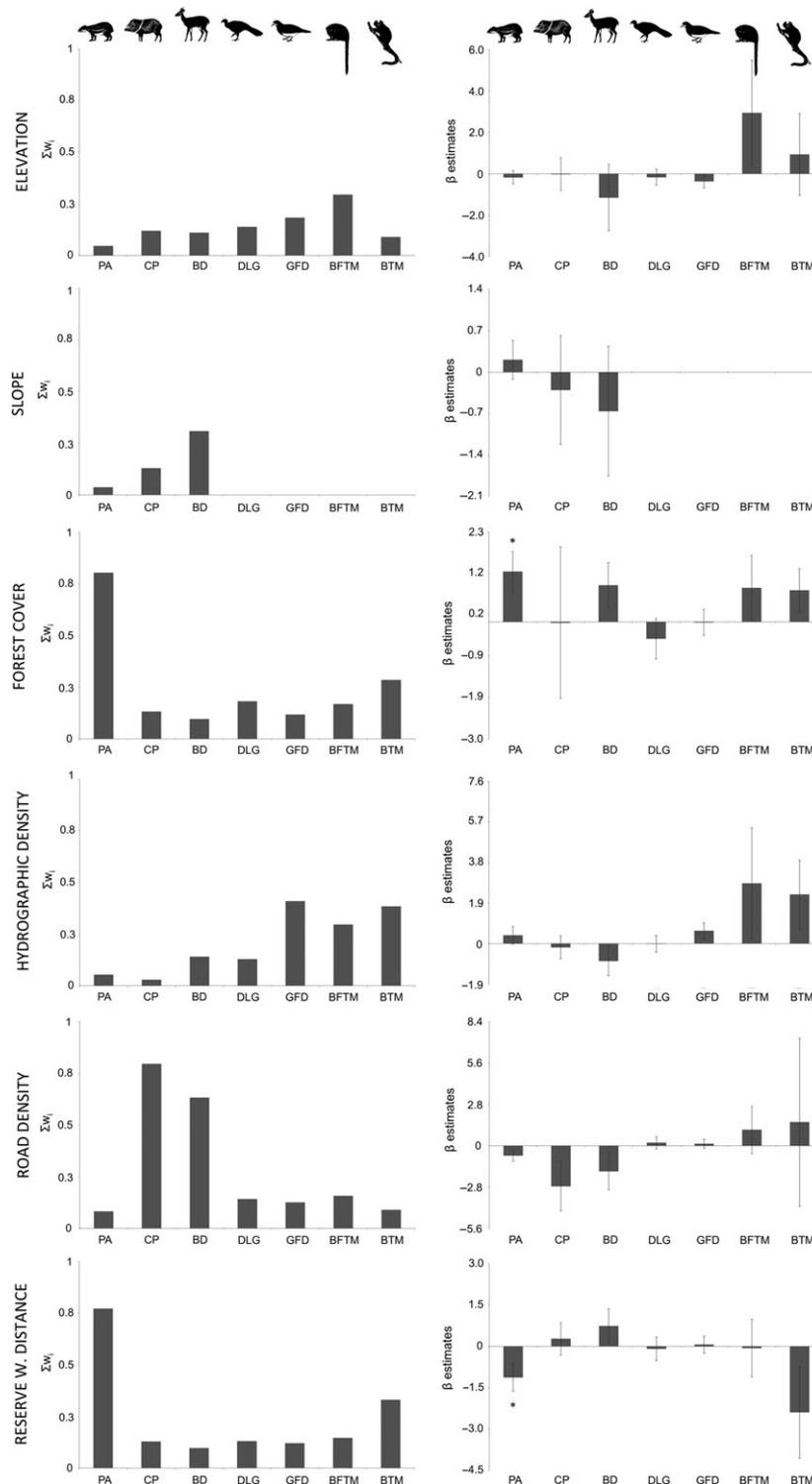
quality forest) was included in the top-ranked occupancy model, with a high relative importance for the three game species (Fig. 3; see Supporting Information Table S4). Evidence ratios of 12, 4, and 3 indicated that anthropogenic-related factors are more closely associated with occupancy for paca, collared peccary, and brocket deer, respectively, than are strictly environmental and geomorphometric characteristics (Evidence ratios for the other species  $\leq 2$ ). We found support for constant occupancy ( $\psi(\cdot)$ ) across sampling sites for the dusky-legged guan, gray-fronted dove, black-fronted titi monkey, and buffy-tufted marmoset (see Supporting Information Table S4).

### Frugivore detection probability

Season, weather, terrain slope, and forest cover were frequently good predictors of frugivore detection probability (Fig. 4; see Supporting Information Table S5). Detection was usually lower in the wet season than in the dry season. Temperature greatly increased the detection of primates, and rainfall increased the detection of the dusky-legged guan. In higher-quality habitats, collared peccaries and black-fronted titi monkeys were more readily detected, whereas dusky-legged guans were less easily detected. Terrain slope decreased paca detection but increased dove detection. Titi



**Figure 2** Summed site occupancy of the seven frugivores – paca *Cuniculus paca*, collared peccary *Pecari tajacu*, brocket deer *Mazama* sp., dusky-legged guan *Penelope obscura*, gray-fronted dove *Leptotila rufaxilla*, black-fronted titi monkey *Callicebus nigrifrons*, and buffy-tufted marmoset *Callithrix aurita* – in a protected area of Atlantic Forest, in south-eastern Brazil. [Color figure can be viewed at wileyonlinelibrary.com]



**Figure 3** Influence of geomorphometric, environmental, and anthropogenic covariates on frugivore occupancy in a large Atlantic Forest remnant, showing the sum of model weights ( $\Sigma w_i$ ) and the associated beta ( $\beta$ ) 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, dusky-legged guan *Penelope obscura*; GFD, gray-fronted dove *Leptotila rufaxilla*; BFTM, black-fronted titi monkey *Callicebus nigrifrons*; BTM, buffy-tufted marmoset *Callithrix aurita*.

monkeys were more detected early in the day than later. Finally, monthly fruit availability had low influence on the detection of several of the species, increasing only the detection of dusky-legged guans.

## Discussion

We determined the occupancy of a diverse group of Neotropical frugivores in a protected area of Atlantic Forest and its immediate surroundings, investigating the relationship between landscape characteristics and site occupancy rates at multiple scales. Expanding our survey over other Atlantic Forest sites and over a greater period of time could be used in future long-term multi-species monitoring programs, enabling estimation of some vital rates such as local extinction and colonization probabilities. Knowledge of factors influencing these vital rates is especially useful for conservation and management. Despite frugivores' important role in regulating plant communities (Wright *et al.*, 2000; Galetti & Dirzo, 2013), most frugivore populations are decreasing and/or are threatened, and several species are still poorly studied, including the species analyzed here (IUCN, 2015). For example, buffy-tufted marmoset *Callithrix aurita* is considered 'vulnerable', red-brocket deer *M. americana* is 'data deficient', and black-fronted titi monkey *Callicebus nigrifrons* is 'near threatened' (IUCN, 2015).

### Influence of human disturbance, protection and geomorphometry

Our general hypothesis that human- and disturbance-related factors would be more important drivers of occupancy than strictly environmental and geomorphometric characteristics was supported for the main game species analyzed – paca *C. paca*, collared peccary *P. tajacu*, and brocket deer *Mazama* spp. Many frugivores are considered important game species and are sensitive to hunting (Redford, 1992; Peres & Palacios, 2007), 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 kind of protection, the most protected area (the reserve) held higher occupancies of frugivores, especially in its center, where most of the land is in fact public and guards actively patrol the area. Furthermore, paca occupancy decreased as the distance increased between sampling site and the reserve. This has also been observed for another key group at the same location (small carnivores; Nagy-Reis *et al.*, 2017).

In addition, paca occupancy was positively correlated with the percentage of high-quality forest cover. Similar to ungulates in the Amazon (*M. gouazoubira*, *M. americana* and *Tayassu pecari*; Licona *et al.*, 2011), the occupancy of large-sized game species in Atlantic Forest (i.e. collared peccaries and brocket deers) was predicted only by human accessibility (here measured by road density), even after incorporating habitat covariates at a finer scale (as

suggested by Licona *et al.*, 2011). Despite the mountainous terrain of our study area and the variation in hydrography throughout our study area, we had overall low support for the effects of geomorphometry and hydrography on frugivore occupancy.

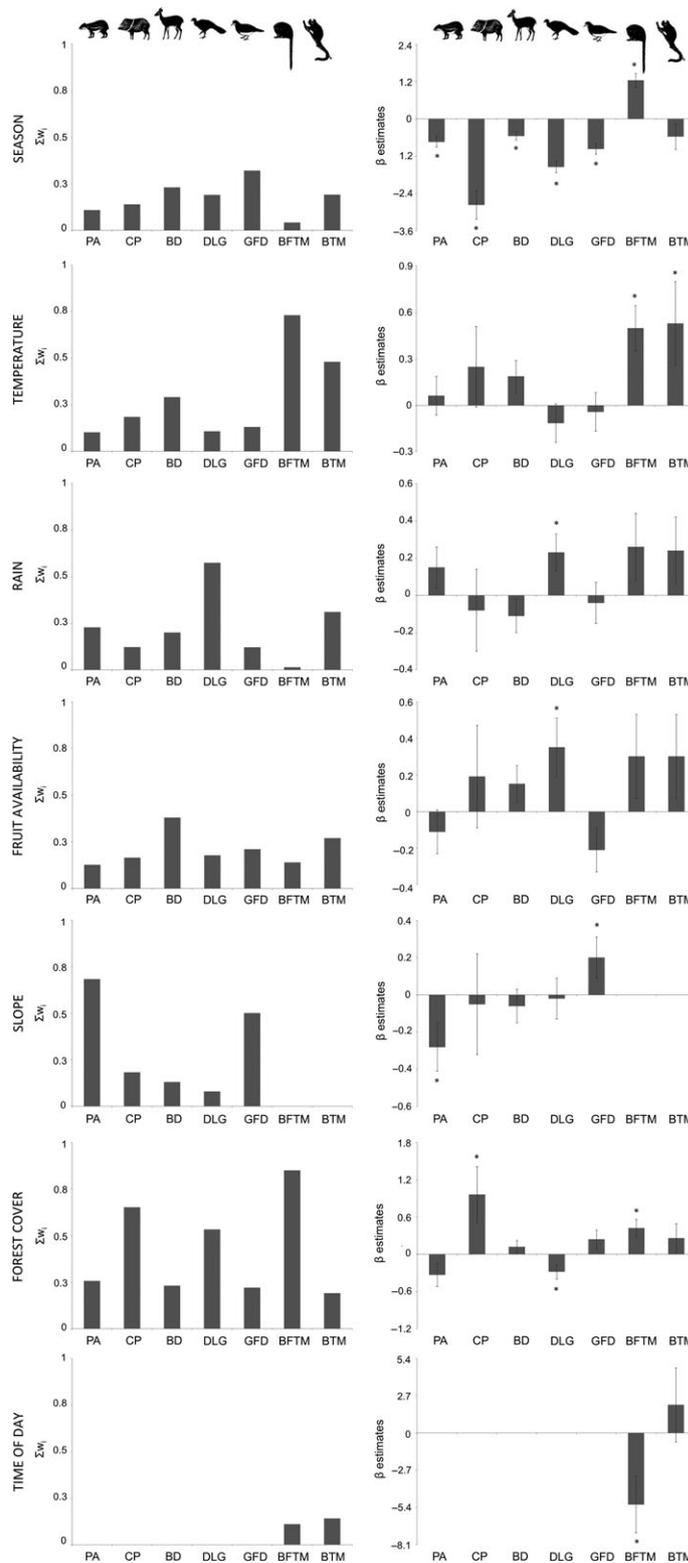
### Biological consequences of frugivore occupancy

Because certain frugivores are preferred game species, and illegal hunting is common in the Atlantic Forest, anthropogenic factors may exert greater pressure on their occurrence than natural characteristics of the habitat. Notably, the species most influenced by human- and disturbance-related factors, paca, collared peccary and brocket deer, are also the largest frugivores in our study area, a fact that may have important implications concerning these species' distinct ecological roles. In contrast to the other analyzed frugivores, collared peccary and brocket deer eat medium- and large-sized seeds more frequently than small ones (Bodmer, 1991b), while pacas can disperse medium-sized seeds as well as smaller seeds (Pimentel & Tabarelli, 2004; Dubost & Henry, 2006; Keuroghlian & Eaton, 2009). Therefore, the reduced occupancy of these frugivores in areas with human- and disturbance-related impacts, may result in declines in the availability and quality of seed dispersal and predation services (Peres & Palacios, 2007), especially for plants with medium and large seeds. In the Atlantic Forest, nature reserves protect a small amount of the remaining forest (9%), and most forest remnants are distant (>25 km) from existing reserves (Ribeiro *et al.*, 2009). We found evidence of some effects of anthropogenic factors on the occurrence of frugivorous game species in one of the few relatively well-preserved and protected Atlantic Forest sites, a fact that gives us troubling insights into how human-dominated biomes may be suffering from loss of ecological services and, consequently, facing modification of local plant communities.

### Management recommendations

Due to the ecological relevance of Neotropical frugivores and their sensitivity to threats, several actions are recommended 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; Moegenburg & Levey, 2003; Kirika *et al.*, 2008). Here, we highlight the main management recommendations arising from our study:

- 1 Different species of frugivores play different ecological roles and may be preferred as game species to varying degrees. We have demonstrated that some frugivores do not respond to a given habitat attribute as intensely as others might. Studying several species of a group and using the landscape characteristics necessary for the species with the most demanding requirements to design and manage landscape and protect the fauna may encompass the requirements of other species (Lambeck, 1997) and, consequently, conserve the ecological functions of the entire group. We therefore



**Figure 4** Influence of each sample and site covariate on frugivores' detection probabilities in a large Atlantic Forest remnant, showing the sum of models' weights ( $\Sigma w_i$ ) and the associated beta ( $\beta$ ) 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, dusky-legged guan *Penelope obscura*; GFD, gray-fronted dove *Leptotila rufaxilla*; BFTM, black-fronted titi monkey *Callicebus nigrifrons*; BTM, buffy-tufted marmoset *Callithrix aurita*.

recommend consideration of a multi-taxa approach to identify the most demanding species and aid in management plans for landscapes and wildlife.

- 2 We determined that high percentages of intermediate and advanced levels of forest succession, close proximity to strictly protected areas (i.e. IUCN Protected Area Category Ia – Strict Nature Reserve; Phillips, 2004), and limited human accessibility (e.g. low road densities) are important landscape characteristics for managing Atlantic Forest frugivores. These factors should be considered when establishing additional protected areas (see Magioli *et al.*, 2015, for some guidelines to maintain functional diversity of Atlantic Forest mammals).
- 3 The establishment of protected areas can decrease habitat loss (Andam *et al.*, 2008) and anthropogenic pressures (Bruner *et al.*, 2001; Peres & Palacios, 2007). In accordance with a previous study of small carnivores (Nagy-Reis *et al.*, 2017), our results suggest that reserves can improve the occupancy of key groups. In addition to more strictly protected areas (e.g. reserves), the frugivores' occupancy patterns found in the surrounding areas suggest that these areas with less protection may also provide suitable habitat if human accessibility is low. Nonetheless, since hunting still occurs illegally in the Atlantic Forest, and illegal hunting 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.
- 4 In addition to a multi-taxa approach, incorporating landscape characteristics at multiple scales and properly dealing with detection probability are fundamental steps in an investigation of species-habitat relationships, as suggested by the following findings. (1) Frugivores' responses to the landscape apparently depended on the scales at which they perceive the habitat. (2) Incorporating detection probability resulted in a relative increase of up to 146% above naïve occupancy, even though we used efficient and valid data collection methods (O'Connell *et al.*, 2011; Gestich *et al.*, 2016). (3) Temperature, precipitation, season, terrain slope, and vegetation cover influenced the detection of most species.

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King, a native English speaker from British Columbia, Canada, proofread the manuscript.

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## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** Test results for spatial independence of detections for Neotropical frugivores sampled with camera traps (1.5 km between sampling sites) in a large Atlantic Forest remnant in Brazil.

**Table S2.** Spearman's correlation matrix of the measured site covariates for a large Atlantic Forest remnant in Brazil.

**Table S3.** Model selection analysis for occupancy ( $\psi$ ) 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 in an Atlantic Forest site in Brazil.

**Table S4.** Model selection analysis (cumulative  $w_i > 0.80$ ) and occupancy (initial  $\psi$ ) 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 in an Atlantic Forest site in Brazil.

**Table S5.** Model selection analysis (cumulative  $w_i > 0.80$ ) 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 in an Atlantic Forest site in Brazil.