Effectiveness of Protected Areas for biodiversity conservation: Mammal occupancy patterns in the Iguaçu National Park, Brazil

Marina Xavier da Silva[a,d,*], Agustin Paviolo[b], Leandro Reverberi Tambosi[c,d], Renata Pardini[e]

[a] Projeto Carnívoros do Iguaçu, Parque Nacional do Iguaçu, BR-469, Km 22.5, CEP 85851-970, Foz do Iguaçu, PR, Brazil
[b] Instituto de Biología Subtropical, Universidad Nacional de Misiones and CONICET, and Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Bertoni 85, N3370AIA, Puerto Iguazú, Misiones, Argentina
[c] Centro de Engenharia, Modelagem e Ciências Sociais Aplicadas, Universidade Federal do ABC, Avenida dos Estados, 5001, CEP 09210-580, Santo André, SP, Brazil
[d] Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, 101, CEP 05508-090, São Paulo, SP, Brazil
[e] Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, 101, CEP 05508-090, São Paulo, SP, Brazil

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ABSTRACT

Protected areas – widely recognized as the main strategy for biodiversity conservation – have greatly expanded, covering ~ 15% of the Earth; however, we still lack detailed information on biodiversity to evaluate their effectiveness. This is particularly urgent for biodiversity hotspots where protected areas are islands within human modified landscapes. We focus on mammals of the Iguaçu National Park – one of the most important parks in the Atlantic Forest hotspot – to evaluate the effectiveness of protected areas in conserving biodiversity. We monitored 300 km^2 with 37 cameras traps during five years to assess if (1) species occupancy declined over time, and (2) if species occupancy/detectability are spatially associated with illegal hunting, proximity to tourism infrastructure and distance from the edge, estimating the proportion of the park where these negative effects are detected. Many species that are rare in most Atlantic Forest remnants presented high occupancy within the park, and no decline in occupancy was observed over time. However, the distribution of 11 species was spatially associated primarily with the distance from the edge and proximity to tourism infrastructure, resulting in a decline, across half of the park area, from 13 to 23% in occupancy and from 19 to 35% in detectability (values averaged among species). These negative effects should be even stronger on smaller protected areas, which are the majority in highly altered hotspots. Re-establishing and properly managing buffer zones and restricting tourism to localized areas are essential to ensure the effectiveness of protected areas for biodiversity conservation.

1. Introduction

Protected Areas (PAs) have long been recognized as essential for biodiversity conservation. Despite some recent dispute on the goals of conservation biology (e.g., Kareiva & Marvier, 2012; Soule, 2013), the PA strategy continues to be consensually seen as a cornerstone of conservation (Mace, 2014). In the last decades, the inclusion of PA issues on the agenda of international conventions has stimulated the creation of many PAs and of PA networks around the world, with the global system currently covering ~ 15% of the Earth's surface (Juffe-Bignoli et al., 2014).

Determining the effectiveness of PAs in representing and maintaining biodiversity is thus of foremost importance (Juffe-Bignoli et al., 2014). A substantial effort has been put in evaluating PA effectiveness using approaches ranging from how much area is protected (e.g.,

Jenkins & Joppa, 2009) to how well PA systems perform in representing biodiversity (e.g., Leroux et al., 2010). While these studies have pointed out an increased coverage of the global PA system and indicated how to close remaining conservation gaps, most protected areas are still 'paper parks', with only 20–50% of global PAs being effectively managed (Geldmann et al., 2013; Watson, Dudley, Segan, & Hockings, 2014).

Several studies addressed this specific issue of how effective PAs are in maintaining biodiversity by comparing deforestation, fires and other impacts inside and outside PAs using remote-sensing technologies, and/or questionnaires, suggesting that PAs reduce many of the studied impacts (Geldmann et al., 2013). Although this type of study has the advantage of allowing regional or global analysis, they do not focus directly on biodiversity measures (e.g., Beaudrot et al., 2016), and should be complemented by more local yet more precise evaluations based on species distributions, population sizes and community structure.

Evaluating and ensuring the effectiveness of PAs for biodiversity conservation is particularly urgent and challenging in biodiversity hotspots. PAs in those hotspots are islands immersed within highly modified landscapes, and are subjected to cryptic yet strong threats such as, hunting, invasive species and other edge effects (e.g. changes in vegetation structure and microclimate and increased chance of fire and logging), which cannot be accurately assessed by using gross metrics, such as changes in forest cover. Large mammals are good indicators for detecting the effects of some of these cryptic threats. They are among the preferred game species (Jerozolimski & Peres, 2003), are subjected to persecution due to human-wildlife conflict (Woodroffe & Ginsberg, 1998), and commonly alter their behavior, avoiding proximity to areas with intensive human presence such as tourist trails and roads (Leblond, Dussault, & Ouellet, 2013; Rogala, Hebblewhite, Whittington, & White, 2011). As a result, few areas in the world harbor intact large mammal faunas (Morrison, Sechrest, Dinerstein, Wilcove, & Lamoreux, 2007).

Brazil stands out both for its biodiversity and for the investment in the establishment of PAs, harboring today the largest PA system in the world (~12.4%) of the global system (WDPA, 2012). However, PA downgrading, downsizing and degazettement, which have become increasingly common in many countries and are currently a global phenomena (Mascia & Pailler, 2011; Watson et al., 2014), have affected the Brazilian PAs as well (Bernard, Penna, & Araújo, 2014). A few studies have evaluated the effectiveness of Brazilian PAs, and they focus mostly in more pristine regions and on the rates of deforestation inside and outside PAs (Carranza, Balmford, & Manica, 2013; Nolte, Agrawal, Silvius, & Soares-Filho, 2013). In contrast, we know little about the effectiveness of the Atlantic Forest PAs – the second largest rainforest in South America with one of the highest species richness and rates of endemism on the planet (Metzger, 2009) – that harbors 70% of the Brazilian population and is reduced to less than 16% of its original extent (Ribeiro, Metzger, Martensen, & Ponzoni, 2009).

One of the most important PAs in the Atlantic Forest is the Iguaçu National Park (INP) in Brazil, which is bordered by PAs in Argentina. Together with adjacent PAs and other forest remnants, it protects approximately 10 000 km² and many endangered species (Di Bitetti, Paviolo, & De Angelo, 2006), and is the only Atlantic Forest PA large enough to harbor forest sites located 12 km from any converted land (Ribeiro et al., 2009). It is also the second most visited National Park in Brazil; in 2016, the park received more than 1.5 million people and generated an income of U$ 8 million. Part of the resources are injected into the Brazilian PA system to be shared among other PAs. If the total economic impact of INP in the region is taken into account (Medeiros, Young, Pavese, & Araújo, 2011), the park generates today around U$ 150 million per year.

Given its importance as one of the last large Atlantic Forest protected remnants and its relevance in terms of visitation and income generation, the INP is ideal to evaluate the effectiveness of protected areas within biodiversity hotspots in conserving biodiversity. By monitoring an area of 300 km² during five years (2009–2013), we here focus on the temporal and spatial dimensions of occupancy patterns of terrestrial large mammals. We investigate (a) if species occupancy declined over time, and (b) if species occupancy or detectability are spatially associated with illegal hunting, proximity to tourism infrastructure and distance from the edge to converted land, estimating the proportion of the park where these negative effects are detected.

2. Material and methods

2.1. Study area

The Iguaçu National Park is located in the southwest portion of Brazil, close to the international border with Argentina and Paraguay (Fig. 1A), and is covered mostly by semi-deciduous Atlantic Forest and by the highly threatened Araucaria Forest in its northern part. The climate is humid temperate with mean annual precipitation of 1 712 mm and mean annual temperature of 20.7C without a dry season (Peel, Finlayson, & Mcmahon, 2007). The INP covers 1 852 km² and is adjacent to the Iguazú National Park in Argentina with its 677 km² (Fig. 1A). Together, they are core areas for long-term conservation in the Upper Paraná Atlantic Forest ecoregion harboring high levels of biodiversity (Di Bitetti et al., 2006) and one of the most spectacular natural sights in South America: the Iguaçu falls. Both parks were declared Word Heritage Areas by UNESCO.

The INP is surrounded by 14 municipalities with a human population estimated in more than 446 000 inhabitants. The occupation of the region started in the 1950s through federal incentives, leading to rapid forest conversion and culminating with the transformation into one of the most important Brazilian soybean production areas, with heavy use of fertilizers and agrochemicals. Nowadays large crop farms and smaller cattle farms dominate the landscapes beyond the INP, with few remaining forest patches (Fig. 1A).

2.2. Sampling design

We assessed the occupancy patterns of terrestrial large mammals using a regular grid established on the western part of the INP. In total, we established 37 sites 4 km apart from each other, covering around 300 km² (one-sixth of the INṔs area). Grid location was chosen to encompass a large variation in key spatial aspects associated with potential threats or impacts to mammals (i.e. width of the park, distance to tourism infrastructure and quality of neighboring areas; Fig. 1A). The grid included all main tourism attractions and associated infrastructure, encompassing a wide variation (from 0 to 31 km) in the distance to tourism infrastructure. It also covered both the narrowest (3 km from edge to edge) and wider areas of the park (17 km from edge to edge), including areas adjacent to highly altered landscapes as well as those bordered by the Iguazú National Park in Argentina (i.e. areas inserted in the largest tract of Atlantic Forest in the region).

2.3. Data collection

2.3.1. Mammal sampling

In each of 37 sites, we installed two camera-traps 40 cm above ground level. We monitored all the sites simultaneously during three periods of three months each in three different years (from July to October 2009, from October 2010 to January 2011, and from February to May 2013). During each sampling period, we visited the sites every 20 days to replace films, batteries, silicon and keep the area in front of the camera clear. Each month was considered a capture session, and capture history matrices of nine capture sessions (three from each year) were created for each species.

2.3.2. Spatial covariates

We focused on three spatial covariates that represent common threats in PAs.

2.3.2.1. Hunting pressure. Hunting was calculated from a georeferenced database created by the INP Protection Sector, which coordinates park ranger activities, containing all records of illegal activities encountered in the park from 2009 to 2012. We calculated the sum of the number of hunting records and associated activities found from 2009 to 2012 in a 2-km radius (i.e. half the distance between sites) around each of the 37 sites. From all records in the database, we considered only those clearly related to hunting (or to palm tree extraction, which is commonly performed by hunters) for which it was possible to discern between old and new events: the presence of hunting platforms, hunting trails and/ or hunting camps, and evidence of recent palm tree extraction.

2.3.2.2. Proximity to tourism infrastructure. As tourism attractions and associated infrastructure are spatially aggregated within the park
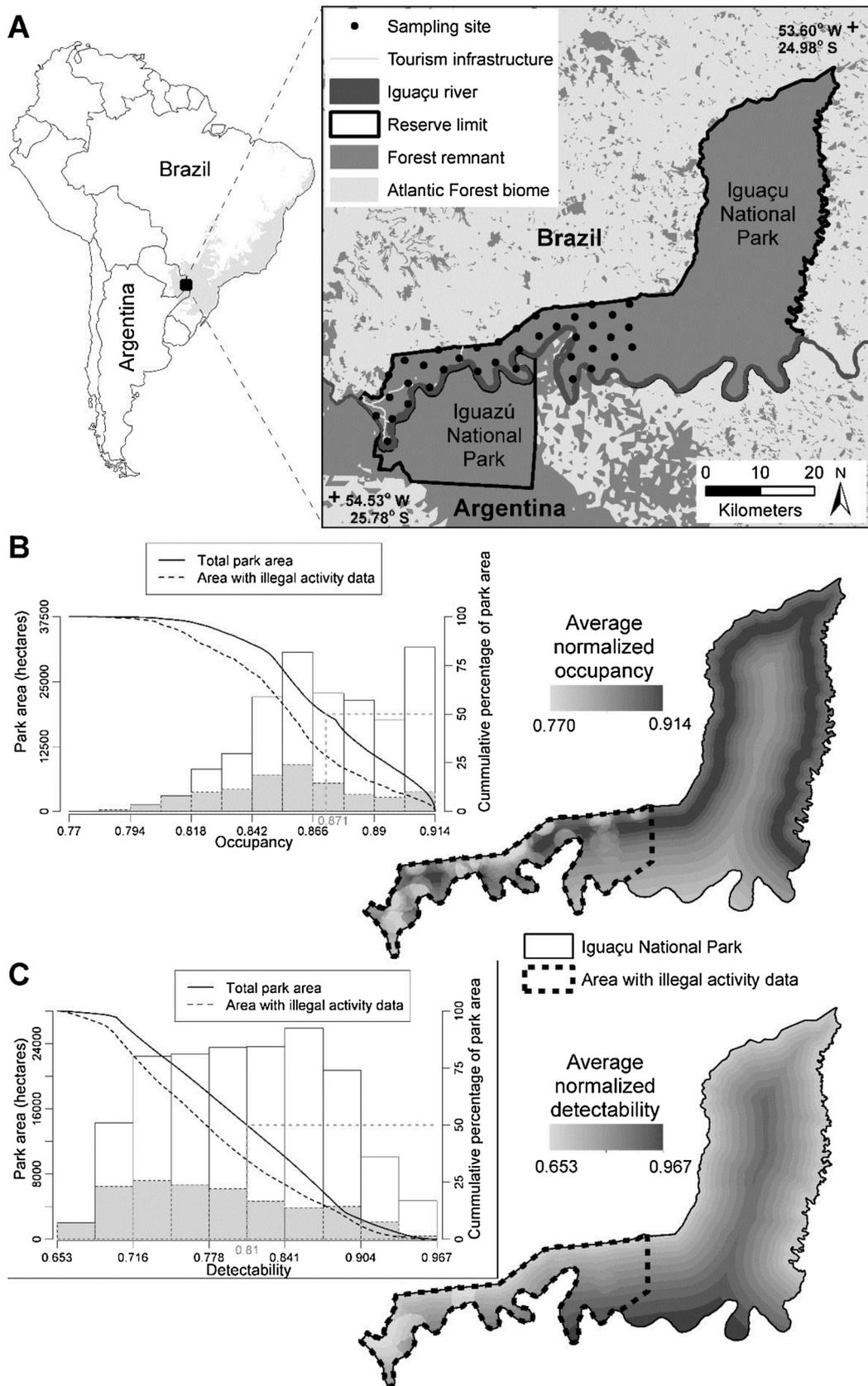
Fig. 1. (A) Map of Brazil showing the remnants of Atlantic Forest and in more detail the limits of the Iguaçu and Iguazú national parks, in Brazil and Argentina, the 37 sampling sites as black dots and the location of tourism infrastructure. Maps of the Iguaçu National Park showing variation in the average normalized occupancy (B) and detectability (C) among 16 native terrestrial large mammals (all analyzed species, except the domestic dog). Within both (B) and (C) histograms of the area (bars) and cumulative percentage area (lines) of INP within classes of average normalized occupancy or detectability, considering the entire park (white bars, full line) and the area of the park with hunting information (grey bars, dashed line).

(Fig. 1A), we chose to use a categorical variable that represents the presence/absence of *tourism infrastructure* within the 2-km radius of each of the 37 sites.

2.3.2.3. Distance from the edge of the park. We were interested to quantify edge effects from adjacent human-modified landscapes associated with species invasion, proximity to human-wildlife conflict areas, and attraction to resources provided by crops and livestock. As such, we quantified for each site the nearest distance to the edge of the park bordered by converted land. This excluded the southern limits of the park, which are bordered by protected forest (Iguazú National Park), and/or by the large Iguaçu River, which is 1-km wide in average, presents many rapids, including also one of the largest waterfalls in the world, the Iguaçu Falls (Fig. 1A). We consider that the Iguaçu River is a natural barrier that effectively reduces the chance of movement of mammals between the park and converted land, decreasing edge effects associated with species invasion, proximity to human-wildlife conflict areas, and attraction to resources provided by crops and livestock.

2.4. Sampling effort and sampling period

Sampling effort slightly varied across sites due to camera trap malfunction and was calculated as the number of sampling days when camera traps were active in each of the nine capture sessions in each site. Similarly, to account for the fact that the sampling was carried out in different months in 2009, 2010 and 2013, we defined a categorical variable, representing the different sampling periods in the different years.

2.5. Data analysis

2.5.1. Occupancy modeling

For each species, we used both single-season (MacKenzie et al., 2002) and multi-season (MacKenzie, Nichols, Hines, Knutson & Franklin, 2003)occupancy models to estimate the effects of spatial covariates on species occupancy and detectability in the INP. These models have two parameters in common: occupancy (ψ), and detectability (p). In contrast to single-season models, occupancy can change between seasons (i.e. between the three years), but not within seasons (i.e. within each year), in multi-season models. Occupancy dynamics is then governed by two additional parameters: probability of colonization of unoccupied sites (γ), and probability of local extinction at occupied sites (Φ).

Given the small size of the sampled area in each site relative to the home range of most large mammals, we interpreted occupancy estimates as the proportion of sites used by the species (MacKenzie et al., 2006), assuming random movement of the target species in and out of sites. Because species are usually more easily detected at sites with higher abundance (MacKenzie, 2005), we interpreted detectability as a proxy of site use intensity, as have been done elsewhere (e.g., Ahumada, Hurtado, & Lizcano, 2013; Cassano, Barlow, & Pardini, 2014). Thus, in both single and multi-season models, the three spatial covariates (hunting, proximity to tourism infrastructure and distance from the edge) were used as site covariates for both occupancy (ψ) and detectability (p). The survey covariates (sampling effort and sampling period) were used as covariates for detectability (p) only. Probability of colonization (γ) and probability of extinction (Φ) were kept constant in multi-season models. We analyzed data from all terrestrial large mammal species that have been recorded in at least 30% of the 37 sites (Table A.1). For all except one of the analyzed species, detectability was close to or higher than 0.15, as recommended (MacKenzie et al., 2002) (Fig. 2).

For each species, we compared a set of candidate models (considering both single − and multi-season models) with different combinations of spatial covariates (maximum of two spatial covariates per parameter) in a two-step approach designed to allow comparing models

with site-covariates in both occupancy (ψ) and detectability (p). In the first step, we compared (1) models that had occupancy constant − $\psi(.)$ − and detectability as a function of spatial covariates, spatial covariates and sampling effort, and survey covariates, with (2) models that had detectability constant − $p(.)$ − or as a function of sampling effort − p (effort) − and occupancy as a function of spatial covariates (Table A.2). In the second step, we compared (1) the selected models from the first step (those with ΔAICc ≤ 2 relative to the first-ranked model) with (2) models that had covariates in both occupancy (ψ) and detectability (p) (Table A.2). These were created by combining into single models the covariates originally present in either occupancy (ψ) or detectability (p) in the models from the first step that were more plausible than the reference model (those with ΔAICc ≤ 2 relative to the $\psi(.)$ $p(.)$ model) (Table A.2). Spatial covariates were standardized by mean and standard deviation when there were convergence problems. Models in all steps were ranked according to the Akaike's Information Criterion corrected for small samples (Burnham & Anderson, 2002). Analyses were run in R (R Core Team, 2013) using the package Unmarked (Fiske & Chandler, 2011).

When multi-season models were among selected models, we compared mean ψ between seasons (years) using the confidence intervals (CI). We considered ψ varied between seasons (years) when (1) CIs of different years did not overlap, or (2) CIs overlapped, but the confidence interval of the difference of mean ψ between years did not include zero (Payton, Greenstone, & Schenker, 2003).

2.5.2. Quantifying PNI area affected by threats

To extrapolate the predicted occupancy and detectability of each species to the entire INP area, we generated 100-m spatial resolution maps of the three spatial covariates. For hunting pressure, we used the georeferenced database containing the illegal activities described above, and assigned the number of illegal activities registered in a 2-km radius buffer around each pixel. As illegal activities have been recorded by the park staff in just a subset of the INP, we highlighted in the maps the area for which we have information on hunting pressure (Fig. 1B-C). For proximity to tourism infrastructure, we calculated whether there was a tourism infrastructure in a 2-km radius buffer around each pixel, resulting in a binary map for the entire park. For the distance from the edge, we generated an Euclidean distance map, with the nearest distance of each pixel to the edge of the park bordered by converted land, again excluding the southern limits of the park, which are bordered by protected forest (Iguazú National Park), and/or by the large Iguaçu River (see Data collection − Spatial covariates).

We then applied the predict function of the package Unmarked to the first-ranked occupancy model for each species to extrapolate occupancy and detectability of each species across the entire park. To generate occupancy and detectability maps considering all native species together, we first normalized the data for each species across the park. For each species, the minimum occupancy (and detectability) values within the park were set to 0 and the maximum occupancy (and detectability) value was set to 1. Then, for each pixel, we summed the normalized occupancy (and detectability) values of all native species and divided by the number of species. This methodological procedure ensures that all species have the same weight, and no single species dominates, the normalized average values.

3. Results

With a total sampling effort of 9 360 traps-night, we recorded 26 terrestrial large mammal species of which 17 were analyzed (Table A.1). Considering estimates from the first-ranked model, mean occupancy ranged from $\psi = 0.20$ (± 0.13) for the giant-anteater (*Myrmecophaga tridactyla)* to $\psi = 0.999$ (± 0.001) for red brocket deer (*Mazama americana*), and mean detectability from $p = 0.05$ (± 0.02) for jaguarundi (*Puma yagouaroundi*) to $p = 0.73$ (± 0.04) for agouti (*Dasyprocta azarae*) (Fig. 2).
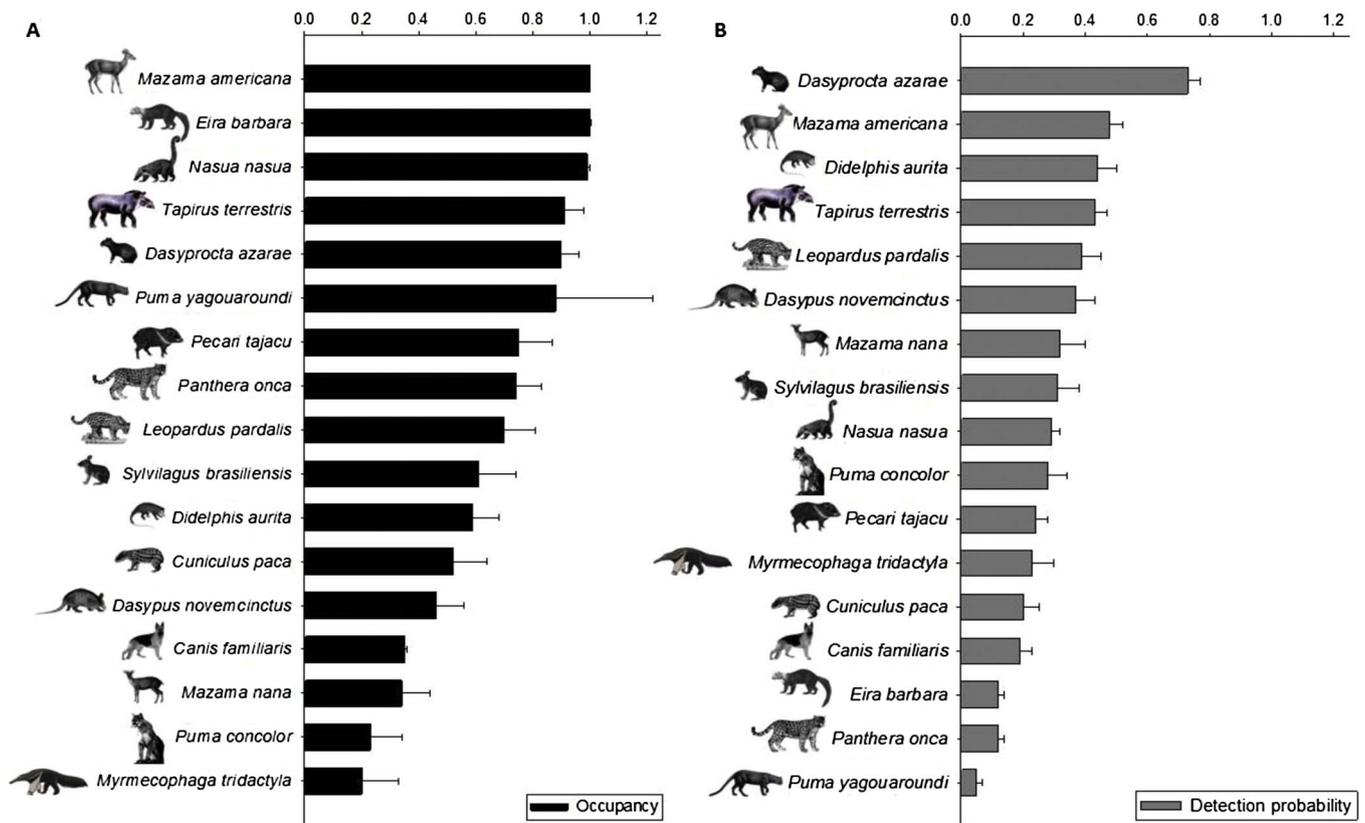
Fig. 2. (A) Mean occupancy and (B) mean detectability for each of the 17 analyzed terrestrial large mammals across the Iguaçu National Park. Lines represent the standard error.

For 10 out of the 17 species, the first-ranked model was a multi-season model (Table 1), indicating that occupancy dynamics is important. However, using the confidence interval, a significant difference in occupancy between years was observed for jaguarundi and puma (*Puma concolor*) only (Fig. 3). For jaguarundi, occupancy in 2010 and 2013 was higher than in 2009 and for puma the occupancy in 2013 was higher than in 2009.

For 11 out of the 17 species, spatial covariates were indeed important to determine their spatial distribution across the park, influencing either occupancy (Fig. A.1) or detectability (Fig. A.2), as neither of the two models without spatial covariates − the reference model ψ(.) p(.) and the model ψ(.)p(effort) − were among the selected models (Table 1).

Detectability may be affected by site covariates that influence camera trap effectiveness (besides those altering species abundance). However, because we kept the area in front of the cameras clear (see Data collection) and vegetation structure did not strongly vary across sampling sites (all located within forests), we assume that the relationship between detectability and the three site covariates is driven mainly by differences in site use intensity. Given that we interpret both occupancy and detectability as related to site use (either use/nonuse, or use intensity, respectively), from now on we describe and interpret the results on the effects of hunting pressure, proximity to tourism infrastructure and distance from the edge considering together their effects on both occupancy and detectability for the sake of simplicity.

For nine of these 11 species with consistent response to spatial covariates, the selected models included distance from the edge of the park as a covariate of either occupancy or detectability (Table 2). Most of these species − tapir (*Tapirus terrestris*), ocelot (*Leopardus pardalis*), jaguar (*Panthera onca*), paca (*Cuniculus paca*) and agouti − responded positively to edge distance, while three − giant-anteater, domestic dog (*Canis familiaris*) and peccary (*Pecari tajacu*) − responded negatively to edge distance. For jaguarundi the effect of distance from the edge of the park was positive on detectability, but negative on occupancy. For nine

species, selected models included proximity to tourism infrastructure as a covariate (Table 2). While jaguar, ocelot, jaguarundi, big-eared opossum (*Didelphis aurita*) and domestic dog responded positively to proximity to tourism infrastructure, tayra (*Eira barbara*), tapir, peccary and giant-anteater responded negatively to this covariate. Finally, for four species the selected models included hunting as a covariate (Table 2). Occupancy or detectability of agouti, paca and giant-anteater decreased, while jaguar occupancy increased, where hunting was more frequent.

Extrapolating these effects for the entire INP area, and averaging normalized occupancy and detectability values among the 16 analyzed native species (i.e. excluding the domestic dog), revealed that no area of the park presented maximum occupancy or detectability values for all the species. Average occupancy varied from 0.77 and 0.91 across the park, and in 50% of the park area species occupancy was on average 13% to 23% lower than maximum values (≪0.87 to 0.77) (Fig. 1B). Average detectability varied from 0.65 to 0.97 across the park, and in 50% of the park area species detectability was on average 19% to 35% lower than maximum values (≪0.81 to 0.65) (Fig. 1C). These results are conservative given that we are not considering the effects of hunting in a considerable part of the park, for which this information in not available. Indeed, considering only the area of the park for which hunting pressure data was available, values of average occupancy and average detectability are lower than for the whole park (full and dashed lines in Fig. 1B–C).

4. Discussion

Our findings confirm that the Iguaçu National Park still harbors a rich terrestrial large mammal fauna, including many keystone species such as large herbivores and top predators. Many of the species with high occupancy within the park are rare or extinct in most Atlantic Forest remnants. Additionally, we did not find evidence of temporal declines in occupancy over the five-year period for any of the terrestrial

Table 1

Selected occupancy models (ΔAICc ≤ 2) for 17 terrestrial large mammals (in alphabetic order) in the Iguaçu National Park. For each model, information on the number of parameters (K), maximum likelihood (LogLik), Akaike Information Criterion corrected for small samples (AICc), difference between the AICc of the model and the first-ranked model (ΔAICc), and estimated coefficients with respective standard error, is provided. H = hunting pressure; T = proximity to tourism infrastructure; E = distance from the edge of the park; Eff = sampling effort; Per = sampling period.

Species	Models	K	LogLik	AICc	ΔAICc	T (ψ)	H(ψ)	T(p)	E(ψ)	H (p)	E (p)	Eff	2009	2010	2013
Canis familiaris	ψ(T + E)p(eff)	5	−54.42	120.78	0.00	22.20 (20.8)			−31.05 (29.3)			0.09 (0.07)			
	ψ(T + E)p(.)	4	−55.96	121.17	0.39	28.50 (34.0)*			−39.20 (47.0)*						
Cuniculus paca	ψ(.)p(H + E)	4	−88.27	185.79	0.00					−0.71 (0.41)	0.54 (0.24)				
	ψ(.)p(E)	3	−90.00	186.72	0.94						0.74 (0.22)				
	ψ(E)p(H + E)	5	−87.43	186.79	1.01				0.60 (0.47)	−0.59 (0.42)	0.48 (0.22)				
Dasyprocta azarae	ψ(H)γ(.)Φ(.)p(E + eff)	7	−175.23	368.31	0.00		−0.35 (0.21)				0.24 (0.01)	0.05 (0.01)			
Dasypus novemcinctus	ψ(.)γ(.)Φ(.)p(T)	5	−136.88	285.69	0.00			−1.29 (0.66)							
	ψ(.)γ(.)Φ(.)p(per)	6	−135.68	286.17	0.48								−0.60 (0.47)	0.53 (0.58)*	−0.81 (0.70)
	ψ(.)γ(.)Φ(.)p(.)	4	−138.49	286.22	0.53										
	ψ(E)γ(.)Φ(.)p(T)	6	−135.75	286.30	0.61			−1.34 (0.65)	−0.65 (0.46)						
	ψ(T)p(per)	5	−137.23	286.40	0.71	−2.13 (1.12)							−1.22 (0.27)	0.65 (0.35)	−0.68 (0.43)
	ψ(.)γ(.)Φ(.)p(T + eff)	6	−136.00	286.79	1.10			−1.43 (0.67)				0.02 (0.02)*			
	ψ(E)γ(.)Φ(.)p(.)	5	−137.55	287.04	1.35				−0.58 (0.46)				−1.20 (0.27)	0.62 (0.35)	−0.71 (0.43)
	ψ(.)p(per)	4	−139.06	287.38	1.69										
	ψ(H)γ(.)Φ(.)p(.)	5	−137.79	287.51	1.82		0.08 (0.07)								
	ψ(.)γ(.)Φ(.)p(T + E)	6	−136.40	287.59	1.90			−1.45 (0.68)			0.30 (0.30)*				
	ψ(.)γ(.)Φ(.)p(eff)	5	−137.87	287.67	1.98							0.02 (0.02)*			
Didelphis aurita	ψ(T)γ(.)Φ(.)p(per)	7	−152.94	323.74	0.00	7.03 (15.87)*							−0.04 (0.30)*	0.85 (0.41)	−1.67 (0.51)*
Eira barbara	ψ(.)p(T + eff)	4	−107.09	223.42	0.00			−1.54 (0.74)				0.07 (0.03)			
Leopardus pardalis	ψ(.)γ(.)Φ(.)p(T + E + eff)	7	−151.95	321.77	0.00			2.03 (0.48)			0.65 (0.16)	0.06 (0.02)			
	ψ(E)γ(.)Φ(.)p(T + E + eff)	8	−150.79	322.74	0.97			2.00 (0.48)	0.84 (0.6)		0.60 (0.16)	0.06 (0.02)			
Mazama americana	ψ(.)p(H + eff)	4	−206.20	421.65	0.00					0.04 (0.02)		0.05 (0.01)			
	ψ(.)p(eff)	3	−208.20	423.12	1.47							0.05 (0.01)			

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Table 1 (*continued*)

Species	Models	K	LogLik	AICc	ΔAICc	T (ψ)	T(p)	H(ψ)	H (p)	E(ψ)	E (p)	Eff	2009	2010	2013
Mazama nana	ψ(.)γ(.)Φ(.)p(eff)	5	−86.66	185.26	0.00							0.06 (0.03)			
	ψ(.)γ(.)Φ(.)p(.)	4	−88.19	185.63	0.37										
	ψ(.)p(T + E + eff)	5	−86.87	185.67	0.41		1.23 (0.54)				−0.55 (0.31)	0.05 (0.03)			
	ψ(.)p(T + eff)	4	−88.27	185.78	0.52		0.92 (0.54)					0.05 (0.03)			
	ψ(.)γ(.)Φ(.)p(T + E)	6	−85.65	186.10	0.84		1.19 (0.67)				−0.76 (0.36)				
	ψ(.)p(eff)	3	−89.70	186.12	0.86							0.06 (0.03)			
	ψ(.)p(T + E)	4	−88.48	186.21	0.95		1.45 (0.53)				−0.56 (0.31)				
	ψ(.)γ(.)Φ(.)p(E)	5	−87.23	186.39	1.13						−0.56 (0.37)				
	ψ(E)p(eff)	4	−88.73	186.70	1.44					−0.57 (0.43)		0.06 (0.03)			
	ψ(.)p(T)	3	−90.09	186.90	1.64		1.19 (0.52)								
	ψ(.)γ(.)Φ(.)p(E + eff)	6	−86.05	186.90	1.64						−0.47 (0.39)	0.05 (0.03)			
Myrmecophaga tridactyla	ψ(H + E)γ(.)Φ(.)p(T)	7	−59.02	135.90	0.00	−8.64 (34.51)*		−3.66 (2.46)		−3.59 (2.67)					
	ψ(H + E)γ(.)Φ(.)p(.)	6	−61.49	137.79	1.89			−3.78 (2.49)		−3.51 (2.50)					
Nasua nasua	ψ(.)p(eff)	3	−186.24	379.21	0.00							0.03 (0.01)			
	ψ(.)p(T + eff)	4	−185.15	379.55	0.34		−0.51 (0.36)					0.04 (0.01)			
	ψ(T)p(eff)	4	−185.41	380.07	0.86	−8.34 (0.01)						0.03 (0.01)			
	ψ(T + E)γ(.)Φ(.)p(eff)	7	−181.50	380.85	1.64	−38.16 (56.8)*				−10.83 (13.7)*		0.04 (0.01)			
	ψ(.)γ(.)Φ(.)p(eff)	5	−184.48	380.89	1.68							0.04 (0.01)			
	ψ(.)p(H + eff)	4	−185.91	381.07	1.86				0.01 (0.02)*			0.03 (0.01)			
Panthera onca	ψ(E)p(.)	3	−93.72	194.17	0.00					4.55 (2.33)					
	ψ(E)p(eff)	4	−93.16	195.58	1.41					4.45 (2.21)		0.02 (0.02)*			
	ψ(T + E)p(.)	4	−93.35	195.96	1.79	4.44 (38.69)*				4.15 (2.22)					
	ψ(H + E)p(.)	4	−93.40	196.05	1.88			0.17 (0.27)*		6.53 (5.03)					
Pecari tajacu	ψ(T + E)p(per)	6	−132.10	278.99	0.00	−2.52 (1.25)				−0.82 (0.55)			−2.39 (0.40)	1.70 (0.46)	1.58 (0.46)
	ψ(.)p(per)	4	−135.43	280.11	1.12								−2.39 (0.40)	1.70 (0.46)	1.58 (0.46)
Puma concolor	ψ(.)γ(.)Φ(.)p(T + eff)	6	−102.10	219.01	0.00		1.05 (0.52)					0.32 (0.15)			
	ψ(.)γ(.)Φ(.)p(eff)	5	−104.20	220.34	1.33							0.36 (0.16)			
Puma yagouaroundi	ψ(.)p(T)	3	−57.58	121.89	0.00		1.38 (0.61)								
	ψ(T + E)γ(.)Φ(.)p(T)	7	−52.62	123.10	1.21	27.34 (40.3)*	1.13 (0.60)			−45.17 (73.2)*					
	ψ(.)p(T + E)	4	−57.12	123.49	1.61		1.38 (0.58)				0.27 (0.27)*				
Sylvilagus brasiliensis	ψ(.)γ(.)Φ(.)p(H)	5	−121.20	254.34	0.00				−0.41 (0.22)						
	ψ(.)γ(.)Φ(.)p(.)	4	−122.95	255.15	0.81										
	ψ(.)γ(.)Φ(.)p(H + eff)	6	−120.51	255.82	1.47				−0.40 (0.23)			0.02 (0.02)*			
	ψ(.)γ(.)Φ(.)p(eff)	5	−121.99	255.91	1.57							0.03 (0.02)			

Coefficients

Table 1 (*continued*)

Species	Models	K	LogLik	AICc	ΔAICc	Coefficients								
						T (ψ)	H(ψ)	H (p)	E(ψ)	E (p)	Eff	2009	2010	2013
Tapirus terrestris	ψ(T)p(E + eff)	5	−184.52	380.97	0.00	−2.35 (1.41)				0.46 (0.13)	0.07 (0.01)			
	ψ(.)p(E + eff)	4	−186.09	381.42	0.46					0.46 (0.13)	0.07 (0.01)			

*Indicates a weak effect (estimate ± 1 SE overlaps 0).

large mammal species in the park. However, our results highlight that the spatial distribution of most terrestrial large mammals have been negatively affected by edge effects, tourism or, at a lesser extent, hunting. Combining these effects across species, we showed that species occupancy and detectability are lower than observed maximum values in a considerable area of the park.

4.1. Effectiveness of the Iguaçu National Park

The INP is among the few Atlantic Forest areas that still harbor a mostly intact and abundant large mammal assemblage. From the 25 recorded native mammals, eight are considered threatened or near threatened according to the National and/or the IUCN red list (Table A.1), and some of those, such as tapir and jaguar, present high occupancy across the park. Previous inventories suggest that few PAs within the Atlantic Forest, all located in Southeastern Brazil, still harbor similarly well-conserved large mammal faunas (Galetti et al., 2009). In contrast, human-modified landscapes outside PAs (e.g., Espartosa, Pinotti, & Pardini, 2011) and even some PAs (e.g., Cassano, Barlow, & Pardini, 2012) in this region present very simplified large mammal faunas, dominated by medium-sized generalist species, and lacking most large-bodied ungulates and felids of conservation concern.

Moreover, the INP still harbors most of the terrestrial large mammals known to occur in the park ~20 years ago, at the time of the first systematic study on mammals (Crawshaw, 1995). Our study actually confirmed the occurrence of the giant-anteater until now recorded only by hair found in two jaguar scats (Cândido-Jr, D'amico, Oliveira, & Quadros, 2003). The only exception is the white-lipped peccary, which once represented 77% of the jaguar diet in the park (Crawshaw, 1995), but has become uncommon (Azevedo & Conforti, 2008), and was not recorded in our study.

Indeed, we found no evidence of temporal decline in the occupancy of mammal species across the park within a five-year period, not even for species of conservation concern as the jaguar whose populations declined drastically in the past in the INP region (Paviolo, de Angelo, Di Blanco, & Di Bitetti, 2008), indicating that the rate of decline of this endangered species may have been reduced in recent years. In contrast, we found that the occupancy of two relatively common species − jaguarondi and puma − recently increased in the park. Nevertheless, given the relatively short time frame of our study compared to the longevity of most large mammals, our inferences on temporal variation are limited. Assessing long term trends in occupancy are of foremost importance for future studies evaluating the effectiveness of PAs for conserving biodiversity.

Despite the short-term temporal stability in occupancy for most species, our spatial analysis do, however, indicate that not all area of the park is effective in maintaining the occurrence and abundance of terrestrial large mammals. Proximity to tourism infrastructure, proximity to the edge of the park and hunting combined reduced on average the occupancy and the detectability of native mammal species in at least 13 and 19% of maximum observed values, respectively, across half of the INP area. The magnitude of these impacts may be much higher, as our estimates do not take into account hunting within a large area of the park, or the milder edge effects from the converted land along the southern border, which is separated from the park by the large Iguaçu River. In addition to a reduction in the current effective area of the park, these cryptic threats may lead to population declines over time, if not properly addressed and managed.

4.2. Threats to the fauna of the park

Several terrestrial large mammals were negatively affected by edge effects from adjacent human-modified landscapes (i.e. had occupancy or detectability positively associated with the distance to the edge of the park bordered by converted land), including both frugivores (tapir, paca and agouti) and carnivores (ocelot and jaguar). For large-bodied
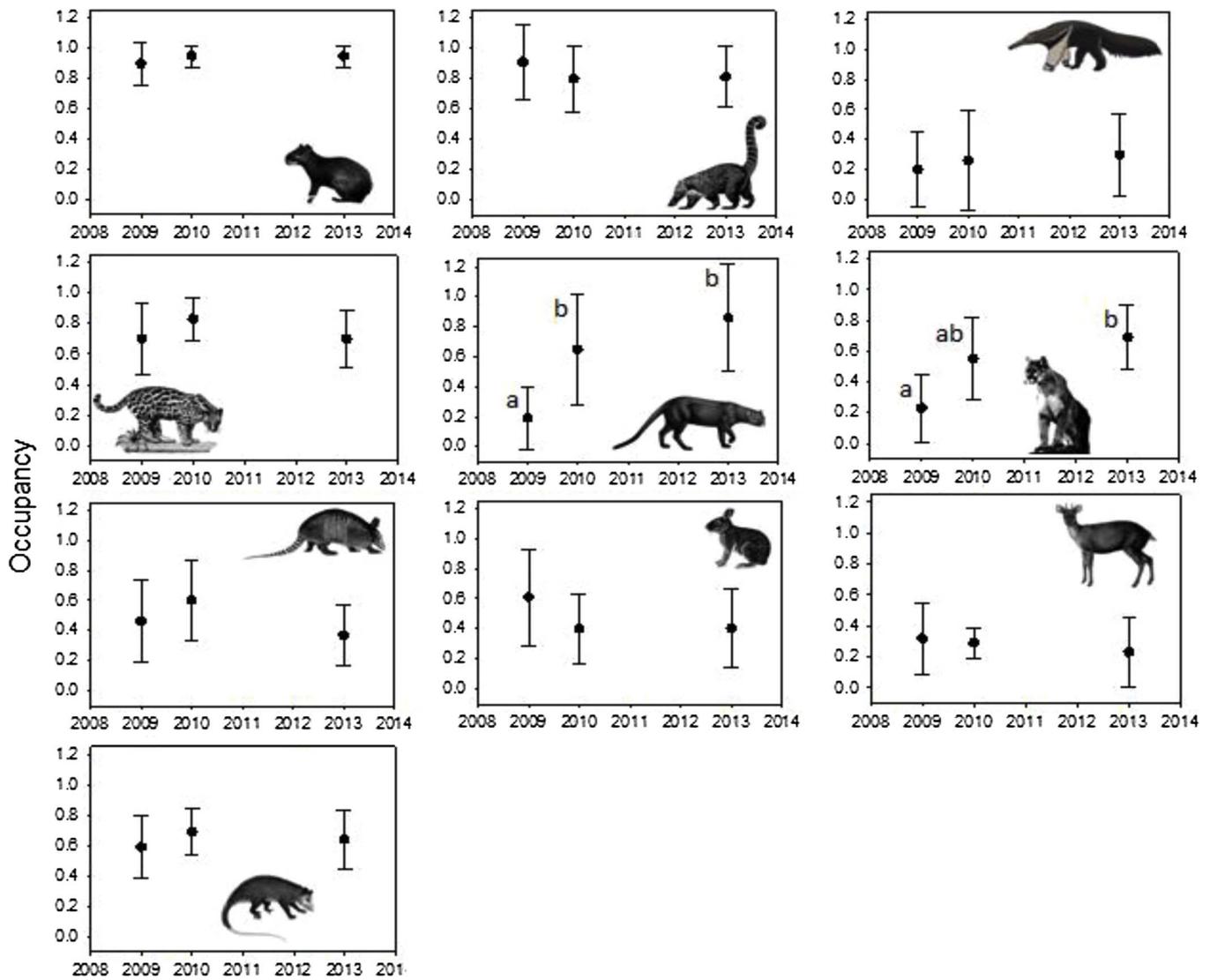
Fig. 3. Mean occupancy (and confidence interval) per year for each of the 10 terrestrial large mammals in the Iguaçu National Park for which the first-ranked model was a multi-season model (Table 1). Distinct letters indicates mean occupancy differed between years.

Table 2

Spatial covariates included in the selected occupancy models of 11 terrestrial large mammals in the Iguaçu National Park. + covariate with positive effect in all selected models, − covariate with negative effect in all selected models. Dark grey to white: covariate present in all, some or none of the selected models. Complete results of model selection in Table 1. Species are ordered in terms of their response to the distance from the edge of the park (positive, negative, and no response).

	Distance from the edge		Proximity to tourism		Hunting pressure	
	Ψ	*p*	Ψ	*P*	Ψ	*p*
Dasyprocta azarae		+			−	
Cuniculus paca	+	+				−
Tapirus terrestris		+	−			
Leopardus pardalis	+	+		+		
Panthera onca	+		+		+	
Pecari tajacu	−		−			
Myrmecophaga tridactyla	−			−	−	
Canis familiaris	−		+			
Puma yagouaroundi	−	+	+	+		
Didelphis aurita			+			
Eira barbara				−		

mammals that range widely and therefore come into frequent contact with reserve limits and beyond, the adjacent altered areas can act as population sinks (Schuette, Wagner, Wagner, & Creel, 2013), mainly by overexposing animals to human-induced mortality, such as road kills, hunting and persecution (Woodroffe & Ginsberg, 1998). Human-wildlife conflicts in particular are fast becoming one of the most urgent threats to large predator survival worldwide (Treves & Karanth, 2003) as well as in the INP region (Xavier da Silva, Brocardo, Rodrigues, & Vogliotti, 2013). In addition, disturbances and habitat loss in human-modified landscapes surrounding PAs may also favor biological invasions (Laurance et al., 2002). The domestic dog distribution across the INP is associated with the edge of the park, the opposite pattern displayed by several frugivores and carnivores of conservation concern, being an example of an edge-induced invasion. Recently the ubiquity and negative consequences of domestic dog invasion in Brazilian PAs have been highlighted (Lessa, Guimarães, Bergallo, Cunha, & Vieira, 2016), and domestic dog presence and abundance have been shown to be the main driver of declines in native mammal populations in Atlantic Forest remnants outside PAs (Cassano et al., 2014).

However, two native species − the giant anteater and the collared peccary − were more common near the edge of the INP (i.e. had occupancy or detectability negatively associated with the distance to the edge of the park bordered by converted land). The giant-anteater has a broad distribution across Central and South America being more abundant in open, savanna-like biomes (Kreutz, Fischer, & Linsenmair, 2012) and in areas where jaguars − its main predator − are absent (Quiroga, Noss, Boaglio, & Di Bitetti, 2016). The observed association with the edge of the park may thus be related either to edge-induced changes in vegetation towards more open forests, or to predator avoidance (as the jaguar showed opposite responses to all studied spatial variables compared to the giant-anteater). Similarly, the positive response of the collared peccary to the edge may be related to the importance of crop plantations outside the park as food sources (Pérez & Pacheco, 2006), or to the avoidance of jaguars.

Tourism at the INP although spatially restricted is intense. Many tourism activities within the park require frequent traffic of jeeps, boat trailers, employees and tourists, which may affect large mammals that have been shown to avoid the proximity to humans (Leblond et al., 2013). A negative impact of tourism on diurnal vertebrates was also observed in other Atlantic Forest national parks (Cunha, 2010). At the INP, the species negatively affected by the proximity to tourism infrastructure are either commonly hunted (peccary and tapir), are known to be very secretive as the giant anteater (Reyes, Matamoros, & Glowinski, 2010), or are not strictly nocturnal as the tayra that is active throughout the day. In contrast, the native species positively affected by the proximity to tourism infrastructure within the park are mainly felids, which are nocturnal and known to use trails and roads for moving through the forest (Harmsen, Foster, Silver, Ostro, & Doncaster, 2010). As touristic trails and roads are the only ones available at the INP, and given that their nocturnal habits make possible for felids to explore these areas during periods with no human activity, their natural preference for trails is probably the reason for the positive association of these species with tourism infrastructure.

Paca and agouti are among the most frequently hunted species within the INP (Ivan Baptiston, personal communication) and elsewhere in the Neotropics (Jerozolimski & Peres, 2003), and our results suggest they are negatively affected by hunting in the park. Although they present high fecundity, these two medium-sized frugivore rodents that are important seed dispersers are indeed disappearing from many Atlantic Forest remnants outside PAs (e.g., Espartosa et al., 2011), with possible dramatic consequences for forest regeneration (Jorge & Howe, 2009). It is important to highlight though that measuring hunting pressure accurately is notoriously difficult. Although our index of hunting pressure was based on a rare and large database on the records of illegal hunting accumulated over the years by park rangers, it may not represent hunting pressure perfectly for all species (hunted for

different reasons and with different techniques). Hence, it is possible that the effects of hunting are underestimated here compared to the effects of the proximity to tourism infrastructure or distance to the edge, both of which are easier to measure accurately.

4.3. Conclusions and conservation implications

Any extrapolation exercise has limitations associated with focusing on only some factors (those considered to be the most important), difficulties in accurately mapping all and each of the factors (e.g. hunting pressure, or edge effects when edges are not homogeneously similar), among others. However, in contrast to most estimates of the effectiveness of PAs based on gross metrics of deforestation from satellite images (Naughton-Treves, Holland, & Brandon, 2005), our estimates of INP's effectiveness is based on an extensive empirical dataset collected across 300 km^2, encompassing ample variation in the factors considered to be important to terrestrial large mammals. Moreover, our results on the proportion of the park where negative cryptic effects on terrestrial large mammals are detected are certainly conservative. Not only were the effects of hunting not considered in a portion of the park, but also we opted not to consider the effects of the edge of the park bordered by the Iguaçu River, as our experience suggests this large river significantly reduces mammal movements between the park and converted land.

Hence, our findings suggest that, despite the integrity of forests within the INP, cryptic threats, such as hunting, biological invasion, and other edge- and tourism-associated threats, do affect the fauna inside the park, considerably reducing the effective area for maintaining the occurrence and abundance of large mammals. Although we found no evidence of temporal declines in occupancy during the short time frame of our study, these cryptic threats that today are responsible for the spatial declines in occupancy and detectability across the park may lead to temporal declines in occupancy in the long run, if not properly addressed and managed.

If this is the case for one of the most extensive PAs that is adjacent to other parks as the INP, the consequences of such cryptic threats should be even stronger in smaller or more isolated PAs, which are the majority within the Atlantic Forest. In such a spatial context where PAs are forest islands in human-modified landscapes, common measures of PAs effectiveness such as rate of deforestation (Nolte et al., 2013) are not useful and can even lead to biased conclusions. Direct information on biological assemblages and populations is needed and should be incorporated into monitoring programs within management plans for PAs, and used to complement more regional or global analysis of PA effectiveness (e.g., Beaudrot et al., 2016).

This is not to say, however, that the INP or other Atlantic Forest PAs are not valuable for biodiversity conservation. On the contrary, our results corroborate the idea that they are the only places where a rich large mammal fauna can still be found in the Atlantic Forest (Galetti et al., 2009). The regional importance of these few PAs that still harbor well-conserved faunas is in fact the reason for prioritizing management actions for monitoring, controlling and minimizing these cryptic threats that we have shown to influence their effectiveness.

Our findings suggest that most cryptic threats come from outside as either species invasion, such as that by the domestic dog, or road kills, hunting and persecution that make several native species less common near the edges of the park with human-modified landscapes. These findings highlight the urgent need to legally re-establish and enforce the adequate management of buffer zones around PAs. In the INP region, for instance, one more hydroelectric power plant on the Iguaçu River was installed less than 500 m from the edge of the INP.

The intense tourism in the INP also negatively impacted some large mammals, representing a clear alert message on the danger of uncontrolled tourism and of encouraging the unlimited growth of tourism in PAs. Recently, the reopening of the road "Estrada do Colono" that cuts 18 km of forest within the INP is under legal consideration as a

road park for tourism (although several other political and economic interests are involved), greatly expanding the area of the park that would be under the impacts of tourism infrastructure. To ensure bio-diversity conservation as well as recreation and education provided by tourism, it is necessary to constantly review tourism rate targets, and keep the tourism attractions and infrastructure in localized areas of PAs.

Although the effects of hunting within the park were only evident for two game species, it is alarming that it has affected two rodent species with high fecundity. It is important to keep in mind that measuring hunting pressure is difficult and may lead to underestimate hunting effects, and that part of the widespread edge-induced impacts at INP is in fact related to hunting and persecution at and beyond park boundaries, which in the past have led to severe depletion of the jaguar population. To reduce this kind of impact it is necessary to combat illegal activities inside parks and surroundings (Geldmann et al., 2013) by supporting park rangers, mitigating human-wildlife conflict, and enforcing buffer zones systems taking into account the livelihoods of the local communities (Xavier da Silva et al., 2013)

As a result of some of these threats to the Iguaçu National Park such as the installation of a hydroelectric dam and the intended reopening of the Estrada do Colono, the United Nations Educational, Scientific and Cultural Organization (UNESCO) gave an ultimatum to the Brazilian government threatening to withdraw the title of Human Natural Heritage to the park (Carazzai, 2014). After decades of expansion of its PA system, Brazil is now risking its natural capital and biodiversity by creating legal mechanisms to allow development projects inside and around PAs (Ferreira et al., 2014). Our results indicates that even large PAs are affected by cryptic threats, suggesting that expanding human activities near and inside PAs may, in the long term, disintegrate the effectiveness of the largest PA system in the world.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2017.11.001.

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