

Marina Xavier da Silva

Efetividade de áreas protegidas para a
conservação da biodiversidade: padrões de
ocupação de mamíferos no Parque Nacional do
Iguaçu

Effectiveness of protected areas for
biodiversity conservation: mammal occupancy
patterns in the Iguaçu National Park

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Epígrafe

Sobre urubus e formigas

Sem florestas, tamanduás raleiam.
Sem tamanduás, formigas proliferam.

Sem caçadores, a fauna prolifera.
Sem justa punição, marginais proliferam.

Com marginais, nós, animais, acepilhamos.
Sem Educação, integridade acepilha.

Sem punição, honestidade raleia.
Sem honestidade, Sociedade se acepilha.

Com Sociedade organizada, Educação prolifera.
Com leis íntegras, cumpridas, Sociedade prolifera.

Nem muita enchente, nem seca, pouco é o cuidado com nossas águas.
Não que não tenha leis, falta cumprimento.
Não que não se tenha integridade, falta acreditação.
Não que não se tenha honestidade, falta humanos direitos.
Não que não tenha coragem, falta arrimo.

Urubu é pouco, muito é o lixo.
Fiscalização não é pouca, muito é o marginal.
Animais não é muito, floresta que é pouca.
Educação é pouca porque a Sociedade se está esgarçada.
Dedicação é muita. Mas, sobra impunidade.

Não que falte polícia, sobra bandido.
Não que falte tamanduás, sobram formigas.

Carlos AF De Giovanni
Colega e chefe da Rebio Perobas – PR

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Índice

Introdução geral	01
Resumo	03
Abstract	04
Introduction	07
Methods	09
Study area	09
Sampling design	10
Data Collection	11
Mammal sampling	11
Spatial covariates	11
Sampling effort and year	12
Data analysis	12
Occupancy modeling	12
Model fitting and selection	13
Results	18
Discussion	28
Terrestrial large mammal fauna of Iguaçu National Park	28
Distance from the edge of the park	29
Proximity to tourism attraction/ infrastructure	31
Hunting pressure	31
Temporal variation in occupancy	32
Conclusions and conservation Implication	32
Acknowledgements	34
References	35
Appendices	43
Conclusão geral	47

Introdução geral

Áreas protegidas (APs) são consensualmente reconhecidas como primordiais para a conservação da biodiversidade (Bruner et al. 2001; Chape et al. 2005; DeFries et al. 2005), tendo sido incorporadas em inúmeras conferências internacionais sobre meio ambiente e ampliadas ao redor do mundo (Chape et al. 2005; UNEP-WCMC 2008). Dada sua importância global, garantir a efetividade destas áreas é de suma importância. Diversos trabalhos buscaram avaliar o sistema de áreas protegidas globalmente, com alguns deles, focados especificamente na efetividade das APs para a conservação da biodiversidade (Bruner et al. 2001; Laurance et al. 2012; Joppa et al. 2008; Naughton-Treves et al. 2005). Apesar de globais, a maioria dos trabalhos de efetividade baseiam-se em medidas indiretas, como taxas de desmatamentos e incêndios (Bruner et al. 2001; Joppa et al. 2008). No entanto, mesmo que as florestas sejam mantidas dentro das áreas protegidas, muitas ameaças podem estar afetando a biodiversidade, como caça, invasão de espécies e doenças (Joppa et al. 2008).

O Brasil é um dos países com maior biodiversidade do planeta, possui o maior sistema de áreas protegidas no mundo, que representa cerca de 12% do total (WDPA 2012), mas muito pouco se sabe sobre a efetividade de suas APs para a conservação da biodiversidade. O Parque Nacional do Iguaçu (PNI), é uma das APs mais importantes da Mata Atlântica, tanto pelo seu tamanho, sua conexão com outros fragmentos florestais expressivos na Argentina (aproximadamente 1 milhão de ha) (Di Bitetti et al. 2006), como pelo número de visitantes (1.5 milhões de visitantes/ano), arrecadação e geração de renda, sendo reconhecido como um dos parques mais bem geridos do país. Como os demais remanescentes de Mata Atlântica, entretanto, o PNI se insere em paisagens altamente alteradas por atividades humanas, o que deve aumentar as ameaças sobre as comunidades biológicas que abriga.

Considerando a importância do PNI em termos de extensão, geração de renda e gestão, essa dissertação teve por objetivo avaliar a efetividade desta área protegida na conservação da biodiversidade, através da análise do padrão de ocupação de mamíferos terrestres de maior porte. Para tanto, uma área de 300 km² com 37 sítios amostrais contendo armadilhas fotográficas foi monitorada durante cinco anos (2009 - 2013) para verificar se caça, proximidade a atrativos turísticos e a distância da borda do parque afetam o padrão de ocupação e detecção dos mamíferos. Espera-se que o

padrão de ocupação não seja afetado pelos fatores de ameaça estabelecidos se o PNI estiver sendo efetivo na conservação da biodiversidade.

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Resumo

Áreas protegidas são consensualmente reconhecidas como a principal estratégia para a conservação da biodiversidade. Avaliar a efetividade destas áreas, especialmente em biomas como a Mata Atlântica onde as áreas protegidas são como ilhas de floresta em paisagens altamente alteradas pelo homem, é de suma importância. O Parque Nacional do Iguaçu (PNI) abriga um dos maiores remanescentes de Mata Atlântica do Brasil, possui alta visitação turística, assenta-se sobre solos férteis, sofrendo muitas pressões advindas das paisagens antropizadas adjacentes, e é considerado um dos parques mais bem geridos no país. Este trabalho buscou avaliar a efetividade desta área protegida através da análise do padrão de ocupação de 17 espécies de mamíferos terrestres de maior porte em relação à proximidade a atrativos turísticos, distância da borda do parque e pressão de caça. Informações sobre ocupação foram obtidas entre 2009 e 2013 através de armadilhas fotográficas distribuídas sistematicamente em 37 sítios amostrais em cerca de 300 km², um sexto da área do parque. Muitas espécies raras ou localmente extintas em outros remanescentes de Mata Atlântica apresentaram altas taxas de ocupação no PNI, que juntamente com poucas áreas protegidas do sudeste do Brasil representam as únicas áreas do bioma que ainda abrigam uma fauna de grandes mamíferos intacta. No entanto, a distribuição de 11 das 17 espécies analisadas não foi homogênea, tendo sido afetada por pelo menos um dos fatores de ameaça estudados, principalmente a distância da borda do parque e proximidade a atrativos turísticos. O efeito negativo destas ameaças deve ser ainda mais forte em áreas protegidas menores e mais isoladas, que representam a maioria em biomas muito alterados como a Mata Atlântica. Medidas como o restabelecimento e manejo de zonas tampão, a manutenção de atrativos turísticos em áreas restritas, o combate efetivo das atividades ilícitas e a redução de conflitos entre animais silvestres e o homem, são fundamentais para a efetividade de áreas protegidas para conservação da biodiversidade no longo prazo.

Abstract

Protected areas are widely recognized as the main strategy for biodiversity conservation. Evaluating the effectiveness of these areas, especially in biomes such as the Atlantic Forest where protected areas are forest islands immersed in highly altered landscapes, is of paramount importance. The Iguazu National Park (INP) harbors one of the largest Atlantic Forest remnants in Brazil, receives vast number of tourists, is located on productive soils, suffering many threats from the adjacent human-modified landscapes, and is considered one of the best managed parks in the country. This study aimed at evaluating the effectiveness of this protected area through the analysis of the occupancy patterns of 17 terrestrial large mammals relative to the proximity to tourism attractions, distance from the edge of the park and hunting pressure. Occupancy information was obtained from 2009 to 2013 with camera traps distributed systematically across 37 sites covering around 300 km², one-sixth of the park. Many species that are rare or locally extinct in other Atlantic Forest remnants presented high occupancy within the INP, which together with few protected areas from southeastern Brazil represent the only areas of this biome that still harbor an intact large mammal fauna. The distribution of 11 of the 17 analyzed species was not homogeneous across the park, however, being affected by at least one of the studied threat factors, mainly the distance from the edge of the park and proximity to tourism attractions. The negative effects of these threats should be even stronger on smaller and more isolated protected areas, which are the majority in highly altered biomes such as the Atlantic Forest. Measures such as the re-establish and management of buffer zones, the maintenance of tourism in restricted areas, the effective combat of illicit activities and the reduction of human-wildlife conflicts are essential to the effectiveness of protected areas for biodiversity conservation in the long run.

Effectiveness of Protected Areas for biodiversity
conservation: mammal occupancy patterns in the Iguazu
National Park

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Abstract

Protected areas are widely recognized as the main strategy for biodiversity conservation, with the global system covering today ~12% of the Earth's surface. Despite the importance of evaluating the effectiveness of these areas, most studies albeit focusing on global or regional scales did not include information on biodiversity. This detailed information is particularly urgent in countries as Brazil that harbors the largest protected area system worldwide, and in biomes such as the Atlantic Forest where protected areas are forest islands within human-modified landscapes. We here focus on the Iguaçu National Park – one of the most important Atlantic Forest protected areas - and on terrestrial large mammals as a case study to evaluate the effectiveness of protected areas in conserving biodiversity. We monitored 300 km² with 37 camera traps during five years to assess if hunting, proximity to tourism attractions and distance from the edge of the park affect species distribution. While many species that are rare or locally extinct in most Atlantic Forest remnants presented high occupancy, the distribution of 11 species across the park was affected mainly by distance from the edge and proximity to tourism attractions. These negative effects are expected to be even stronger on smaller/ more isolated protected areas, which are the majority in highly altered biomes such as the Atlantic Forest. Re-establishing and properly managing buffer zones, restricting tourism to localized areas, combating illicit activities and reducing human-wildlife conflicts are essential to ensure the effectiveness of protected areas for biodiversity conservation in the long run.

Key-words: Atlantic Forest, conservation units, edge effect, hunting, mammals, tourism

Introduction

Protected Areas (PAs), defined as areas recognized, dedicated and managed to achieve the long-term conservation of nature with associated ecosystem services and cultural values (UNEP-WCMC 2008), have long been recognized as essential for biodiversity conservation (Bruner et al. 2001; Chape et al. 2005; DeFries et al. 2005). Despite some recent dispute on the goals of conservation biology between the more traditional view that advocates that nature should be protected for its own sake (Cafaro and Primack 2014; Soule 2013; Soule 1985) and the view that focus also on human well-being (Marvier 2014), the PA strategy continues to be consensually seen as a cornerstone of conservation (Kareiva and Marvier 2012). In the last decades, the inclusion of PA issues on the agenda of environmental international conferences (i.e. Earth Summit, Convention on Biological Diversity – CBD, Millennium Development Goal) has stimulated the creation of many PAs around the world, with the global system currently covering ~12% of the Earth's surface (Chape et al. 2005; UNEP-WCMC 2008). Indeed, the increase of PA coverage was the main response to the 2010 biodiversity target (Butchart et al. 2010).

Determining the effectiveness of PAs in representing and maintaining biodiversity is thus of foremost importance (Chape et al. 2005; Gaston et al. 2006; Geldmann et al. 2013; Rodrigues et al. 2004). A substantial effort have been made to evaluate PA effectiveness using approaches ranging from how much area is protected (Jenkins and Joppa 2009; Schmitt et al. 2009) to how well regional and/or global PA systems perform in representing biodiversity (Leroux et al. 2010; McDonald and Boucher 2011; Rodrigues et al. 2004). Despite the increased coverage of the global PA system and the identification of conservation gaps and biases, however, most protected areas are still 'paper parks', with no effective management and unlikely to deliver effective conservation (Geldmann et al. 2013; Terborgh and Schaik 2002).

Several studies addressed this specific issue of how effective PAs are in maintaining biodiversity by comparing deforestation, fires, roads and other impacts inside and outside PAs using remote-sensing technologies (Joppa et al. 2008; Naughton-Treves et al. 2005) and/or questionnaires (Bruner et al. 2001; Laurance et al. 2012) that rarely included information on biodiversity (Geldmann et al. 2013; Laurance et al. 2012). Although all of these studies suggest that PAs reduce many of the studied impacts, they have been criticized for the insufficient quality and length of time of the available satellite images (Naughton-Treves et al. 2005) and for the

substantive and genuine knowledge of questionnaire respondents who might also be interested in reporting PA success (Bhagwat et al. 2001; Vanclay 2001). Moreover, results may be biased since PAs are commonly located in the most pristine and least accessible sites or may be the focus of cultural processes that discourage disturbance (Vanclay 2001). Most importantly, although allowing for regional or global analysis of the effectiveness of PAs, most studies do not focus directly on biodiversity measures (Brooks et al. 2009), and should be complemented by more local yet more precise evaluations based on species distributions, population sizes and community structure.

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, representing ~12,4% of the global system (WDPA 2012). Few studies, however, evaluated the effectiveness of Brazilian PAs. Most of those focused on the rates of deforestation inside and outside PAs (in the Amazon - Nolte et al. (2013) and in the Cerrado - Carranza et al. (2013). Moreover, PA downgrading, downsizing and degazettement, which have become increasingly common in many countries and are currently global phenomena (Mascia and Pailler 2011), have affected the Brazilian PA system given the pressures from agribusiness, and for generating electricity (Bernard et al. 2014). This scenario is particularly problematic in the Atlantic Forest, the second largest rainforest in South America with one of the highest species richness and rates of endemism on the planet (Metzger 2009), but which harbors 70% of the Brazilian population, is reduced to less than 16% of its original extent, and has only 1,62% of its area in PAs (Ribeiro et al. 2009). Evaluating and ensuring the effectiveness of Atlantic Forest PAs is thus even more urgent and challenging given that PAs act as forest islands in highly modified landscapes and are thus subjected to cryptic yet strong threats such as hunting and invasive species, whose impacts cannot be measured through deforestation only.

Large mammals are good indicators for detecting the effects of some of these cryptic threats. They are not only among the preferred game species (Jerozolinski and Peres 2003), but also among the most affected by hunting given the low abundance and fecundity (Bodmer 1995). Apex predators are also vulnerable given the large home range requirements, low population densities, slow growth rates and persecution due to human-wildlife conflict (Woodroffe and Ginsberg 1998). Large mammals thus commonly alter their behavior, avoiding human proximity as tourist trails and roads

(Leblond et al. 2013; Rogala et al. 2011). As a result, few areas in the world harbor intact large mammal faunas (Morrison et al. 2007). However, many characteristics that make large mammals good indicators of human impacts were also commonly reported as obstacles for studying these species, especially in tropical forests. Nowadays the use of camera traps (Ahumada et al. 2013) and the development of occupancy models (MacKenzie et al. 2006) make feasible the analysis of large mammal distribution across relatively large areas.

One of the Atlantic Forest regions that has historically been important for studies on mammals is the *Green Corridor* formed by the Iguazu National Park (INP) in Brazil and PAs in Argentina (Crawshaw 1995; Di Bitetti et al. 2010; Di Bitetti et al. 2008; Paviolo et al. 2008; Paviolo et al. 2009b). The INP is one of the most important PA in the Atlantic Forest being the only one harboring forest 12 km from any edge (Ribeiro et al. 2009). Together with adjacent PAs and other forest remnants of the *Green Corridor* it protects approximately 1 million ha and many endangered species (Di Bitetti et al. 2006). It is also the second most visited National Park in Brazil, receiving more than 1,5 million people and generating an income of US\$ 7 million in 2012, resources that are injected into the Brazilian PA system to be shared among other PAs. If the total economic impact of PNI in the region is taken into account, the park generates in a very conservative perspective around US\$ 90 million per year.

Given its importance in terms of extension, example of resource generation and management, and threats to biodiversity, we here focus on the Iguazu National Park and on occupancy patterns of terrestrial large mammals as a case study to evaluate the effectiveness of protected areas in conserving biodiversity. We monitored an area of 300 km² with 37 camera traps stations during five years (2009 – 2013) to access if illegal hunting, proximity to tourism attractions/ infrastructure and distance from the edge of the park affect occupancy and detection probability of mammals. We expect that these spatial covariates should not influence species occupancy patterns if the INP has been effective in conserving biodiversity.

Methods

Study area

The Iguazu National Park (INP) lies on the western limit of Paraná state, southwest of Brazil (25°05'S - 25°41'S, 53°40'W-54°38'W) close to the international

border with Argentina and Paraguay. The study area is characterized by Köppen as humid subtropical climate (Cfa) with mean annual precipitation of 1712 mm and mean annual temperature of 20.7 C (Maack 2012). The INP covers 1852 km² and is adjacent to the Iguazú National Park in Argentina with its 677 km² (Fig. 1). 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. 2003) and one of the most spectacular natural sights in the South America: the Iguazu falls. Because of these characteristics, both parks were declared World Heritage Areas by UNESCO (BRASIL 2000). The INP is covered mostly by semi-deciduous Atlantic Forest and, to a lesser extent also by the highly threatened Araucaria Forest in its northern part.

The INP is surrounded by 14 municipalities with human population estimated in more than 446,000 (IBGE 2014). The occupation of the region started in the fifties through federal incentives, which stimulated migration especially from *gauchos* from south Brazil, leading to rapid forest conversion and culminating with the transformation of the region in one of the most important Brazilian soybean production areas. Nowadays large crop farms and smaller cattle farms dominate the landscapes beyond the INP, with few remaining forest patches. Deforestation coupled with the heavy use of fertilizers and agrochemicals have increased erosion and decreased water quality and soil production (BRASIL 2000). More recently the changes in environmental laws have also affected the INP region as other Protected Areas in Brazil.

Sampling design

We accessed the occupancy patterns of terrestrial large mammals using a regular grid established on the west part of the INP. In total, we established 37 sites 4 km apart from each other, covering around 300 km² (one-sixth of the INP's area). Grid location was selected to encompass a large variation in spatial factors expected to impact mammals (i.e. illegal hunting, proximity to tourism infrastructure and distance from the edge of the park) Thus all main tourism attractions and associated infrastructure are enclosed in the grid, which also covers the narrowest area of the park (i.e. closer to the edge and with greater accessibility for people, including those carrying out illegal activities as poaching and palm tree extraction) (Fig. 1).

Data collection

Mammal sampling

In each of 37 sites we installed two camera-traps fixed 40 cm above ground level, settled to work for 24 hours with 5 min interval between photos. We monitored all the sites simultaneously during three periods of three months each (in 2009, 2010 and 2013). We visited the sites every 20 days to exchange films, batteries, silicon and keep the area in front of the camera clean. Monitoring periods of one month were considered distinct capture surveys. Capture history matrices of nine capture surveys (three from each year) in each of the 37 sites were created for each species.

Spatial covariates

We focused on three spatial covariates that represent common threat factors in national parks. These covariates were quantified for each of the 37 sites and used as site-covariates in the occupancy models. All the spatial covariates were calculated using the tools of the software Arc Map (ESRI®ArcMap™10.1).

Hunting pressure - Hunting was calculated from a georeferenced database created by the INP sector that coordinates park rangers (Setor de Proteção), containing all the illegal activities encountered in the park from 2009 on. We calculated the number of records of hunting and associated activities (i.e. hunting platforms, hunting trails, traps, hunting camps, palm tree extraction) found in a 2-km radius (i.e. half the distance between sites) area around each of the 37 sites (Fig. 2A).

Proximity to tourism attractions/ infrastructure - The INP is the second most visited park in Brazil receiving more than 1 million tourists per year. As tourism attractions and associated infrastructure although numerous are spatially localized (Fig. 1), we chose to use a categorical variable that represents the presence/ absence of *tourism attractions/ infrastructure* in the proximities (i.e. within the 2-km radius area) of each site (Fig. 2B).

Distance from the edge of the park - To quantify the edge effects from adjacent human-modified landscapes, we quantified for each site the nearest distance to the northern limit of the park, since the remaining limits are bordered by protected forest and/or the Iguaçu River (Fig. 2C).

Sampling effort and year

Besides spatial covariates used as site covariates, two survey covariates were used in occupancy models. Sampling effort varied across sites and surveys 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 surveys for each site. Year is a categorical variable, representing the years of 2009, 2010 and 2013.

Data analysis

Occupancy modeling

We used both single-season (MacKenzie et al. 2002) and multi-season (MacKenzie et al. 2003) occupancy models to estimate the effects of spatial covariates on occupancy and detection probability of mammal species in the INP. Results from fitting different occupancy models to the same data are comparable, including model selection metrics such as AIC (MacKenzie et al. 2006). The use of both types of models allows comparing the fit between models that differ in assumptions, especially the closure assumption; sites are assumed to be “closed” to changes in occupancy during the survey period (all capture surveys) in single-season models. Although the occupancy estimator in single-season models may be relatively robust to violation of the closure assumption if interpreted as the proportion of sites “used” by the species (MacKenzie et al. 2005), we chose to use also the multi-season models to be able to evaluate the importance of occupancy dynamics over the time frame of the study.

The two model approaches have two common parameters: occupancy probability (ψ), the probability that a species is present at a site, and detection probability (p), the probability that a species will be detected at a site where it is present. In contrast to single-season models, site occupancy can change between seasons (primary periods, in this study between the three years), but not within seasons (secondary periods, in this study within each year), in multi-season models. Occupancy dynamics then is governed by two additional parameters: the probability of colonization of unoccupied sites (γ), and the probability of local extinction at occupied sites (Φ) (MacKenzie et al. 2003). 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. The parameter p is interpreted as a proxy of site use intensity.

Model fitting and selection

For both single- and multi-season models, the three spatial covariates (hunting, proximity to tourism attractions/ infrastructure and distance from the edge of the park) were used as site covariates of both occupancy (ψ) and detection probability (p), while sampling effort and year were used as survey covariates of detection probability (p) only. Probability of colonization (γ) and probability of extinction (Φ) were thus 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 1).

For each species and type of model (single- and multi-season), we compared a set of candidate models with different combinations of spatial covariates (maximum of two spatial covariates per parameter) in a two-step approach modified from Bailey et al. (2004). In the first step, we first held occupancy constant, $\psi(.)$, and allowed detection probability to vary with spatial covariates, $\psi(.) p(\text{spatial cov})$ (six models), with spatial covariates and sampling effort, $\psi(.) p(\text{spatial cov}+\text{effort})$ (six models), and with survey covariates, $\psi(.) p(\text{survey cov})$ (two models). Next, we held detection probability constant, $p(.)$, and allowed occupancy to vary with spatial covariates, $\psi(\text{spatial cov}) p(.)$ (six models). We also included six additional models with occupancy varying with spatial covariates and detection probability with sampling effort, $\psi(\text{spatial cov}) p(\text{effort})$ (six models) and a constant model, $\psi(.) p(.)$, for reference (Table 2).

In the second step we selected the first-ranked model among both the $\psi(\text{spatial cov}) p(.) / \psi(\text{spatial cov}) p(\text{effort})$ models and the $\psi(.) p(\text{spatial cov}) / \psi(.) p(\text{spatial cov}+\text{effort}) / \psi(.) p(\text{survey cov})$ models, which were more plausible than the constant model (those with $\Delta\text{AICc} \leq 2$ relative to the $\psi(.) p(.)$ model), and combined then into $\psi(\text{spatial cov}) p(\text{spatial cov})$, $\psi(\text{spatial cov}) p(\text{spatial cov}+\text{effort})$ or $\psi(\text{spatial cov}) p(\text{survey cov})$ models. The combined models were compared to the selected models of the first step (those with $\Delta\text{AICc} \leq 2$ relative to the first ranked model). 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 for small samples (Burnham and Anderson 2002). Analyses were run in R (R Core Team 2013) using the package Unmarked (Fiske and 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 overlap, but the confidence interval of the difference of mean ψ between years did not included zero (Payton et al. 2003).

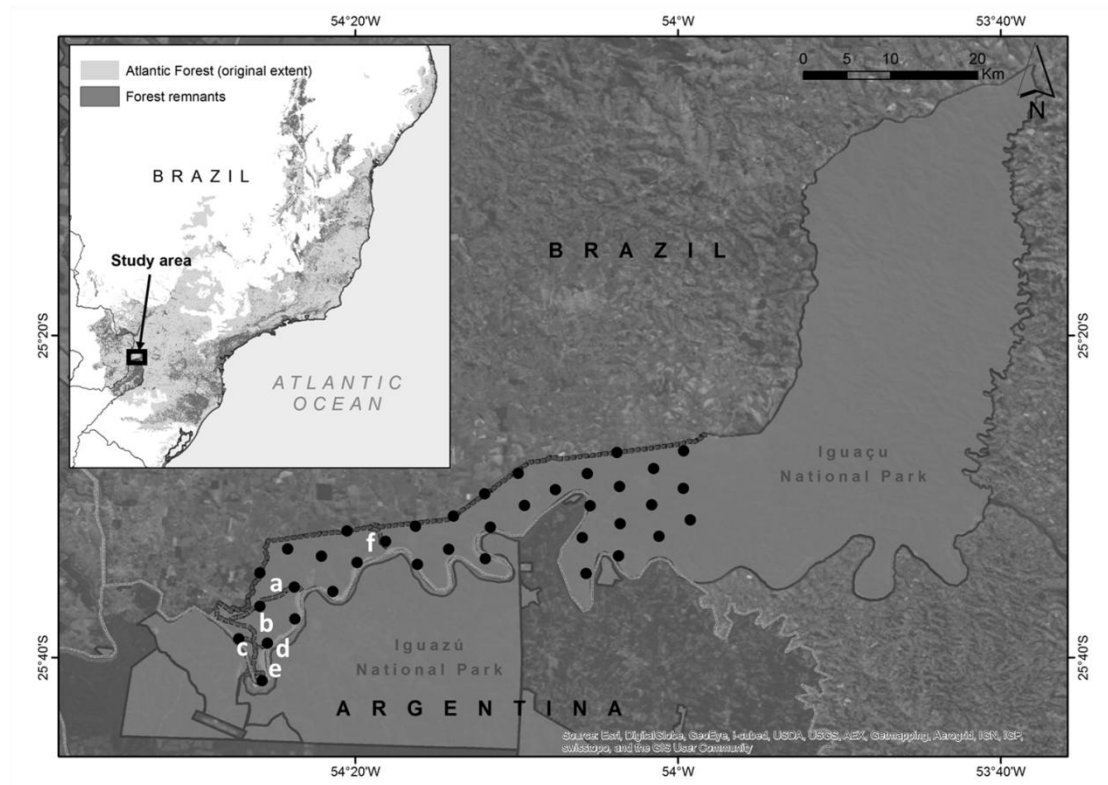


Fig. 1. Map of Brazil, showing the original distribution of the Atlantic Forest, current remnants, and the location of the study area. Limits of the two main protected areas of the Upper Paraná Atlantic Forest ecoregion: The Iguazu National Park in Brazil and the Iguazú National Park in Argentina. Black dots indicate the location of the 37 sampling sites, dashed grey line the northern limit adjacent to human-modified landscapes, and white letters the tourism attractions and infrastructure: a) Poço Preto trail, b) Road, c) Macuco Safari trail, d) Bananeiras trail, e) Hotel and Iguazu Falls view, f) Linha Martins trail.

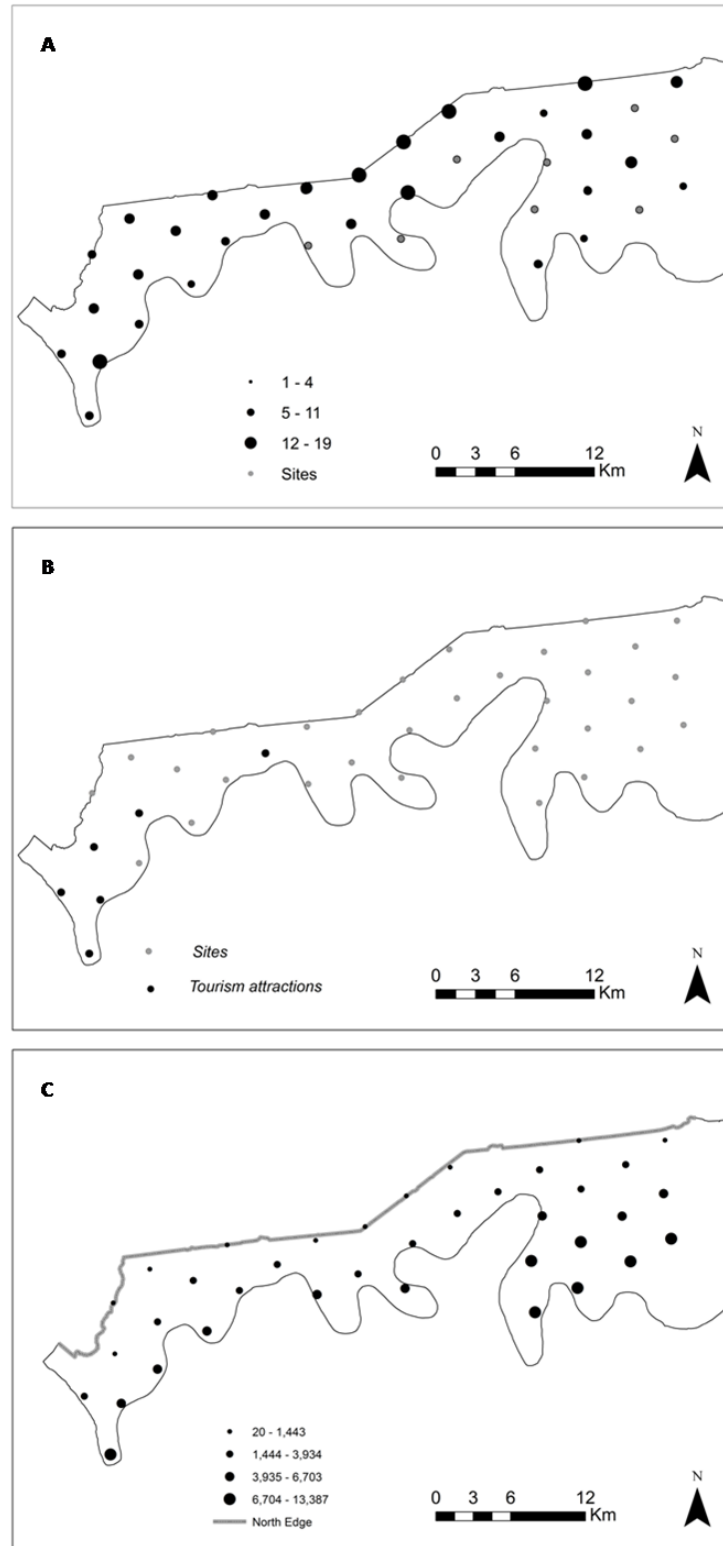


Fig. 2. Representation of the camera trap grid, showing the variation of spatial covariates across the 37 sampling sites in the Iguazu National Park. The sizes of dots are proportional to the values of different spatial covariates. (A) Hunting pressure, (B) Proximity to tourism attractions, (C) Distance from the edge of the park (northern limit).

Table 1. Large terrestrial mammals recorded across the 37 sampling sites in the Iguazu National Park, showing the number of sites where each species was recorded, the naive occupancy (observed proportion of occupied sites), and the number of detections (number of survey sessions with records summed across the 37 sites).

Species	Common name	# Sites	Naive occupancy	# Detections
Ordem Artiodactyla				
<i>Mazama americana</i> *	red brocket deer	35	95	155
<i>Pecari tajacu</i> *	collared peccary	24	65	57
<i>Mazama nana</i> *	dwarf brocket deer	15	41	30
Ordem Carnivora				
<i>Nasua nasua</i> *	coati	34	92	92
<i>Leopardus pardalis</i> *	ocelot	30	81	96
<i>Eira barbara</i> *	tayra	24	65	37
<i>Puma concolor</i> *	puma	20	54	46
<i>Panthera onca</i> *	jaguar	19	51	30
<i>Puma yagouaroundi</i> *	jaguarundi	12	32	15
<i>Canis familiaris</i> *	domestic dog	11	30	23
<i>Procyon cancrivorus</i>	crab-eating raccoon	9	24	11
<i>Leopardus tigrinus</i>	oncilla	4	11	5
<i>Leopardus wiedii</i>	margay	4	11	4
<i>Cerdocyon thous</i>	crab-eating fox	3	8	4
<i>Galictis cuja</i>	lesser grison	3	8	2
Ordem Cingulata				
<i>Dasybus novemcinctus</i> *	nine-banded armadillo	24	65	57
<i>Cabassous tatouay</i>	greater naked-tailed armadillo	1	3	1
<i>Euphractus sexcinctus</i>	six-banded armadillo	2	5	3
Ordem Didelphimorphia				
<i>Didelphis aurita</i>	big-eared opossum	32	86	90
Ordem Lagomorpha				
<i>Sylvilagus brasiliensis</i> *	tapeti	22	59	45
Ordem Perissodactyla				
<i>Tapirus terrestris</i> *	lowland tapir	34	92	128
Ordem Pilosa				
<i>Myrmecophaga tridactyla</i> *	giant-anteater	12	32	19
<i>Tamandua tetradactyla</i>	lesser anteater	1	3	1
Ordem Rodentia				
<i>Dasyprocta azarae</i> *	agouti	37	100	216
<i>Cuniculus paca</i> *	lowland paca	13	35	31
<i>Hydrochaeris hydrochaeris</i>	capybara	5	14	7

* Species that were analyzed.

Table 2. Single and multi-season occupancy models included in each of the two steps of the model selection for investigating the importance of spatial covariates on the distribution of terrestrial large mammals in the Iguazu National Park.

Models	Step 1	Step 2
MacKenzie et al. (2002)	$\Psi(.)p(\text{spatial cov})$	Step 1 models with $\Delta\text{AICc} \leq 2$ relative to the first ranked model
	$\Psi(.)p(\text{spatial cov}+\text{eff})$	
	$\Psi(.)p(\text{year})$	
	$\Psi(.)p(\text{eff})$	$\Psi(\text{first ranked spatial cov}) p(\text{first ranked spatial and/or survey cov})$
	$\Psi(\text{spatial cov})p(.)$	
	$\Psi(\text{spatial cov})p(\text{eff})$	
	$\Psi(.)p(.)$	
MacKenzie et al. (2003)	$\Psi(.)\gamma(.)\Phi(.)p(\text{spatial cov})$	Step 1 models with $\Delta\text{AICc} \leq 2$ relative to the first ranked model
	$\Psi(.)\gamma(.)\Phi(.)p(\text{spatial cov}+\text{eff})$	
	$\Psi(.)\gamma(.)\Phi(.)p(\text{year})$	
	$\Psi(.)\gamma(.)\Phi(.)p(\text{eff})$	$\Psi(\text{first ranked spatial cov})\gamma(.)\Phi(.)p(\text{first ranked spatial and/or survey cov})$
	$\Psi(\text{spatial cov})\gamma(.)\Phi(.)p(.)$	
	$\Psi(\text{spatial cov})\gamma(.)\Phi(.)p(\text{eff})$	
	$\Psi(.)\gamma(.)\Phi(.)p(.)$	

Results

With a total sampling effort of 9360 traps-night, we recorded 26 terrestrial (Appendices 1-4) large mammal species of which 17 were analyzed (Table 1). While the white-lipped peccary was not recorded, corroborating the hypothesis that it has gone locally extinct in the park, we confirmed, for the first time, the occurrence of the giant-anteater (*Myrmecophaga tridactyla*) in the INP. Considering estimates from the first-ranked model, mean occupancy ranged from $\psi = 0.20 (\pm 0.13)$ for the giant-anteater to $\psi = 1 (\pm 0.001)$ for red brocket deer (*Mazama americana*), and mean detection probability from $p = 0.05 (\pm 0.02)$ for jaguarundi (*Puma yagouaroundi*) to $p = 0.73 (\pm 0.04)$ for agouti (*Dasyprocta azarae*) (Fig. 3). Tayra (*Eira barbara*), coati (*Nasua nasua*), tapir (*Tapirus terrestris*) and agouti all had $\psi \geq 0.90$, while puma (*Puma concolor*), Brazilian dwarf brocket deer (*Mazama nana*), and domestic dog (*Canis familiaris*) had $\psi < 0.40$ (Fig. 3).

The constant model $\psi(.)p(.)$ was among the selected models for only three species: the Brazilian dwarf brocket deer, nine-banded armadillo (*Dasypus novemcinctus*) and tapeti (*Sylvilagus brasiliensis*), indicating weak response of these species to spatial covariates (Table 3). For other three species - red brocket deer, coati and puma - selected models included the model $\psi(.)p(\text{effort})$, indicating that sampling effort explained occupancy and/or detection probability of these species as well as spatial covariates (Table 3). For the remaining 11 species, nor the $\psi(.)p(.)$ neither the $\psi(.)p(\text{effort})$ models were among selected models, indicating that spatial covariates are indeed important to determine their distribution across the park (Table 4).

For nine of the 11 species with consistent response to spatial covariates, the selected models included distance from the edge of the park as a covariate (Table 4). Most of these species – tapir, ocelot (*Leopardus pardalis*), jaguar (*Panthera onca*), paca (*Cuniculus paca*) and agouti - responded positively to edge distance, while three - giant-anteater, domestic dog and peccary (*Pecari tajacu*) - responded negatively to edge distance. For jaguarundi the effect of distance from the edge of the park was positive on detection probability, but negative on occupancy. For nine species, selected models included proximity to tourism attractions as a covariate (Table 4). While ocelot, jaguarundi, big-eared opossum and domestic dog responded positively to proximity to tourism attractions, tayra, tapir, peccary and giant-anteater responded negatively to this covariate. Finally, for four species the selected models included hunting as a covariate (Table 4). Occupancy or detection probability of agouti, paca

and giant-anteater decreased, while jaguar occupancy increased, where hunting was more frequent.

Ocelot, jaguarundi and jaguar responded similarly to the same covariates, which included a positive response to proximity to tourism attractions besides a predominantly positive response to distance from the edge of the park (Table 4). For ocelot two multi-season models were selected, both indicating that detection probability increases further from the edge, close to tourism attractions and with sampling effort. The second-ranked model indicates that occupancy also increases further from the edge. For jaguarundi, three models were selected (the second-ranked being a multi-season model). All of them indicate that detection probability increases with the proximity to tourism attractions with the second-ranked model indicating also that occupancy increases close to the edge and to tourism attractions (but these effects on occupancy were weak as the standard error of coefficients included zero), and the third-ranked indicating that detection probability increases also further from the edge (but this effect was also weak, hindering conclusive interpretations regarding the effects of distance from the edge for this species). For jaguar, four single-season models were selected. All of them indicate that occupancy increases further from the edge, with the second-ranked indicating also that detection probability increases with sampling effort (but this was a weak effect). The third-ranked model indicates that occupancy increases also close to tourism attractions (but the effect of tourism was weak), while the fourth-ranked model indicates that occupancy increases also with hunting (but again the effect of hunting was weak).

As the cats, the domestic dog and the opossum also responded positively to the proximity to tourism attractions, (Table 4). For domestic dog two single-season models were selected both indicating that occupancy increased close to the edge and to tourism attractions, with the first-ranked model indicating also that detection probability increases with sampling effort (effects of the second-ranked model were weak). For big-eared opossum, only one multi-season model was selected indicating occupancy increases close to tourism attractions and detection probability varied between years (but both effects were weak).

In contrast to the cats and domestic dogs, three species (tayra, tapir and peccary) responded negatively to proximity to tourism attractions, some of them responding also to distance from the edge (Table 4). The only selected model for tayra (a single-season model) indicates that detection probability increases further from

tourism attractions and with sampling effort. For tapir two single-season models were selected both indicating that detection probability increases further from the edge and with sampling effort. The first-ranked model indicates also that occupancy increases further from tourism attractions. For peccary, two single-season models were selected both with detection probability as function of year, with the first-ranked model indicating also that occupancy increases close to the edge but further from tourism attractions.

Finally, three species (agouti, giant-anteater and paca) responded negatively to hunting (among other factors) (Table 4). For agouti only one multi-season model was selected, indicating that occupancy increases where hunting is less frequent and detection probability further from the edge and with sampling effort. For giant-anteater two multi-season models were selected both indicating that occupancy increases close to edge and where hunting is less frequent, with the first-ranked model indicating also that detection probability increases further from tourism attractions (but this effect of tourism was weak). For paca three single-season models were selected. The first- and third-ranked models indicate that detection probability increases where hunting is less frequent and further from the edge, with the third-ranked model indicating also that occupancy increases further from edge. The second-ranked model indicates that detection probability increases further from the edge.

For ten species (agouti, coati, giant-anteater, ocelot, jaguarundi, puma, nine-banded armadillo, tapeti, big-eared opossum and Brazilian dwarf brocket deer) multi-season models were among selected models and for six of them (big-eared opossum, agouti, giant-anteater, ocelot, puma and tapeti) these were the only selected models, indicating that occupancy dynamics is important. Using the confidence interval, a significant difference in occupancy between years was observed for jaguarundi and puma only (Fig. 4). For jaguarundi, occupancy in 2010 and 2013 was higher than in 2009 and for puma the occupancy in 2013 was higher than in 2009.

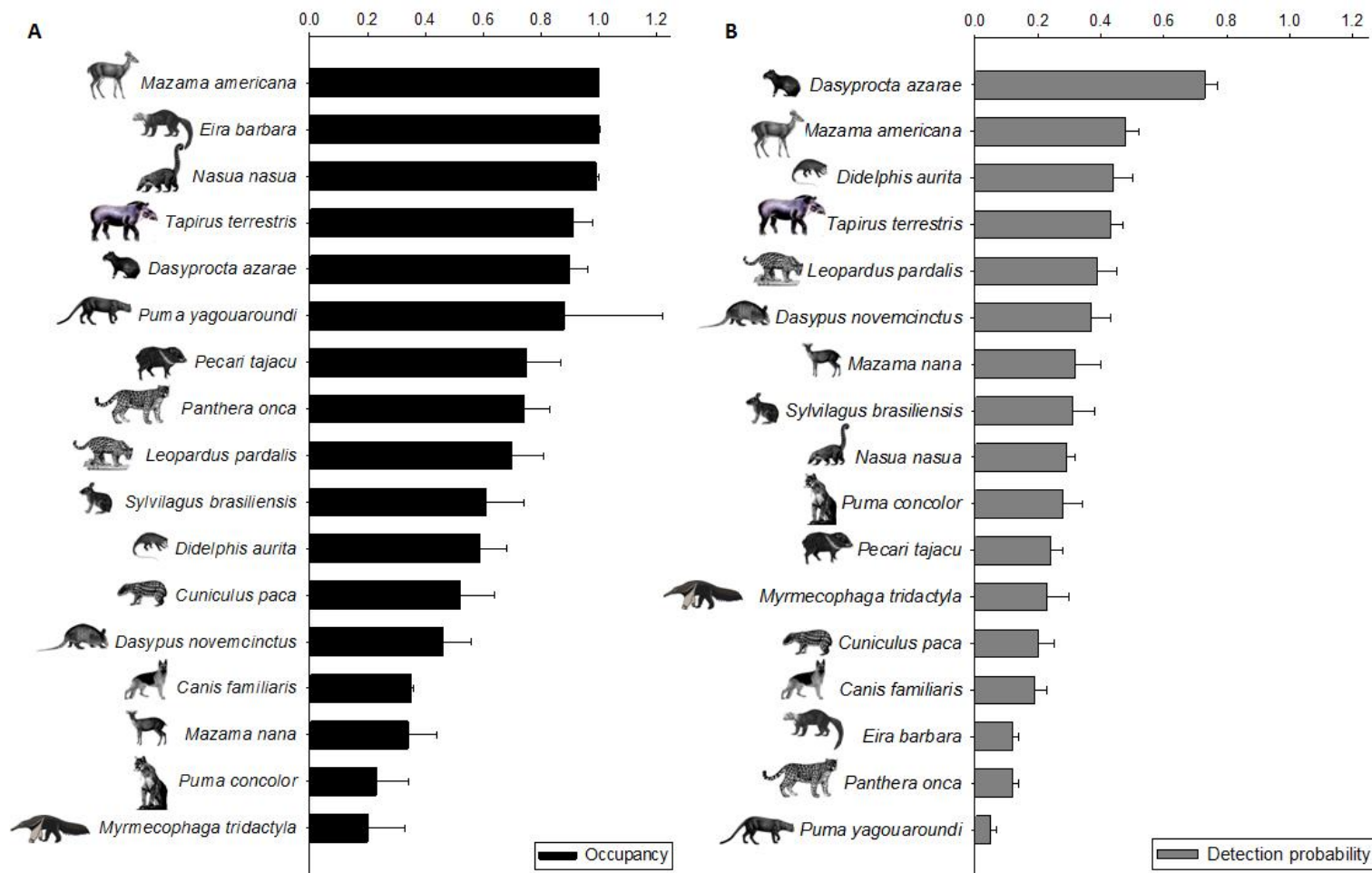


Fig. 3. (A) Mean occupancy and (B) mean detection probability in descending order for 17 terrestrial large mammals in the Iguazu National park. Bars represent the standard error.

Table 3. Selected ($\Delta AICc \leq 2$) occupancy models for six terrestrial large mammals (in alphabetic order) in the Iguazu National Park. For each model, information on the number of parameters (K), maximum likelihood (LogLik), Akaike Information Criterion for small samples (AICc), difference between the AICc of the model and the first-ranked model ($\Delta AICc$), weight of evidence (wi), and estimated coefficients with respective standard error, is provided. H= hunting pressure; T= proximity to tourism attractions; E= distance from the edge of the park; Eff= sampling effort; Year= sampling year.

Species	Models	K	Log Lik	AICc	$\Delta AICc$	wi	Coefficients									
							T (ψ)	T(p)	H(ψ)	H (p)	E(ψ)	E (p)	Eff	2009	2010	2013
<i>Dasypus novemcinctus</i>	$\psi(.)\gamma(.)\Phi(.)p(T)$	5	-136.88	285.69	0	0.18		-1.29 (0.66)								
	$\psi(.)\gamma(.)\Phi(.)p(year)$	6	-135.68	286.17	0.48	0.14								-0.6 (0.47)	0.53 (0.58)*	-0.81 (0.7)
	$\psi(.)\gamma(.)\Phi(.)p(.)$	4	-138.49	286.22	0.53	0.14										
	$\psi(E)\gamma(.)\Phi(.)p(T)$	6	-135.75	286.3	0.61	0.13		-1.34 (0.65)			-0.65 (0.46)					
	$\psi(T)p(year)$	5	-137.23	286.4	0	0.62	-2.13 (1.12)							-1.22 (0.27)	0.65 (0.35)	-0.68 (0.43)
	$\psi(.)\gamma(.)\Phi(.)p(T+eff)$	6	-136	286.79	1.1	0.1		-1.43 (0.67)					0.02 (0.02)*			
	$\psi(E)\gamma(.)\Phi(.)p(.)$	5	-137.55	287.04	1.35	0.09					-0.58 (0.46)					
	$\psi(.)p(year)$	4	-139.06	287.38	0.97	0.38								-1.20 (0.27)	0.62 (0.35)	-0.71 (0.43)
	$\psi(H)\gamma(.)\Phi(.)p(.)$	5	-137.79	287.51	1.82	0.07			0.08 (0.07)							
	$\psi(.)\gamma(.)\Phi(.)p(T+E)$	6	-136.4	287.59	1.9	0.07		-1.45 (0.68)				0.30 (0.30)*				
	$\psi(.)\gamma(.)\Phi(.)p(eff)$	5	-137.87	287.67	1.98	0.07							0.02 (0.02)*			

<i>Mazama americana</i>	$\psi(.)p(H+eff)$	4	-206.2	421.65	0	0.57	0.04 (0.02)	0.05 (0.01)
	$\psi(.)p(eff)$	3	-208.2	423.12	1.47	0.28		0.05 (0.01)
<i>Mazama nana</i>	$\psi(.)\gamma(.)\Phi(.)p(eff)$	5	-86.66	185.26	0	0.26		0.06 (0.03)
	$\psi(.)\gamma(.)\Phi(.)p(.)$	4	-88.19	185.63	0.37	0.22		
	$\psi(.)p(T+E+eff)$	5	-86.87	185.67	0	0.2	1.23 (0.54)	-0.55 (0.31) 0.05 (0.03)
	$\psi(.)p(T+eff)$	4	-88.27	185.78	0.11	0.19	0.92 (0.54)	0.05 (0.03)
	$\psi(.)\gamma(.)\Phi(.)p(T+E)$	6	-85.65	186.1	0.84	0.17	1.19 (0.67)	-0.76 (0.36)
	$\psi(.)p(eff)$	3	-89.7	186.12	0.45	0.16		0.06 (0.03)
	$\psi(.)p(T+E)$	4	-88.48	186.21	0.53	0.16	1.45 (0.53)	-0.56 (0.31)
	$\psi(.)\gamma(.)\Phi(.)p(E)$	5	-87.23	186.39	1.13	0.15		-0.56 (0.37)
	$\psi(E)p(eff)$	4	-88.73	186.7	1.03	0.12		-0.57 (0.43) 0.06 (0.03)
	$\psi(.)p(T)$	3	-90.09	186.9	1.23	0.11	1.19 (0.52)	
<i>Nasua nasua</i>	$\psi(.)\gamma(.)\Phi(.)p(E+eff)$	6	-86.05	186.9	1.64	0.11		-0.47 (0.39) 0.05 (0.03)
	$\psi(.)p(eff)$	3	-186.24	379.21	0	0.32		0.03 (0.01)
	$\psi(.)p(T+eff)$	4	-185.15	379.55	0.34	0.27	-0.51 (0.36)	0.04 (0.01)
	$\psi(T)p(eff)$	4	-185.41	380.07	0.86	0.21	-8.34 (0.01)	0.03 (0.01)

	$\psi(T+E)\gamma(.)\Phi(.)p(\text{eff})$	7	-181.5	380.85	0	0.17	-38.16 (56.8)*	-10.83 (13.7)*	0.04 (0.01)
	$\psi(.)\gamma(.)\Phi(.)p(\text{eff})$	5	-184.48	380.89	0.04	0.17			0.04 (0.01)
	$\psi(.)p(H+\text{eff})$	4	-185.91	381.07	1.86	0.13		0.01 (0.02)*	0.03 (0.01)
<i>Puma concolor</i>	$\psi(.)\gamma(.)\Phi(.)p(T+\text{eff})$	6	-102.1	219.01	0	0.54	1.05 (0.52)		0.32 (0.15)
	$\psi(.)\gamma(.)\Phi(.)p(\text{eff})$	5	-104.2	220.34	1.33	0.28			0.36 (0.16)
<i>Sylvilagus brasiliensis</i>	$\psi(.)\gamma(.)\Phi(.)p(H)$	5	-121.2	254.34	0	0.18		-0.41 (0.22)	
	$\psi(.)\gamma(.)\Phi(.)p(.)$	4	-122.95	255.15	0.81	0.12			
	$\psi(.)\gamma(.)\Phi(.)p(H+\text{eff})$	6	-120.51	255.82	1.47	0.08		-0.40 (0.23)	0.02 (0.02)*
	$\psi(.)\gamma(.)\Phi(.)p(\text{eff})$	5	-121.99	255.91	1.57	0.08			0.03 (0.02)

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

Table 4. Selected ($\Delta AICc \leq 2$) occupancy models for 11 terrestrial large mammals (in alphabetic order) in the Iguazu National Park. For each model, information on the number of parameters (K), maximum likelihood (LogLik), Akaike Information Criterion for small samples (AICc), difference between the AICc of the model and the first-ranked model ($\Delta AICc$), weight of evidence (wi), and estimated coefficients with respective standard error, is provided. H= hunting pressure; T= proximity to tourism attractions; E= distance from the edge of the park; Eff= sampling effort; Year= sampling year

Species	Models	K	LogLik	AICc	$\Delta AICc$	wi	Coefficients									
							T (ψ)	T(p)	H(ψ)	H (p)	E(ψ)	E (p)	Eff	2009	2010	2013
<i>Canis familiaris</i>	$\psi(T+E)p(\text{eff})$	5	-54.42	120.78	0	0.49	22.2 (20.8)				-31.0 (29.3)		0.09 (0.07)			
	$\psi(T+E)p(.)$	4	-55.96	121.17	0.39	0.4	28.5 (34.0)*				-39.2 (47)*					
<i>Cuniculus paca</i>	$\psi(.)p(H+E)$	4	-88.27	185.79	0	0.45				-0.71 (0.41)		0.54 (0.24)				
	$\psi(.)p(E)$	3	-90	186.72	0.94	0.28						0.74 (0.22)				
	$\psi(E)p(H+E)$	5	-87.43	186.79	1.01	0.27				-0.59 (0.42)	0.60 (0.47)	0.48 (0.22)				
<i>Dasyprocta azarae</i>	$\psi(H)\gamma(.)\Phi(.)p(E+\text{eff})$	7	-175.23	368.31	0.00	0.71			-0.35 (0.21)			0.24 (0.01)	0.05 (0.01)			
<i>Didelphis aurita</i>	$\psi(T)\gamma(.)\Phi(.)p(\text{year})$	7	-152.94	323.74	0.00	0.77	7.03 (15.87)*							-0.04 (0.30)*	0.85 (0.41)	-1.67 (0.51)*
<i>Eira barbara</i>	$\psi(.)p(T+\text{eff})$	4	-107.09	223.42	0	0.79		-1.54 (0.74)					0.07 (0.03)			
<i>Leopardus pardalis</i>	$\psi(.)\gamma(.)\Phi(.)p(T+E+\text{eff})$	7	-151.95	321.77	0	0.62		2.03 (0.48)				0.65 (0.16)	0.06 (0.02)			
	$\psi(E)\gamma(.)\Phi(.)p(T+E+\text{eff})$	8	-150.8	322.74	0.97	0.38		2 (0.48)			0.84 (0.6)	0.6 (0.16)	0.06 (0.02)			
<i>Myrmecophaga tridactyla</i>	$\psi(H+E)\gamma(.)\Phi(.)p(T)$	7	-59.02	135.9	0	0.6		-8.64 (34.51)*	-3.66 (2.46)		-3.59 (2.67)					

	$\psi(H+E)\gamma(.)\Phi(.)p(.)$	6	-61.49	137.79	1.89	0.23		-3.78 (2.49)	-3.51 (2.50)			
<i>Panthera onca</i>	$\psi(E)p(.)$	3	-93.72	194.17	0	0.32			4.55 (2.33)			
	$\psi(E)p(\text{eff})$	4	-93.16	195.58	1.4	0.16			4.45 (2.21)	0.02 (0.02)*		
	$\psi(T+E)p(.)$	4	-93.35	195.96	1.79	0.13	4.44 (38.69)*		4.15 (2.22)			
	$\psi(H+E)p(.)$	4	-93.4	196.05	1.88	0.13		0.17 (0.27)*	6.53 (5.03)			
<i>Pecari tajacu</i>	$\psi(T+E)p(\text{year})$	6	-132.1	279	0	0.64	-2.52 (1.25)		-0.82 (0.55)	-2.39 (0.40)	1.70 (0.46)	1.58 (0.46)
	$\psi(.)p(\text{year})$	4	-135.43	280.11	1.12	0.36				-2.39 (0.40)	1.70 (0.46)	1.58 (0.46)
<i>Puma yagouaroundi</i>	$\psi(.)p(T)$	3	-57.58	121.89	0	0.28		1.38 (0.61)				
	$\psi(T+E)\gamma(.)\Phi(.)p(T)$	7	-52.62	123.1	0	0.33	27.3 (40.3)*	1.13 (0.60)	-45.2 (73.2)*			
	$\psi(.)p(T+E)$	4	-57.12	123.49	1.61	0.13		1.38 (0.58)		0.27 (0.27)*		
<i>Tapirus terrestris</i>	$\psi(T)p(E+\text{eff})$	5	-184.52	380.97	0	0.56	-2.35 (1.41)		0.46 (0.13)	0.07 (0.01)		
	$\psi(.)p(E+\text{eff})$	4	-186.09	381.42	0.46	0.44			0.46 (0.13)	0.07 (0.01)		

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

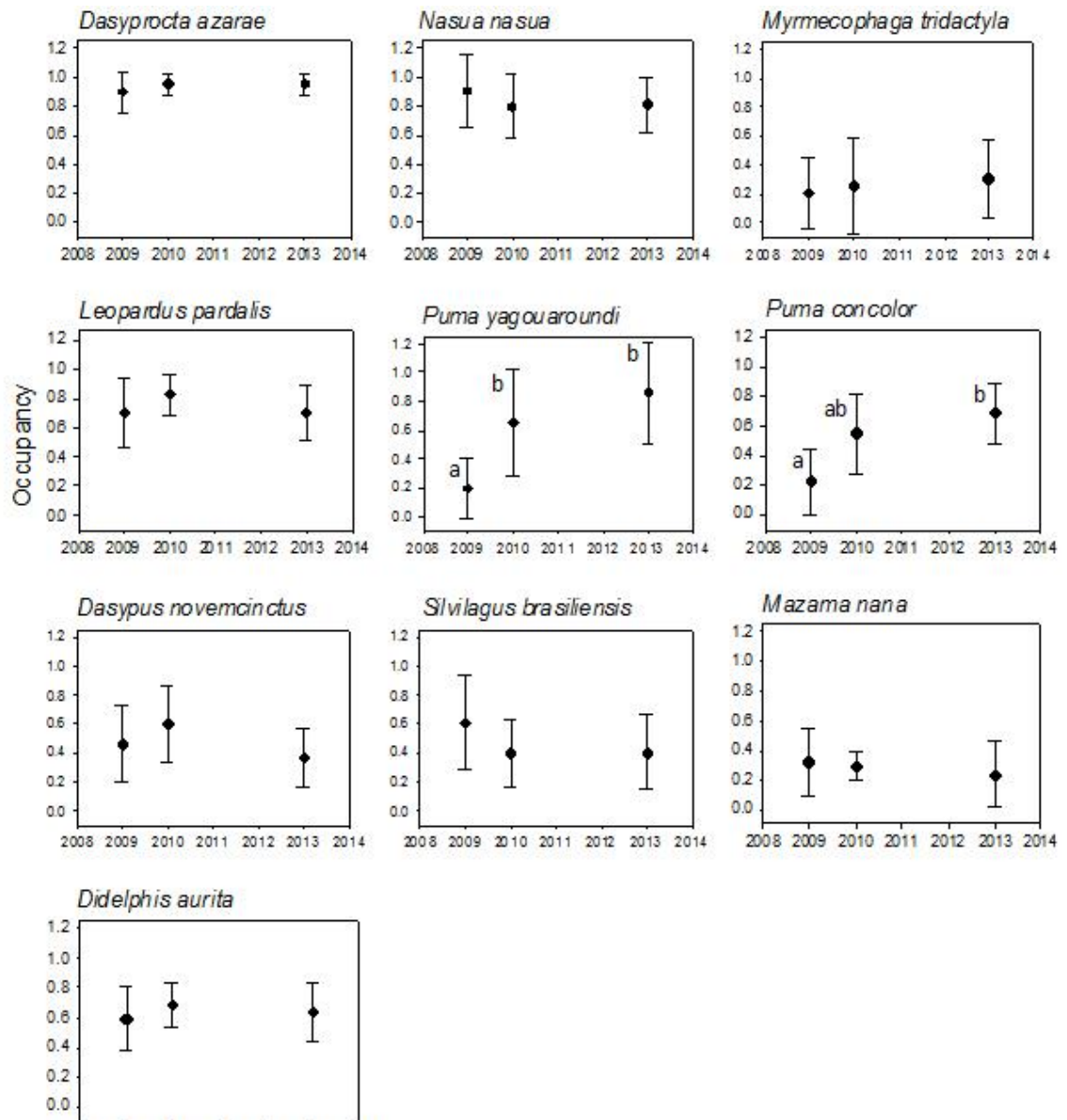


Fig. 4. Mean occupancy and confidence interval across the three study years for 10 terrestrial large mammals in the Iguazu National Park. Distinct letters indicates mean occupancy differs among years.

Discussion

On the one hand, our results confirm that the Iguaçu National Park still harbors a rich terrestrial large mammal fauna, including many key-stone species as large herbivores and top predators. Many of the recorded species with high occupancy within the park are rare or extinct in most Atlantic Forest remnants. On the other hand, we show that most large mammal species are not evenly distributed across the park, with occupancy negatively affected by edge effect, tourism and, at a lesser extent, hunting.

In the following paragraphs, we first discuss the regional importance of the INP by comparing its terrestrial large mammal fauna to that found at other PAs and remnants of Atlantic Forest. We then interpret the results from modeling occupancy and detection probability for 11 species to discuss the main threats to this fauna at INP. Finally, we highlight the implications of our results to the management of PAs in general and of the INP in particular aiming the long term conservation of biodiversity.

Terrestrial large mammal fauna 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. Few PAs, all in Southeastern Brazil (i.e. Sooretama Biological Reserve/ Linhares Forest Reserve, Carlos Botelho State Park, Ilha do Cardoso State Park, Jureia-Itatins Ecological Station), still harbor similarly well-conserved large mammal faunas in the Atlantic Forest (Galetti et al. 2009; Jorge et al. 2013). Human-modified landscapes outside PAs present very simplified large mammal faunas dominated by medium-sized generalist species and missing most large-bodied ungulates and felids of more conservation concern (Espartosa et al. 2011); the same is the case of even some of the Atlantic Forest PAs (Cassano et al. 2012).

On a regional scale, the INP nowadays 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), and in the adjacent Argentinean park (Di Bitetti et al. 2010; Paviolo et al. 2008). Our study actually confirmed the occurrence of the giant-anteater until now recorded only by hair found in two jaguar scats (Cândido-Jr et al. 2003). Photographic records not only confirmed the occurrence of this species during all study years but also suggest that the species is reproducing within the park given the large number of records of females with cubs. However, our study also

confirmed the extirpation of the white-lipped peccary in the INP. White-lipped peccary together with the sympatric collared peccary are the most important forest-dwelling ungulates both in terms of the livelihoods of human populations that depends on subsistence hunting and as seed predators and prey for top predators (Redford 1992). In the INP peccaries represented 77% of the jaguar diet (Crawshaw 1995). The absence of white-lipped peccary and the low density of collared peccary in the INP were first reported by Cascelli de Azevedo and Conforti (2008) who found no conclusive evidence on the reasons for this decline in the park (as it is also the case for white-lipped peccaries at other areas in the Amazon from where the species has been declining; (Fragoso 1997), the most supported hypothesis being the combination of illegal hunting and jaguar predation. The high occupancy observed for the collared peccary in this study together with the occurrence albeit in very low density of the white-lipped peccary in the adjacent Argentinean park and their known ability to cross rivers represent a hope for population recovering of both peccaries in the INP.

Distance from the edge of the park

Several terrestrial large mammals were negatively affected by edge effects from adjacent human-modified landscapes, with distance from the edge included in the selected models with negative effects for both frugivores (tapir, paca and agouti) and carnivores (ocelot and jaguar). For large-bodied mammals that range widely and therefore come into frequent contact with reserve limits and beyond, the adjacent altered areas can act as population sinks, mainly by overexposing animals to human-induced mortality, such as road kills, hunting and persecution (Woodroffe and Ginsberg 1998). A recent study in Kenya showed that in fact distance to active human settlements and land use induced temporal changes in carnivore occupancy, suggesting that these animals adjust their distribution in reaction to human use (Schuette et al. 2013). This sink effect of adjacent human-modified landscapes is probably most strong in the case of the jaguar, for which accumulated evidence suggest a severe population decline in the INP region in the past (Crawshaw 1995; Galetti et al. 2013; Paviolo et al. 2008). Although our results suggest that jaguars are not affected by hunting within the park, the species do suffer strong persecution outside park boundaries. Indeed, human-wildlife conflicts are fast becoming one of the most urgent threats to large predator survival worldwide (Treves and Karanth 2003) as well as in the INP region (Xavier et al. 2013).

The tapir - a megafrugivore that eats large amounts of fruits and disperse large quantities of seeds often at long distances (Jorge et al. 2013) – despite presenting high occupancy in the INP was also affected by edge effects. Although our results suggest that the levels of hunting within the INP was not strong enough to depress tapir populations, tapir occupancy and detection probability were higher further from areas easily accessed by hunters in the adjacent forest remnants including the Argentinean park (Cruz 2012), and further from tourism attractions and infrastructure in the INP. This suggests that both human avoidance behavior and hunting at and beyond park limits are responsible for the edge effect observed for tapir in the INP. Hunting at and beyond park limits seems also to be the reason for the negative edge effect observed for paca and agouti, since these species are those most clearly affected by hunting within the park (see below).

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 an example of an edge-induced invasion. Recently the ubiquity and negative consequences of domestic dog invasion in Atlantic Forest remnants has been highlighted in several studies (Galetti and Sazima 2006; Paschoal et al. 2012; Srbek-Araujo and Chiarello 2008; Torres and Prado 2010) with domestic dog presence and abundance being the factors best explaining the occurrence of native mammal species in forests outside PAs (Cassano et al. 2014; Frigeri 2013). In fact, domestic dog distribution across the INP indicates a positive edge effect, the opposite pattern displayed by several frugivores and carnivores of conservation concern. However, two native species - the giant anteater and the collared peccary - also responded positively to the edge in the INP. The giant-anteater has a broad distribution across Central and South America being common in open, savanna-like biomes, with the importance of forest to the species not well understood (Kreutz et al. 2012). The observed positive edge effect may be associated with the ability to explore both the forests inside the park and more open areas beyond its limits. The positive response of the collared peccary to the edge may be associated with predator avoidance, since its major predator, the jaguar, showed the opposite pattern, and/ or with the importance of crop plantations outside the park as food sources.

Proximity to tourism attractions/ infrastructure

Tourism at the PNI 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 in roads (Leblond et al. 2013) and trails (Rogala et al. 2011). A negative impact of tourism on diurnal vertebrates was also observed in another national park at the Atlantic Forest (Cunha 2010). At the INP, the proximity to tourism attractions negatively affected tapir, tayra, giant-anteater and collared peccary, while felids (jaguar, jaguarondi, and ocelot) and domestic dogs were associated with touristic areas.

The species negatively affected by human presence related to tourism are either commonly hunted (peccary and tapir), are known to be very secretive as the giant anteater (Portillo Reyes et al. 2010), or are not strictly nocturnal as the tayra that is active throughout the day. In contrast, the native species associated with touristic areas within the park are all felids, which are nocturnal and known to use trails and roads for moving through the forest (Carbone et al. 2001; Harmsen et al. 2010) either for hunting (Harmsen et al. 2010) or scent marking (Rabinowitz and Nottingham 1986). As touristic trails and roads are the only ones available in 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 activity.

Hunting pressure

Paca, collared peccary, red brocket deer and agouti are the most frequently hunted species within the INP (Ivan Baptiston, personal communication) and elsewhere in the Neotropics (Bodmer 1995; Cullen et al. 2000; Jerozolinski and Peres 2003; Paviolo et al. 2009a). Current levels of hunting within the INP indeed negatively affected occupancy/ detection probability of two of these species, agouti and paca. These two medium-sized frugivore rodents that are important seed dispersers (Levin 2007; Smythe 1987) and affect plant recruitment in Neotropical forests (Jorge and Howe 2009) are disappearing from many Atlantic Forest remnants outside PAs (Cassano et al. 2012; Chiarello 1999) with possible dramatic consequences for forest regeneration (Jorge and Howe 2009). Our results suggest, however, that at current levels, hunting is not affecting the populations of red brocket

deer and especially collared peccaries, which presented an increase in detection probability over the study years in the INP. Nevertheless, despite strongly affecting only two species, it is noteworthy that hunting at INP impacted species with high fecundity in areas within large source populations. The giant-anteater also showed a negative association with areas where hunting is more frequent, indicating again the secretive nature of this species that probably avoids humans but is not commonly hunted.

Temporal variations in occupancy

Although not among the main objectives of this study, we were able to check for temporal variation in occupancy during the last five years within the INP. Despite the fact that occupancy dynamics was important for several species, with multi-season models selected for most terrestrial large mammals, occupancy levels were fairly stable for most of them. For any of the species of conservation concern we observed a decline in occupancy levels, not even for the jaguar whose populations declined drastically in the past in the INP region (Paviolo et al. 2008), indicating that the rate of decline of this endangered species has been reduced in recent years. On the contrary, the only observed significant change in occupancy levels was the increase for two species of little conservation concern, the jaguarondi and puma. In fact, pumas still occupy most of their continental distribution being present in many forest remnants where the jaguar is locally extinct (De Angelo et al. 2011). Nevertheless, the time frame of our study is too short compared with the longevity of most large mammals, and inferences on temporal variation should be taken with caution (Ahumada et al. 2013). Long term information is needed to enable adequate inferences on changes in mammal occupancy over time.

Conclusions and conservation implications

Despite the integrity of forests within the Iguazu National Park, our findings suggest that cryptic, often ignored threats such as hunting, biological invasion, and other edge- and tourism-associated threats do affect the fauna inside parks, imperiling their ability to effectively contribute to biodiversity conservation in the long run. If this is the case for one of the most extensive PAs that is adjacent to other parks as the INP, 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 (Bruner et al. 2001; Joppa et al. 2008) are not useful and can even lead to biased conclusions. Direct information on biological assemblages and populations are needed and should be incorporated into monitoring programs within management plans for PAs. This detailed local information should also be used to complement more regional or global analysis of PA effectiveness (Bruner et al. 2001; Laurance et al. 2012; Naughton-Treves et al. 2005).

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 and abundant large mammal fauna can still be found in the Atlantic Forest (Galetti et al. 2009). They even highlight the Iguazu National Park as one of the most important areas for large mammal conservation in the Atlantic Forest given the high occupancy of several species that are rare elsewhere. Nevertheless, our study clearly show that this fauna is not evenly distributed across the park and are negatively affected by edge effects, tourism and hunting, which if not properly controlled and managed can substantially reduce the value of the park in the long run.

Our findings suggest that the most important threat to the fauna 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 results highlight the urgent need to legally re-establish and enforce the adequate management of the buffer zones around PAs, which as part of several legal measures that led to the downgrading, downsizing and degazettement of PAs were weaken or totally removed from many PAs in Brazil (Bernard et al. 2014; Mascia and Pailler 2011). In the INP region, for instance, this process occurred to allow the installation of one more hydroelectric power plant on the Iguazu River less than 500 m from the edge of the INP. As observed by DeFries et al. (2005), disturbances and habitat loss surrounding protected areas has reduced their capacity to conserve species by decreasing their effective size and their ability to maintaining ecological processes.

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 biodiversity 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 already affected two rodent species with high fecundity. It is also important to keep in mind 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 adopt drastic measures to combat illegal activities inside parks and surroundings (Geldmann et al. 2013), such as supporting park rangers, mitigating human-wildlife conflict (Xavier et al. 2013), and enforcing buffer zones systems taking into account the livelihoods of the local communities.

As a result of some of these threats to the Iguazu 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 (Bernard et al. 2014). In the long term, this will disintegrate the effectiveness of the largest PA system in the world.

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Appendices



Appendix 1 Arctiodactyla. A) *Mazama americana* (male), B) *Mazama nana* (male), C) *Pecary tajacu* (female with cubs). Didelphimorphia D) *Didelphis aurita*. Cingulata E) *Euphractus sexcinctus*, F) *Cabassous tatouay*, G) *Dasypus novemcinctus*. Lagomorpha H) *Sylvilagus brasiliensis*.



Appendix 2. Carnivora A)*Nasua nasua*, B)*Eira barbara*, C)*Canis familiaris*, D)*Procyon cancrivorus*, E)*Galictis cuja*, F)*Cerdocyon thous*.



Appendix 3. Carnivora A)*Panthera onca* (female), B)*Leopardus pardalis* (male), C)*Leopardus wiedii*, D)*Puma concolor* (male), E)*Puma yagouaroundi*, F)*Leopardus tigrinus* (male).



Appendix 4. Rodentia A)*Hydrochaeris hydrochaeris* (female with cubs), B)*Cuniculus paca*, C)*Dasyprocta azarae* (female with cubs). Pilosa D)*Myrmecophaga tridactyla* (female with cub), E)*Tamandua tetradactyla* (female with cub). Perissodactyla F)*Tapirus terrestris*.

Conclusão geral

A despeito da integridade das florestas do Parque Nacional do Iguaçu (PNI), nossos resultados sugerem que ameaças crípticas e freqüentemente ignoradas como caça, invasões biológicas e outras ameaças associadas às áreas adjacentes e ao turismo afetam a fauna em áreas protegidas, pondo em risco a habilidade destas áreas de efetivamente contribuir para a conservação da biodiversidade no longo prazo. Se esse é o caso para uma das áreas protegidas mais extensas e que é adjacente a outros parques como o PNI, é provável que o efeito dessas ameaças crípticas seja ainda mais forte em áreas protegidas menores e mais isoladas, que são maioria na Mata Atlântica. Em contextos espaciais em que áreas protegidas são ilhas de florestas imersas em paisagens modificadas pelo homem, medidas comumente utilizadas para inferir sobre a efetividade destas áreas, como a taxa de desmatamento (Bruner et al. 2001; Joppa et al. 2008), não são úteis e podem até levar a conclusões enviesadas. Informações diretas sobre populações e comunidades biológicas são necessárias e deveriam ser incorporadas em programas de monitoramento dentro dos planos de manejo de áreas protegidas. Essa informação detalhada e local deveria também ser usada para complementar as análises regionais ou globais sobre efetividade de áreas protegidas (Bruner et al. 2001; Laurance et al. 2012; Naughton-Treves et al. 2005).

Esses resultados não implicam, no entanto, que o PNI ou outras áreas protegidas da Mata Atlântica não sejam valiosas para a conservação da biodiversidade. Ao contrário, nossos resultados corroboram a idéia de que essas áreas são os únicos lugares onde uma fauna de mamíferos de maior porte rica e abundante pode ser encontrada na Mata Atlântica (Galetti et al. 2009). Os resultados inclusive apontam o Parque Nacional do Iguaçu como uma das áreas de Mata Atlântica mais importantes para a conservação de mamíferos de maior porte, dados os altos níveis de ocupação encontrados para muitas espécies que são raras em outros locais. No entanto, nosso estudo mostra claramente que esta fauna não está distribuída homogeneamente no parque e é afetada negativamente por efeitos de borda, turismo e caça, que se não adequadamente controlados e manejados podem reduzir substancialmente o valor do parque no futuro.

Nossos resultados sugerem que a ameaça mais importante para a fauna vem de fora, na forma de invasão de espécies como a do cachorro doméstico, ou de atropelamentos, caça e perseguição, que fazem várias espécies serem menos comuns próximo às bordas do parque adjacentes a paisagens modificadas pelo homem. Isto

evidencia a urgência em se re-estabelecer legalmente e fazer cumprir um manejo adequado nas zonas tampão ao redor de áreas protegidas, as quais foram enfraquecidas ou completamente removidas, como parte de uma série de medidas legais que prejudicaram as áreas protegidas do Brasil (Bernard et al. 2014; Mascia and Pailler 2011). Como observado por DeFries e colaboradores (2005), distúrbios e perda de habitat ao redor de áreas protegidas têm reduzido a capacidade dessas áreas de conservar espécies ao diminuir seu tamanho efetivo e a sua habilidade de manter processos ecológicos.

O turismo intenso no Parque Nacional do Iguaçu também impactou negativamente alguns mamíferos de maior porte, representando uma mensagem clara de alerta sobre o perigo do turismo descontrolado ou de encorajar o crescimento ilimitado do turismo em áreas protegidas. Para garantir a conservação da biodiversidade, assim como a recreação e educação proporcionadas pelo turismo, é necessário constantemente rever as metas turísticas e manter os atrativos e infra-estrutura turísticos restritos a poucos locais nas áreas protegidas.

Embora os efeitos da caça dentro do parque tenham sido evidentes apenas para duas espécies cinegéticas, é alarmante que tenha afetado duas espécies de roedores que apresentam alta fecundidade. É importante notar também que parte dos efeitos de borda que foram comuns se deve a caça e perseguição nos (e fora dos) limites do parque, as quais levaram no passado a depleção da população de onças. É fundamental que se adotem medidas de combate às atividades ilegais dentro dos parques e arredores (Geldmann et al. 2013), como dar apoio e suporte a polícia florestal, mitigar conflitos entre homem e animais silvestres (Xavier et al. 2013), e fazer cumprir o sistema de zonas tampão, levando em consideração a forma de sustento das comunidades locais.

Como resultado das ameaças que vem afetando o Parque Nacional do Iguaçu, a UNESCO (United Nations Educational, Scientific and Cultural Organization) deu um ultimato ao governo brasileiro ameaçando retirar o título de Patrimônio Natural da Humanidade do parque (Carazzai 2014). Depois de décadas de expansão de seu sistema de áreas protegidas, o Brasil está agora arriscando seu capital natural e sua biodiversidade ao criar mecanismos legais para permitir projetos de desenvolvimento dentro e ao redor de suas áreas protegidas (Bernard et al. 2014). No longo prazo, isto deve desintegrar a efetividade para a conservação da biodiversidade do maior sistema de áreas protegidas do mundo.

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