

UNIVERSIDADE ESTADUAL DE SANTA CRUZ PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

EFEITO DE FATORES NATURAIS E ANTRÓPICOS NOS PADRÕES DE OCUPAÇÃO DE MESOCARNÍVOROS EM DOIS GRANDES REMANESCENTES DE MATA ATLÂNTICA DO SUL DA BAHIA

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ILHÉUS 2024

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RESUMO

A diversidade e distribuição de espécies está intimamente relacionada às características de um local, seja ela natural ou causada pelas atividades humanas. Os mesocarnívoros são mamíferos predadores de menor porte que geralmente se beneficiam da ausência de predadores de topo, proliferando em ambientes onde estes últimos foram extintos. O objetivo deste estudo foi estimar a ocupação e explorar os padrões de ocupação de habitat da comunidade de mesocarnívoros em duas unidades de conservação (UC) na Mata Atlântica: o Parque Nacional do Pau Brasil e a RPPN Estação Veracel. Especificamente, testamos se a ocupação de pontos amostrais no interior dessas UC pode ser explicada por variações no ambiente natural (área basal de árvores e declividade do terreno) e fatores antrópicos (proximidade às estradas e aos limites das UC). Ao utilizar armadilhas fotográficas distribuídas em 61 pontos amostrais durante quatro campanhas de três meses de amostragem, detectamos 10 espécies de mesocarnívoros (Cerdocyon thous, Conepatus semistriatus, Didelphis aurita, Eira barbara, Galictis cuja, Herpailurus yagouarundi, Leopardus gutullus, Leopardus wiedii, Nasua nasua, Procyon cancrivorus). A riqueza observada e estimada foram similares, indicando 9 espécies no Parque Nacional do Pau Brasil e 7 espécies na RPPN Estação Veracel. Houve variabilidade na detecção das espécies entre as campanhas, com valores consistentemente baixos observados para a maioria das espécies, exceto para C. thous. As probabilidades médias de ocupação de todas as espécies variaram entre as campanhas e áreas, sendo N. nasua a espécie mais comum nas duas UC. A instalação de armadilhas fotográficas em estradas ou trilhas teve associação positiva com a detecção de C. thous e Leopardus spp. e negativa com a detecção de E. barbara e N. nasua. A maioria das espécies teve sua ocupação relacionada a alguma covariável. Nasua nasua foi mais comum em florestas maduras, com maior área basal, e C. thous evitou essas áreas. Didelphis aurita foi mais comum em áreas mais distantes de estradas, sendo o oposto observado para C. thous. Por fim, houve uma tendência geral para que as espécies prevaleçam na periferia das reservas. O estudo indica que ambas as áreas abrigam uma grande diversidade de mesocarnívoros da Mata Atlântica, porém, a baixa ocupação média das espécies sugere a existência de fatores limitando os tamanhos populacionais.

Palavras-chave: carnívoros, modelo de ocupação de comunidades, uso do habitat, floresta tropical, áreas protegidas

ABSTRACT

Species diversity and ditribution is closely linked to the local characteristics, whether natural or caused by human activities. Mesocarnivores are small predatory mammals that usually benefit from top predator absence, proliferating in areas where the latter has been locally extinct. The objective of this study was to estimate occupancy and explore habitat use patterns of the mesocarnivore community in two protected areas (PA) in the Atlantic Forest: Pau Brasil National Park and Veracel Station Private Natural Heritage Reserve (PNHR). Specifically, we tested if site occupancy within the PA was explained by variation in the natural environment (tree basal area and terrain declivity) and anthropogenic factors (distance to roads and PA limits). By using camera traps in 61 sites along four 3-months seasons, we detected 10 mesocarnivore species (Cerdocyon thous, Conepatus semistriatus, Didelphis aurita, Eira barbara, Galictis cuja, Herpailurus yagouarundi, Leopardus gutullus, Leopardus wiedii, Nasua nasua, Procyon cancrivorus). Observed richness and estimated richness were similar, with 9 species in Pau Brasil National Park and 7 species in Veracel Station PNHR. There was variability in species detection among seasons, with consistently low values observed for most species, except for C. thous. Mean occupancy probabilities varied among species and seasons, with N. nasua being the most common species in both areas. The placement of camera traps along roads or trails was positively associated with detection of C. thous and Leopardus spp. and negatively associates with E. barbara and N. nasua. Most species' occupancy was related to some covariate. Nasua nasua had higher occupancy in mature forests, with higher basal area, while C. thous avoided these areas. Didelphis aurita had higher occupancy in areas farther from roads, the opposite being observed for C. thous. Finally, there was a general trend for species to prevail at the periphery of reserves. The study indicates that both study areas harbor a high diversity of Atlantic Forest mesocarnivores, however, the low average species occupancy suggests the existence of limiting factors constraining the population levels.

Key words: carnivores, community occupancy model, habitat use, tropical forest, protected areas

I. INTRODUÇÃO GERAL

Este trabalho é fruto de uma parceria construída com o Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros (CENAP) do Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) e o Instituto Pró-carnívoros, por meio do Dr. Marcelo Magioli, que me oportunizou o uso de parte dos dados do projeto intitulado "Estudo Populacional e Conservação de Onças-Pintadas da Porção Norte da Mata Atlântica: RPPN Estação Veracel -PARNA do Pau-Brasil". A parceria foi construída na fase inicial do projeto apresentado ao Programa de Pós-Graduação em Ecologia e Conservação de Biodiversidade (PPGECB), quando, por sugestão da minha orientadora, contactei o Dr. Marcelo para conhecer a base de dados utilizada no artigo "The role of protected and unprotected forest remnants for mammal conservation in a megadiverse Neotropical hotspot", publicado na revista Biological Conservation em 2021 por Magioli e colaboradores. O Dr. Marcelo acabou por se tornar um dos meus coorientadores e permitiu o meu acesso a base de dados já filtrados para as espécies de mamíferos carnívoros, meu grupo de interesse. A ausência do registro da onça-pintada na área de estudo e a baixa quantidade de registros de algumas outras espécies me chamou atenção, aguçando meu interesse inicial de investigar a ocorrência e distribuição de carnívoros em uma região de Mata Atlântica exuberante, porém com um longo histórico de ocupação humana. Assim, a partir de conversas com minha orientadora, Dra. Camila, e o Dr. Marcelo, consolidamos a ideia de tentar compreender como a comunidade de mesocarnívoros está estruturada em duas Unidades de Conservação inseridas na Mata Atlântica do extremo sul da Bahia: a Reserva Particular do Patrimônio Natural Estação Veracel e o Parque Nacional do Pau Brasil, que foram parceiros do projeto liderado pelo ICMBio/CENAP e Instituto Procarnívoros e, posteriormente, se tornaram parceiros do meu projeto de mestrado.

Para atingir os objetivos do projeto, pensando e olhando para a estrutura dos dados, a Dr. Camila aconselhou que eu me familiarizasse com os modelos de ocupação, visto que seria uma possível abordagem de análise de dados. Ao me aprofundar em artigos que visavam compreender os padrões de ocupação por mesocarnívoros a partir desses modelos, me deparei com diversas publicações do Dr. Pedro Monterroso e me interessei pela metodologia que ele utilizava em suas análises, além de seus trabalhos serem próximos ao que eu esperava do meu projeto. Por iniciativa própria, entrei em contato com o Dr. Pedro explicitando minha vontade de aprender mais sobre os modelos de ocupação, e ele, gentilmente, aceitou me auxiliar nas análises e se tornar meu coorientador. O Dr. Pedro é associado ao Centro de Investigação em

Biodiversidade e Recursos Genéticos (CIBIO/Biopolis) pertencente a Universidade do Porto, Portugal, e tive o privilégio de fazer um estágio durante oito meses no segundo ano (2024) de mestrado. Neste tempo realizei as análises do meu projeto com o apoio do meu coorientador e de outros membros do WildEcol (laboratório coordenado pelo Dr. Pedro), principalmente do Dr. Gonçalo Curveira-Santos, que me guiou durante todo o processo.

Após esse breve resumo do caminho que me levou à construção deste trabalho, apresento a dissertação intitulada "Efeito de fatores naturais e antrópicos nos padrões de ocupação de mesocarnívoros em dois grandes remanescentes de mata atlântica do sul da Bahia". O principal objetivo desta pesquisa é compreender como os mesocarnívoros presentes em duas Unidades de Conservação no extremo sul da Bahia estão ocupando estas reservas e quais os fatores que estão influenciando a ocorrência desses animais. Visto que o extremo sul da Bahia conta com um longo histórico de ocupação humana e junto com ele, impactos antrópicos como a caça, degradação e perda de habitat, presumi que os mesocarnívoros sofressem com essas perturbações, se tornando menos frequentes em trechos de floresta mais impactados. Em contrapartida, as áreas de estudo contam com uma proteção legal conferida pelo sistema de Unidades de Conservação (SNUC, Lei Nº 9.985, de 18 de julho de 2000.), sendo remanescentes de Mata Atlântica com extensões consideráveis (a RPPN Estação Veracel com cerca de 6 mil hectares e o Parque Nacional do Pau Brasil com cerca de 19 mil hectares), principalmente se tratando do nordeste brasileiro.

Para investigar fatores que interferem na ocorrência dos mesocarnívoros, utilizei um modelo hierárquico de ocupação para a comunidade. Esse modelo é caracterizado por ter um ou mais níveis, um descrevendo o processo observacional (detectabilidade) e outro descrevendo o processo ecológico (probabilidade de ocupação). Além disso, também pode ser usado para avaliar as condições ambientais de um local com a presença de determinadas espécies, o que é fundamental para informar ações de conservação. Considerando que o modelo básico de ocupação tenha como pressuposto que a população seja fechada, ou seja, não são observados natalidade, mortalidade ou migrações, esse modelo não é adequado para estudos de longa duração, como é o caso desse trabalho. Nesses casos, se a intenção da pesquisa for compreender o uso do habitat a partir de modelos de ocupação, uma opção é fazer um "stack" dos dados, em que o mesmo sítio, em tempos diferentes, é considerado uma unidade amostral independente (Mackenzie et al., 2017). Apesar de poder tratar a ocupação de cada espécie isoladamente, optei por utilizar uma abordagem de comunidade ("multi-species"). Este modelo estima a ocupação e detecção para cada espécie e utiliza essas informações como

unidades para calcular métricas em nível de comunidade, como a riqueza, além de reconhecer a variabilidade na distribuição das espécies em uma área (Broms et al. 2015; Dorazio et al. 2006). Essa estrutura também acomoda diferentes respostas das espécies às covariáveis ambientais ao supor que a comunidade é composta por espécies que respondem ao ambiente de forma similar.

II. ARTIGO

Effect of natural and anthropogenic factors on mesocarnivore occupancy patterns in two large remnants from southern Bahia Atlantic Forest

Abstract

Mesocarnivores exhibit diverse responses to natural fluctuations and can provide valuables insights about ecological disturbances. While they may thrive in the absence of top predators, they are also vulnerable to habitat degradation and direct hunting. Utilizing hierarchical community occupancy models and camera-trap data, we assessed mesocarnivore richness, detectability and occupancy in two protected areas within the Atlantic Forest of northeastern Brazil. A total of 10 mesocarnivore species were recorded: seven in RPPN Estação Veracel and nine in Pau Brasil National Park. Cerdocyon thous exhibited the highest detection probability, while Nasua nasua had the highest occupancy probability. In general, species occupancy tended to be low and variable along the time. Camera traps positioned on trails and roads were effective for detecting C. thous and Leopardus spp., whereas N. nasua and Eira barbara were more elusive. N. nasua preferred areas with larger basal area, while C. thous tended to avoid such areas, with slope having no significant effect. Anthropogenic factors like proximity to roads and park boundaries influenced mesocarnivore habitat preferences. Didelphis aurita preferred areas distant from roads, while C. thous showed a preference. Leopardus spp. and N. nasua tended to use areas near protected area boundaries. Despite the rich mesocarnivore diversity in both areas, the low average occupancy suggests barriers hindering populations from reaching higher levels. Anthropogenic factors appear to increase site occupancy by some species, highlighting the complex interplay between human activities and wildlife dynamics in these ecosystems.

Key words: carnivores, community occupancy model, habitat use, tropical forest, protected area.

Introduction

Species diversity is intricately linked to characteristics of the natural environment, with factors such as climate, topography, hydrography, vegetation, and structural heterogeneity shaping both the physical and biological landscape (Srivathsa et al., 2019; da Silva et al., 2018). While natural variation contributes significantly to these dynamics, human activities have caused expressive alterations to ecosystems (Dirzo et al., 2014; Foley et al., 2005), leading to ecological consequences, such as changes in resource availability, species distribution and interspecific interactions (Liu et al., 2007). In many cases, anthropogenic influence can exert a more pronounced impact on populations and community dynamics (e.g. changes in species richness, evenness, and trophic structure) than the natural environment conditions (Buij et al., 2007; Nagy-reis et al., 2017).

Wild mammals have been severely affected by human activities, primarily through overexploitation, and habitat loss and degradation, which pose significant threats to their survival (Galetti et al., 2021). These impacts are particularly evident in tropical forest regions (Dirzo et al., 2014), known for their high diversity of species, including those less adapted to open areas. The conversion of natural habitats into alternative land uses restricts the space available for medium and large mammals, forcing some species to rely on larger forest remnants to persist (Canale et al., 2012; Rios et al., 2022). Moreover, unprotected areas exhibit lower mammal richness if compared to protected remnants of equivalent size, emphasizing the crucial role of safeguarding these fragments, mainly the extensive ones, to maintain the diversity of this group of animals (Magioli et al., 2021; Paolino, 2021). However, even these extensive forest remnants with legal protection face challenges due to human pressures, which pose threats to their integrity and resident wildlife (Bruner et al., 2001; Grelle et al., 2021).

The Atlantic Forest, one of the world's most threatened hotspots (Mittermeier, 2018) located in the Brazilian coast, faces significant challenges in maintaining large protected areas. Indeed, most of the Atlantic Forest remnants are smaller than 50 ha, and only 13% of the area within this biome is maintained as protected areas (SOS Mata Atlântica, 2023). The Atlantic Forest faces an alarming state due to significant reductions in its original vegetation cover, the prevalence of small and isolated remnants, and the local extinction of species, as the jaguar,

resulting from a long history of hunting (Bogoni et al., 2019). Mammal defaunation (accelerated and drastic decline of animal species) occurs is most fragments of the Atlantic Forest (Rios et al., 2022), being the large carnivores the first to disappear (Cardillo et al., 2004; Galetti et al., 2021), triggering changes in entire species assemblages (Pires & Galetti, 2023).

One of the consequences of the reduction or extinction of large carnivore populations is the initiation of effects that propagate through trophic cascades to lower trophic levels, known as top-down effects, such as the mesopredator release (Crooks & Soule, 1999). This release involves the expansion of density, distribution, or changes in the behavior of mesocarnivores (i.e. predators weighing less than 15 kg and occupying an intermediate position in the trophic web) (Brashares et al., 2010; Prugh et al., 2009; Roemer et al., 2009). In the absence of top predators, mesopredator densities are mainly controlled by lower trophic levels (bottom-up effects), such as prey density (Ritchie & Johnson, 2009), and intraguild interactions (Palacios et al., 2012; Sollmann et al., 2012). Furthermore, mesocarnivores show varied responses to intrinsic characteristics such as the presence of water resources, vegetation type, topography, proximity to roads, hunting and domestic dogs (Goulart et al., 2009; Massara et al., 2018; Nagy-Reis et al., 2017; Sévêque et al., 2020; Zapata-Ríos & Branch, 2018). In fragmented landscapes, despite being negatively affected by anthropogenic disturbances, mesopredators can benefit from the availability of prey or foraging opportunities outside forest remnants, allowing them to increase their population densities in the absence of top-down control (Pires & Galetti, 2023).

Occupancy models (sensu Mackenzie et al., 2002) have been increasingly used to understand how the occurrence of species is influenced by both natural and anthropic factors, while accounting for imperfect detection in the observational process (i.e. false absences). Despite widespread interest in understanding species-habitat relationships and assemblage patterns, occupancy is rarely modeled under a community approach (White et al., 2019). These models are capable of correcting biases resulting from imperfect detection, allowing for a more accurate understanding of single species distribution and habitat use within the community (Dorazio & Royle, 2005; Kéry & Schmidt, 2008). Moreover, this approach enables the estimation of species richness and the identification of sites that exhibit high diversity or are particularly important for the community (Guillera-Arroita, 2017). By employing community occupancy models, it is possible to gain a comprehensive understanding of the ecological

dynamics and conservation needs of a group, such as the mesocarnivores, contributing to more effective management and conservation strategies (Curveira-Santos et al., 2021).

The primary objective of this study was to estimate the occupancy and explore the habitat utilization patterns of the mesocarnivore community in two protected areas in the northeast Atlantic Forest: the Pau Brasil National Park and the RPPN (Portuguese acronym for Private Natural Heritage Reserve) Estação Veracel. Combining camera-trapping surveys and hierarchical community occupancy models, we aim to estimate species richness at landscape (protected area) scales, as well as examine the influence of fine-scale environmental and anthropogenic factors on species-specific occupancy patterns. In general, we expect that the occupancy by the mesocarnivores species will be positively impacted by natural factors: (i) Increasing basal area of trees and (ii) low slope - as a larger basal area of trees indicates a more mature and preserved forest, while a low slope suggests flatter terrain that is easier for animal movement - and negatively impacted by anthropic factors: (iii) proximity to protected area limit and (iv) to roads - as proximity to the boundary of the protected area indicates less protection for animals and increased vulnerability to humans and the proximity to roads can also increase the incidence of collisions, noise disturbance, and facilitate the entry of hunters. Since trails and roads can affect the movement of mesocarnivores, we incorporated camera trap location (in roads, trails or forest) as covariates to model species detectability. Given the heterogeneous nature of the mesocarnivore community, we anticipate that species will exhibit varied responses based on their reliance on forest habitats and their susceptibility to human disturbances.

Materials and Methods

Study Areas

The study was conducted in two protected areas (PA): the Pau Brasil National Park (Pau Brasil NP) and RPPN Estação Veracel (RPPN Veracel), both located in the Atlantic Forest, in the southernmost region of Bahia state, Brazil (Fig. 1). These two PAs are core areas of the Central Atlantic Forest Corridor, which, along with other PAs and forest fragments, are intend to form a set of functionally connected remnants from the north of Espírito Santo to the south of Bahia state (MMA, 2006).

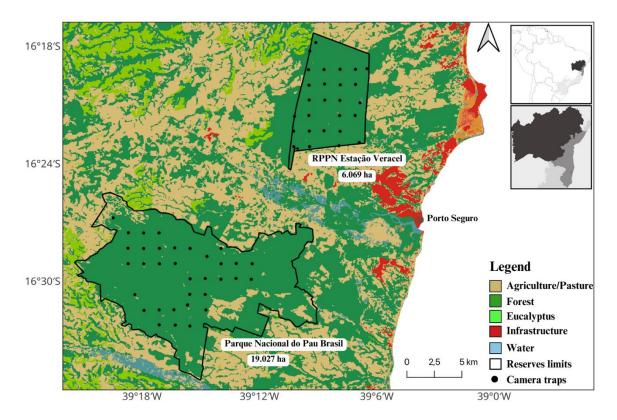


Fig. 1 Map with the camera trap surveyed areas used to model mesocarnivores habitat use in the southern Bahia Atlantic Forest. Protected areas: Pau Brasil National Park (Pau Brasil NP) and Private Reserve of Natural Heritage Estação Veracel (RPPN Veracel).

Pau Brasil NP is a strictly protected PA (Brasil, 2000) covering an area of 19.027 ha. It was established in 1999 and is entirely located in the municipality of Porto Seguro. This PA contains mature vegetation, "muçununga" forests, and permanently or seasonally flooded forests, and it is considered an important refuge for a population of the threatened Brazilwood (Paubrasilia echinata Lam.) timber species (ICMBio, 2016). The park includes unpaved roads restricted to guided tourism, research, and monitoring purposes. RPPN Veracel is a sustainable use PA (Brasil, 2000) and is considered the largest RPPN in the Northeast region of Brazil, covering 6.069 ha. It was created in 1994 by the company Veracel Celulose SA and is located within the municipalities of Santa Cruz Cabrália and Porto Seguro. The reserve contains primary and secondary forests in different successional stages (Veracel, 2016). The reserve has an internal unpaved road for unrestricted circulation and other roads with restricted access for research and monitoring purposes.

The southernmost region of Bahia has a super-humid climate, with regular rainfall distribution throughout the year, ranging from 1,400 mm to 1,800 mm of precipitation. The rainiest quarter in this region is April, May, and June (CPRM, 2002). Like other locations in the

southernmost region of Bahia, the rainfall determines the river regime (intermittent or perennial) present in RPPN Veracel and Pau Brasil NP, with the drainage of these PAs represented by streams, rivers, and lagoons (Veracel, 2016). Due to its similar phytophysiognomy with the Amazon Rainforest, the region is known as Hileia Baiana, located on a "tabuleiros" coast. The land is predominantly flat with altitude ranging from 10 to 100 m.a.s.l., which can be explained by drainage erosive processes, with the presence of cliffs and valleys along the main rivers (CPRM, 2002).

The PAs are separated by approximately 10 km (in a straight line), and there is a collaborative project between Veracel Celulose SA and public and private entities to create a vegetation corridor connecting the two PAs. Both PAs have a history of intense timber extraction and hunting, which are still ongoing despite the current level of protection and enforcement efforts. Despite National Parks having stricter legal protection than RPPNs, the RPPN Estação Veracel is a protected area that undergoes intense surveillance, potentially even more intense than in Pau Brasil NP. Even with the efforts, the jaguar (*Panthera onca*), a keystone species in the ecosystems it inhabits, is already considered locally extinct in both areas, with only the puma (*Puma concolor*) remaining.

Mesocarnivores surveys

The collection of mesocarnivore records was conducted using camera traps, a common and recommended method for studies involving medium-sized mammals (Tobler et al., 2008). Sampling took place between the years 2018 and 2021, by researchers associated with ICMBio/CENAP and Instituto Pró-Carnívoros, during 3-months campaigns: three between August and October (2018, 2019, 2021) and one between April and June (2019).

For this study, we used data collected at 34 sampling stations in Pau Brasil NP and 27 sampling stations in RPPN Veracel (figure 1). The stations were placed in grids with a minimum spacing of 1.4 km, following the TEAM Protocol (Team, 2011). The stations were located on dirt roads, trails, or on the forest (i.e. outside roads and trails), installed at approximately 40 cm above the ground. Bushnell camera traps (Bushnell Trophy Cam HD, Model 119876) were programmed to take three sequential photos with a time interval of 0.6 seconds between shot sequences, operating 24 hours a day. At the end of the four campaigns, each sampling site was sampled for an average of 223 days, ranging from 13 to 310 days.

To organize and help with the identification of mammal photos, we used the Wild.ID 1.0 program (https://github.com/ConservationInternational/Wild.ID). For data organization, we used the package camtrapR (Niedballa et al., 2016). We consulted specialized literature to identify the medium and large-sized mammal species (Emmons & Feer, 1997; Oliveira & Cassaro, 2006). Species nomenclature followed the list of the Brazilian Society of Mammalogy (Abreu et al. 2023). Records of the same species at the same station within 1 hour were removed to avoid data dependency (Goulart et al., 2009).

Natural and anthropogenic covariates

We defined four covariates, grouped as natural or anthropogenic, to explain the occupancy of mesocarnivores (see Appendix 1). Natural covariates consisted in: (i) tree basal area (BASAL) and (ii) slope (SLOPE). Anthropogenic covariates consisted in: (iii) distance to PA limit (LIMIT) and (iv) to internal roads (ROAD). For detectability, we used (v) camera location (roads and trails or forest matrix) as covariable (CAMPLACE).

The information about tree basal area were collected in the field. At each sampling station, two plots measuring 50 x 3 m were set up, forming a cross shape (see Appendix 2). Within this cross area, the number of trees with a circumference at breast height (CBH) > 15 cm was recorded. These CBH values were transformed into basal area and summed. The Euclidian distance to roads and PA limit were collected using Geographic Information System (GIS) software (QGIS 3.28.3.). Slope values were extracted from a 30×30 m of resolution digital elevation model (DEM), the Shuttle Radar Topography Mission (USGS, 2003), downloaded from U.S. Geological Survey (https://earthexplorer.usgs.gov/).

Community occupancy model

To test the effect of anthropogenic and natural covariates on mesocarnivore occupancy, we adopted the hierarchical formulation of the "stacked" single-season community occupancy model. This model allows us to estimate the occupancy probabilities spatially and temporally because of the "stacked" way to incorporate the seasons, besides include detection in a species-specific and community levels (Dorazio & Royle, 2005). This method allows the inclusion of multiple seasons in a single-season type model by treating each season-site combination as a separate site, and then include season as a site covariate. Despite losing the ability to further distinguish the dynamics mechanisms driving the observed data (i.e.

colonization and extinction), thus assuming site temporal independence, the resultant model eases the estimation of model parameters when analysing sparse datasets.

We used the camtrapR package in R (R Core Team, 2022) with the function detectionHistory to create a detection history (1=detected; 0=undetected) for each species in a given 3-day sampling occasion at each site-season combination. Each season had 30 occasions corresponding to 3 days of sampling. We consider the true occupancy (z) of a species (k) at a site (i) as a Bernoulli random variable governed by the probability of occupancy (\psi ki). In our study, we define occupancy probability as the use of a site (i) by the species during the entire sampling period (i.e. 3-month seasons). The observations (yik) of the detections follow a Binomial distribution governed by the detectability (pki) conditioned on the true occupancy state of each species (zki), on the effort (camera traps days working) of each specie at each site (Kki). For inferences about species richness (Wki), we augmented the observation data with all-zero observations (Dorazio & Royle, 2005) of hypothetical species up to total of 11 mesocarnivores that may occur in the study region following the complete list of mammals in the study area (Magioli et al., 2022). The model can be described as:

```
\begin{split} z_{ki} \sim Bernoulli \; (\psi_{ki}) - Latent \; state \\ y_{ijk} \sim Binomial \; (z_{ki} * \; p_{kij}, K_{ki}) - Observation \; process \\ w_{ki} \sim Bernoulli \; (\Omega[i]) - Superpopulation \; process \; (Data \; argumentation) \end{split}
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The specific models for each species in the community are connected through indexing of parameters and latent variables by species, assuming that species-specific parameters are random effects originating from a common underlying distribution governed by community hyperparameters (Kéry & Royle, 2021). These hyperparameters define both the mean community response and the variation among species in relation to a covariate. This approach allows us to account for the interspecific heterogeneity underlying the observed community-level response (Guillera-Arroita, 2017; Iknayan et al., 2014).

In an initial stage (analysis I), we estimated species–specific occupancy and detection probabilities as random effects with area and season specific intercepts $(\beta 0,k,AREA_SEASON[i])$. This allowed us to specifically estimate differences in baseline occupancy across protected areas and seasons contexts and among species, as follows:

 $logit(\psi_{ki}) = \beta \mathbf{0}_{k,\,AREA~SEASON[i]}$ - Ecological process model for occupancy

 $logit(p_{ki}) = \alpha O_{k, AREA \ SEASON[i]}$ - Observation process model for detection probability

We opted not to include covariates in this model due to the imprecise information derived from certain species with limited data, affecting the reliability of the parameters.

In a following stage (analysis II), we select the species which had more precise parameters of occupancy and detectability (*Cerdocyon thous, Didelphis aurita, Eira barabara, Leopardus spp.* and *Nasua nasua*) to construct a model including covariates in the occupancy: tree basal area (BASAL), distance to the road (ROAD), distance to the PA limit (LIMIT), and slope (SLOPE). We also modeled detectability as a function of the location where the camera trap was installed (CAMPLACE), using the forest matrix as a baseline to see the effect of trails and roads. We standardized all covariates before analysis (Pollock et al., 2014), setting their mean values to 0 and standard deviations to 1, except for the CAMPLACE which was used as a categorical covariate. All covariates were tested for correlation using Pearson's correlation test. No high correlation values (> 0.7) were found among the pairs of covariates (see Appendix 1), therefore all covariates were used in the analysis.

We followed the protocol of Zipkin, DeWan & Royle (2009) of fitting a single global model with a limited number of covariates for which there was a strong a priori justification. Considering non-informative prior information, we specified four parameters of the model (occupancy probability and detectability) as a logit-linear function of site covariates:

$$\begin{split} logit(\psi_{ki1}) = \beta 0_{k,\,AREA_SEASON[i]} + \beta 1_{k,\,BASAL[i]} + \beta 3_{k,\,LIMIT[i]} + \beta 4_{k,\,ROAD[i]} + \beta 5_{k,\,SLOPE[i]} - \\ Ecological \,process \,model \,\,for \,\,occupancy \end{split}$$

$$logit(p_{ki}) = \alpha 0_{k,\,AREA_SEASON[i]} + \alpha 1_{k,\,CAMPLACE[i]} \text{- Observation process model for detection}$$
 probability

We analyzed the model using Markov Chain Monte Carlo (MCMC) simulations in JAGS, implemented through the jagsUI package (version 1.5.2) in R (R Core Team, 2022). We ran three chains with 50,000 iterations each, discarding the first 10,000 as burn-in and retaining every 10th iteration. We verified the convergence of the chains through visual inspection of trace plots and used the Gelman–Rubin statistic, with values <1.1 indicating convergence (Gelman et al., 2013). We evaluated model fit by estimating the discrepancy between the deviance residuals of the observed and simulated data from the fitted model (Brooms et al., 2016). We obtained a Bayesian p-value of 0.495 for the first model and 0.503 for the second

model, indicating that both adequately fit to the data. To assess the influence of covariates on occupancy and detection models, we examined the β coefficients and their corresponding 95% Bayesian credibility intervals (BCIs). Strong associations were identified by assessing non-zero overlap in credibility intervals and moderated effects was defined as a value of f factor > 0.9.

Results

Throughout the entire survey periods, we detected 10 species of wild mesocarnivores (Table 1). For the analysis, *Leopardus guttulus* and *Leopardus wiedii* were grouped as an ecospecies (*Leopardus* spp.), effectively totaling 9 species. We obtained a total of 1267 independent records of mesocarnivores: 764 in Pau Brasil NP and 503 in RPPN Veracel. We detected almost all species of mesocarnivores expected to occur in the region (see Appendix 3), resulting in an estimated true richness of 10 species. The true richness within Pau Brasil National Park was estimated at 9 species, while RPPN Veracel harbored 7 species. Two species were only detected in Pau Brasil NP: *Conepatus semistriatus* and *Galictis cuja*, while the remaining seven species were present in both areas. The ocelot (*Leopardus pardalis*), a species expected to occur in the study area, was not recorded (see Appendix 3).

Table 1. Number of independent records of the ten species of mesocarnivores detected in the study area. Protected areas: Pau Brasil National Park (Pau Brasil NP) and Private Reserve of Natural Heritage Estação Veracel (RPPN Veracel). *Leopardus* sp. correspond to unidentified records, which can be either *L. guttulus* or *L. wiedii*.

Scientific name	Common name	Pau Brasil NP	RPPN Veracel
Cerdocyon thous	Crab-eating fox	335	120
Nasua nasua	South American coati	142	224
Didelphis aurita	Big-eared opossum	195	192
Eira barbara	Tayra	59	36
Leopardus wiedii	Margay	17	16
Leopardus spp.		11	5
Herpailurus yagouaroundi	Jaguarundi	3	2
Leopardus guttulus	Southern tiger cat	3	2
Procyon cancrivorus	Crab-eating Raccoon	2	3
Conepatus semistriatus	Triped hog-nosed skunk	1	0

Galictis cuja	Lesser grison	1	0
Total		769	600

In Overall, there was variability in species detectability across seasons (ranging from 0.018 to 0.502), with consistently low values observed for most species (see Appendix 4). *Cerdocyon thous* exhibited the highest detection rates in the initial three seasons for both areas, and in the final season, it displayed the highest detection in Pau Brasil NP, surpassing a threshold of 0.2. On the other hand, *C. semistriatus*, *G. cuja*, *P. cancrivorus*, and *H. yagouarundi* consistently maintained mean detection levels below 0.1 throughout all seasons for both areas.

The mean occupancy probability of all species varied between seasons and area. *Nasua nasua* had the highest occupancy probability in the RPPN Veracel, exceeding 0.75 in all seasons. In the Pau Brasil NP, *N. nasua* had the highest occupancy probability (>0.75) in the season 1 and 4, and *D. aurita* showed the highest occupancy probability (>0.75) in the season 2 and 3. The lowest probabilities in all seasons were observed in *G. cuja*, *C. semistriatus*, *H. yagouarundi*, and *C. thous* (Fig. 2).

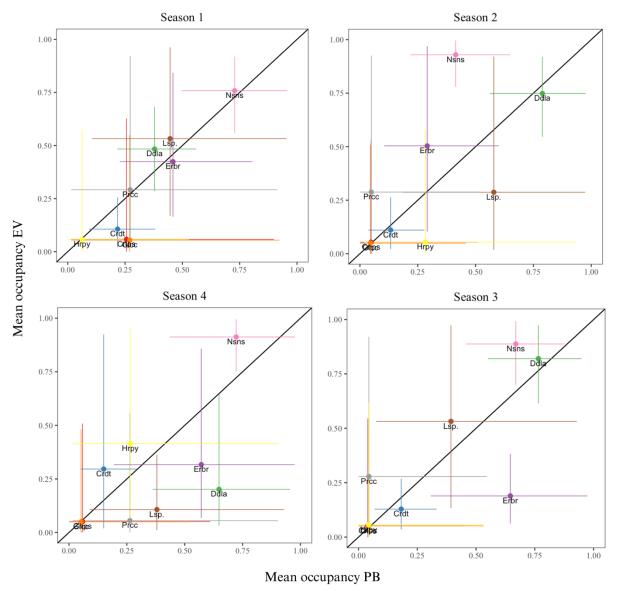


Fig. 2 Species-specific occupancy probability in the four seasons in the two study areas (EV= RPPN Veracel; PB= Pau Brasil NP). Points situated above the diagonal line indicate greater species occupancy in the EV (represented on the y-axis), while points below the diagonal line indicate higher species occupancy in the PB (represented on the x-axis). The error bars depict 95% Bayesian credible intervals. Species codes: crdt-*Cerdocyon thous*; cnps- *Conepatus semistriatus*; ddla-*Didelphis aurita*; erbr- *Eira Barbara*; glcc-*Galictis cuja*; lsp-*Leopardus* spp.; nsns-*Nasua nasua*; prcc-*Procyon cancrivorus*; pmyg- *Herpailurus yagouarundi*.

In analysis II, all species, except *D. aurita*, had their detectability strongly associated with the placement of camera traps on roads or trails (Fig. 3). *Nasua nasua* and *E. barbara* responded negatively [β =-0.381 (range: -0.684 to -0.076) and β =-0.982 (range: -1.774 to -0.190), respectively], while *C. thous* and *Leopardus sp.* responded positively [β =3.776 (range: 2.885 to 4.722) and β =0.185 (range: -0.132 to 0.490), respectively].

Most species had their occupancy related to some site-scale covariate, despite no clear response at the community-level to any of the covariates, as noted from the diffuse hyperparameter posterior distributions. At the species level, *C. thous* had a strong negative response to basal area (β =-0.97, (range: -1.852 to -0.193)) and moderate negative response to the distance to the road (β =-0.572, (range: -1.328 to 0.045)). *Didelphis aurita* had a moderate positive response to the distance from roads (β =0.405, (range: -0.044 to 0.890)). *Leopardus* spp. only responded to the distance from the PA limit (β =-0.512, (range: -1.449 to 0.049)), with a moderate negative relationship. *Nasua nasua* responded to basal area, showing a moderate positive relationship (β =0.422, (range: 1.038 to -0.118)) and a moderate negative response to distance to PA limit (β =-0.282, (range: -0.703 to 0.094)). None of the species had their occupancy substantially influenced by the terrain slope. *Eira barbara* occupancy did not respond to any of the covariates.

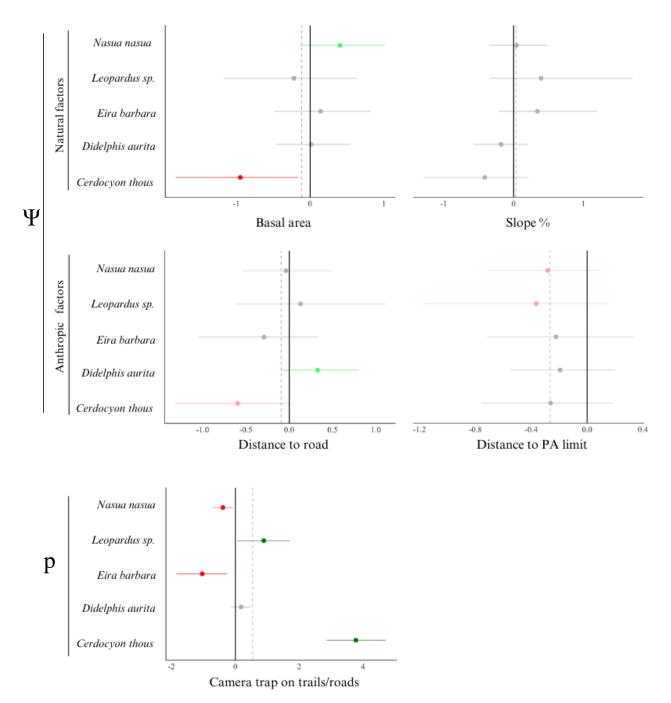


Fig. 3 Effect size of site-scale covariates on occupancy (Ψ) and detectability (p) probabilities for the five studied species with respect to covariates. Points represent the mean, and the horizontal bars represent the standard deviation. Dark red and dark green indicates a strong negative and positive effects, while light red and light green indicates a moderated negative and positive effects, respectively. Grey denotes no effect. Solid black vertical line indicates the intercept, and grey dashed vertical line depict the mean percentile of the community level.

Discussion

The Pau Brasil NP appear to exhibit a higher species richness compared to RPPN Veracel, although all species are expected to occur at both areas. However, detection probabilities for the nine species studied were low across both locations, influencing the accuracy of occupancy probability values. The use of camera traps along trails and roads or within the forest influenced detectability, proving advantageous for *Cerdocyon thous* and *Leopardus sp.*, but detrimental for *Nasua nasua* and *Eira barbara*. At the community level, covariates had no significant effect on occupancy probabilities, highlighting the complex and heterogeneity of the mesocarnivore assemblage. Conversely, at the individual species level, responses to specific covariates were observed, except for slope, which had no apparent impact on species occupancy. *Nasua nasua* occupancy was positively associated with higher basal area, while *C. thous* appeared to benefit from its reduction. Increasing distance to roads was associated with increased occupancy by *D. aurita* and decreased occupancy by *C. thous*. There was a general trend for species to prevail at the periphery of reserves, as evidenced by the higher occupancy rates of *Leopardus spp. and N. nasua* at the reserve limit.

Conepatus semistriatus, G. cuja, H. yagouarundi, and P. cancrivorus were the species with the fewest records, each having less than five observations during the four survey campaigns, generating inaccurate detection and occupancy probability values. This result is not unexpected since these species, except P. cancrivorus, have a low number of records in other camera trap surveys in Atlantic Forest remnants (da Silva et al., 2018; Ferreguetti et al., 2023; Hatakeyama, 2015). For P. cancrivorus, a species that uses swampy areas and arboreal stratum for resting and foraging (Cheida et al., 2013), it is possible that specific sampling is necessary for increasing detection in the study area, with a strategic placement of camera traps in wetlands and in the canopy. The presence of C. semistriatus in Pau Brasil NP, a species typically found in open areas like the Cerrado and Caatinga biomes (Kasper et al., 2009), could be related to the degree of deforestation within the study region. Its detection in grasslands within the protected area is consistent with the hypothesis that habitat alterations from expanding agricultural lands are pushing C. semistriatus into forested regions, including the Atlantic Forest, as observed by Magioli et al. (2020) and Silva-Júnior (2007). The sparce records of some species also suggests that differences in species richness between the protected areas should be interpreted cautiously. We cannot exclude the hypothesis that higher

richness in Pau Brasil NP may stem from its larger area and increased heterogeneity within the reserve due to anthropogenic alterations. However, the species contributing to Pau Brasil NP's richness (*C. semistriatus* and *G. cuja*) had exceedingly rare records and very low detectability. Furthermore, the presence of *C. semistriatus*, a species not typically associated with the Atlantic forest, likely indicates human disturbance.

Overall detection and occupancy probabilities

The greatest detection probability in our study was reported for *C. thous*, with a higher value in the Pau Brasil NP than in RPPN Veracel, being also higher than in other Atlantic Forest fragments (0.23, Dechner et al., 2018; 0.4 Ferreguetti et al., 2023). The other species showed similar detection probability in the two reserves, which are in general lower than values found in larger protected areas of the Atlantic Forest, such as Iguacu National Park and Vale Natural Reserve (da Silva et al., 2018; Wolff et al., 2019), yet higher than values found in Atlantic Forest protected areas immersed in eucalyptus and rubber tree plantations (Dechner et al., 2018; Hatakeyama, 2015). Detectability can be influenced by camera placement, such as observed in our study, and this might explain part of our results, such as the great detectability of *C. thous*. Additionally, detectability is often correlated with population abundance (Burns et al., 2019). In this sense, despite the abundance of carnivores being relatively lower than other trophic groups (Newbold et al., 2020), the low detectability when compared to other studies may signal a population decline within the studied areas (Burns et al., 2019).

Camera traps on trails and roads have been particularly beneficial for detecting species favored by open routes for their movement and foraging (Di Bitteti et al., 2010; Dillon & Kelly, 2007; Monteiro-Alves et al., 2019)., such as *C. thous* and *Leopardus* spp. in our study. This preference is also seen in other felids, as they often choose to use roads or trails over moving through dense forest, a behavior shared by *Leopardus pardalis* in other fragments of Atlantic Forest (Di Bitetti et al., 2006; Goulart et al., 2009). In contrast, *N. nasua* and *E. barbara*, which are predominantly forest dwellers, were less detectable in roads and trails, which is a similar result to other fragments of Atlantic Forest (De Almeida, 2021; Gompper & Decker, 1998; Lima et al., 2020; Presley, 2000). Given the variability of responses, this result reinforces the importance of positioning the camera trap in different locations in studies searching for mammal assemblage data.

At the protected area scale, the occupancy probability found for *C. thous*, *D. aurita*, *E. barbara*, *Leopardus* spp., and *N. nasua* were mostly close to or above the common values reported in literature for Atlantic Forest fragments (see Appendix 5). Among the five taxa, *N. nasua* proved to be the most spread in both areas, displaying the higher occupancy probability. This finding is consistent with other Atlantic Forest remnants, where the South American coati was found to have the highest occupancy probability among mesocarnivores, being an omnivorous species adapted to fragmented forests (da Silva et al., 2018; Dechner et al., 2018; Hatakeyama, 2015).

Influence of natural and anthropogenic factors on site occupancy

Natural factors generated stronger but fewer responses in site occupancy by mesocarnivores, which may result from the relatively low environmental variability in the study areas. Regarding harboring forests with distinct disturbance histories, the protected areas have a relatively flat terrain (excepting for valleys associated to the water drainage) and little edaphic variation, and no recent logging activity. The increase of basal area, indicative of wellpreserved forests featuring large trees, was only important for N. nasua habitat use. This aligns with their preference for forested environments, as identified by Michalski & Peres (2007) and Dutra et al. (2023), and together with results of high overall occupancy in the study areas, suggests that N. nasua permanence in forest fragments may be better explained by a release of intraguild interactions (predation and/or competition) than by adaptation to disturbed areas. In contrast, the C. thous appears to benefit from the reduction in basal area, which is expected since this is an habitat generalist species, thrives in more open and disturbed environments (Beisiegel et l., 2013; De Almeida, 2021; Lucherini, 2015). None of the five species exhibited a response to terrain slope, a response potentially attributable to the intricate interactions between terrain and resource availability. While flatter terrains tend to have a higher abundance of prey (Oliveira et al., 2010), steeper terrains, which in the study area are the valleys, are associated with the presence of water, another essential resource. Alternatively, the importance of slope for the occupation of carnivores may be associated with a more rugged topography, as it has been seen that this is an important factor for the group in mountainous regions (Morell et al., 2021; Nisi et al., 2022).

Anthropogenic factors appear guide more variation in habitat use by mesocarnivores. The high occupancy of *C. thous* in sites near dirt roads was expected given the species is adapted to disturbed open areas (Brady, 1979; De Almeida, 2021; Harmsen et al., 2009; Monteiro-

Alves et al., 2019). The opposite response of *D. aurita*, which is a species particularly vulnerable to hunting (Castilho et al., 2019), could be attributed to the use of these routes by humans and relatively ease of entry for hunters within PAs (Cáceres & Monteiro-Filho, 2007; Laurance et al., 2014). Differently than our initial expectation, increasing distance to the protected area limit decreased the occupancy by *Leopardus* spp. and *N. nasua*. While sites closer to the protected area limit may be subjected to disturbances, the adjacent lands dominated by eucalyptus, agriculture and pasture can provide habitat for small vertebrates, creating opportunities for mesocarnivore foraging near forest edges (Di Bitetti et al., 2010; Henriques et al., 2006; Paglia et al., 1995; Vieira, 2003; Lyra-Jorge et al., 2008; Massara et al., 2018; Rinaldi et al., 2015). Even *N. nasua*, a species that typically prefers more preserved forest areas, can benefit from proximity to adjacent anthropogenic areas (Eisenberg and Redford, 1999).

The few strong responses to natural and anthropogenic factors and the low overall occupancy of the study areas indicate that non-investigated factors may be influencing the mesocarnivore assemblages, such as food availability and/or intra-guild interactions (Di Bitetti et al., 2010; Oliveira et al., 2014). The absence of *Leopardus pardalis*, a strong predator within the mesocarnivores (Oliveira et al., 2010; Massara et al., 2016), was unexpected for the study areas. This may influence the occupancy by the community as well as interactions among the remaining species, which should be evaluated for better understanding of mesocarnivore assembly.

Conclusions and conservation implications

Our research conducted within the Pau Brasil National Park and RPPN Estação Veracel has yielded insights into mesocarnivore species richness, occupancy patterns, and detection probabilities within these two protected areas in the Atlantic Forest. Our findings provide evidence that these protected areas support diverse mesocarnivore assemblages, as evidenced by the record of almost all mesocarnivore species documented in the region, but suggests that these areas are not free from anthropogenic impacts.

Despite the conservation efforts in the protected areas, our research has revealed a significant challenge - the low detectability of most mesocarnivore species. This poses a considerable obstacle to understanding their ecological dynamics and difficult the identification of

fluctuations in population size that can compromise the long-term survival of these animals. The strategic placement of camera traps has proven indispensable in enhancing detectability. Camera traps along trails and roads yielded especially positive results for observing species like *C. thous* and *Leopardus* spp., making it a recommended best practice for future wildlife monitoring in similar habitats. Deploying camera traps within the forest enhanced detectability for *N. nasua* and *E. barbara*. Additionally, sampling in the upper arboreal strata of the forest could facilitate recording not only of these species but also of others, such as *P. cancrivorus* and *D. aurita* (Kierulff et al., 2014).

Natural and anthropogenic factors have been identified as influential in shaping the probability of occupancy for some species, underscoring their importance in the management of these protected areas. Interestingly, only one mesocarnivore species, *N. nasua*, appeared to benefit from stretches of more preserved forests (i.e. stretches with higher tree basal areas). In contrast, species like *Leopardus* spp. and *C. thous* seem to utilize areas adjacent to protected zones or roads, suggesting their resilience and reduced dependence on pristine forest environments. This finding, coupled with the absence of *Panthera onca* and *Leopardus pardalis* and the presence of a species typically associated with open areas, *C. semistriatus*, indicate that Pau Brasil NP and RPPN Veracel have been experiencing anthropogenic disturbances responsible for restructuring mesocarnivores assemblages despite the maintenance of old growth forested areas.

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II. MATERIAL SUPLEMENTAR

Appendix 1. Information about the four covariates included in the occupancy probability for *Cerdocyon thous*, *Didelphis aurita*, *Eira barbara*, *Leopardus* spp. and *Nasua nasua*.

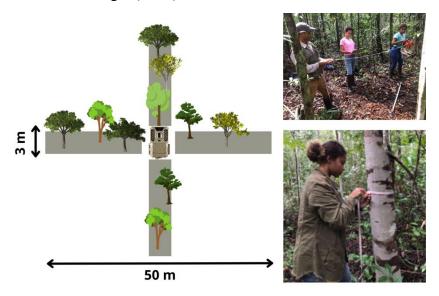
A) Minimum (MIN) and maximum (MAX) values for tree basal area (m2), percentage of slope (%), distance to PA limit (m) and distance to road (m)

Covariates	MIN	MAX
Basal area (m ²)	2838.051	30052.332
Slope %	0.586	42.585
Distance to PA limit (m)	9.799	4814.201
Distance to the nearest		
road (m)	3.254	2474.325

B) Values estimated with Pearson's correlation between the covariates: tree basal area (m2), percentage of slope (%), distance to PA limit (m) and distance to road (m).

	Basal area (m ²)	Slope %	Distance to PA limit (m)	Distance to road (m)
Basal área (m²)	-			
Slope %	-0.046	-		
Distance to PA limit (m)	-0.078	-0.031	-	
Distance to road (m)	0.184	0.028	0.046	-

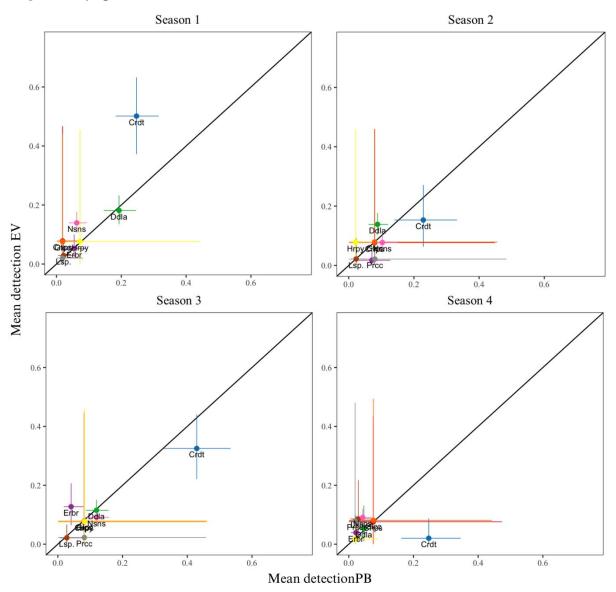
Appendix 2. Schematic drawing representing the basal area collection methodology. At each sampling station, two plots measuring 50 x 3 m were set up, forming a cross shape where the circumference at breast height (CBH) > 15 cm was recorded.



Appendix 3. Species of Order Carnivora and one species of Didelphimorphia known to occur in the RPPN Estação Veracel (RPPN Veracel) and in the Pau Brasil National Park (Pau Brasil NP) – based on Magioli et al. (2022) - and indication of species detected in the present study and considered in the analysis. Species in bold were considered mesocarnivores in this study, and * denotes invasive species.

Tayon	Common name	RPPN Veracel		Pau Brasil NP		Considered
Taxon		Magioli et al. 2022	Present study	Magioli et al. 2022	Present study	in analysis
DIDELPHIMORPHIA						
DIDELPHIDAE						
Didelphis aurita (Wied-Neuwied, 1826)	Black-eared opossum	√	✓	✓	✓	✓
CARNIVORA						
CANIDAE						
Canis lupus familiaris*	Domestic dog	✓	✓	\checkmark	✓	
Cerdocyon thous (Linnaeus, 1766)	Crab-eating fox	\checkmark	✓	✓	✓	✓
Chrysocyon brachyurus (Illiger, 1815)	Maned wolf			✓	\checkmark	
FELIDAE						
Felis catus*	Domestic cat			✓		
Herpailurus yagouaroundi (É. Geoffroy, 1803)	Jaguarundi	√	✓	√	✓	✓
Leopardus guttulus (Schreber, 1775)	Southern tiger cat	✓	✓	✓	✓	✓
Leopardus pardalis (Linnaeus, 1758)	Ocelot	\checkmark				
Leopardus wiedii (Schinz, 1821)	Margay	\checkmark	✓	✓	✓	✓
Panthera onca (Linnaeus, 1758)	Jaguar	✓				
Puma concolor (Linnaeus, 1771)	Puma	✓	✓	✓	✓	
MEPHITIDAE Conepatus semistriatus (Lichtenstein, 1838)	Striped hog-nosed skunk	✓		√	√	✓
MUSTELIDAE						
Eira barbara (Linnaeus, 1758)	Tayra	✓	✓	✓	✓	✓
Galictis cuja (Molina, 1782)	Lesser grison			✓	✓	✓
Lontra longicaudis (Olfers, 1818)	Neotropical otter			✓	✓	
PROCYONIDAE						
Nasua nasua (Linnaeus, 1766)	South American coati	✓	✓	✓	✓	✓
Potos flavus (Schreber, 1774)	Kinkajou		✓		✓	
Procyon cancrivorus (G. Cuvier, 1798)	Crab-eating raccoon	√	√	✓	✓	✓

Appendix 4. Species-specific detection probability in the four seasons in the two study areas (EV= RPPN Estação Veracel; PB= Pau Brasil NP). Points situated above the diagonal line signify greater species occupancy in the EV (represented on the y-axis), while points below the diagonal line indicate higher species occupancy in the PB (represented on the x-axis). The grey error bars depict 95% Bayesian credible intervals. Species codes: crdt-Cerdocyon thous; cnps- Conepatus semistriatus; ddla-Didelphis aurita; erbr- Eira Barbara; glcc-Galictis cuja; lsp-Leopardus spp.; nsns-Nasua nasua; prcc-Procyon cancrivorus; pmyg-Herpailurus yagouarundi.



Appendix 5. Literary review on the frequency of occupation probability found in fragments of Atlantic Forest of the species *Cerdocyon thous*, *Didelphis aurita*, *Eira barbara*, *Leopardus* spp. and *Nasua nasua*. Points are the mean probability occupancy and the grey error bars depict 95% Bayesian credible intervals.

