DRIVERS OF MAMMALIAN COMMUNITIES IN REMNANT FORESTS: A CASE STUDY IN THE ATLANTIC FOREST, SOUTHEASTERN BRAZIL

by

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ABSTRACT

L. Bonjorne de Almeida. Drivers of Mammalian Communities in Remnant Forests: A Case Study in the Atlantic Forest, Southeastern Brazil. 248 pages, 9 tables, 18 figures, 2021.

Humans have modified more than 75% of the Earth's surface, with some regions undergoing more severe modification such as the Atlantic Forest in Brazil which today has only ~12% of its original forest cover remaining. This dissertation investigated how forest amount, landscape context, and anthropogenic factors across the human-dominated Atlantic Forest region of Southeastern Brazil influenced the activity and space use of medium- to large-bodied terrestrial mammals, and by extension the composition and connectivity of mammalian communities. Although species responded differently to landscape and anthropogenic factors, generally 2x2 km landscape units that were <78% forested were less likely to be occupied by forest-dependent frugivores and carnivores than more generalist herbivorous, omnivorous, and insectivorous species. Free-ranging dogs were detected largely independently of people, with both humans and dogs predicted to have a high probability of occurrence across the majority of forest remnants. Although some mammals, such as *Cuniculus paca* and *Dasypus* spp., temporally avoided humans and dogs, other species, such as ocelot and oncilla, shifted their geographic space use to avoid these agents of disturbance. With respect to maintaining community connectivity, only 32% of the key habitats (nodes) in the study region were afforded strict protection from habitat conversion, with nearly one third of the habitat crucial for connectivity remaining at risk of loss to forest conversion. This study indicates that retaining the full complement of medium- to large-mammals in the region likely depends upon retaining and increasing forest amount, connectivity and levels of protection across. A major finding of this study is that a much higher proportion of forest amount (>78%) is needed to ensure persistence of many forest-dependent species, emphasizing the need for reforestation across the highly fragmented Atlantic Forest biome. This has implications for landscape planning should conservation of medium and large-sized mammals be a priority in this region.

Key Words: Atlantic Forest, connectivity, mammals, occupancy, thresholds, conservation

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CHAPTER 1 – BACKGROUND AND INTRODUCTION

Human activities have modified the majority of the Earth's land surface (Vitousek et al. 1997; Ellis and Ramankutty 2008; Ellis et al. 2010; Ellis 2019). The ensuing loss and fragmentation of habitat for wildlife has been, and remains, the main driver of biodiversity loss in the world (Wilcove et al. 1986; Brooks et al. 2002; Pimm et al. 2014; Haddad et al. 2015; Valiente-Banuet et al. 2015). With the human footprint still growing, understanding the function of remnant habitat patches, the role of protected areas, and the adaptability of wildlife to human-dominated landscapes is fundamental for species conservation in the long-term.

Prevailing frameworks for understanding community dynamics in fragmented landscapes extend from island biogeography theory (Diamond 1972; Diamond 1975; Brown 1986; Lomolino and Perault 2001) and metapopulation theory (Levins 1969; Hanski and Gilpin 1991; Hanski 2001; Akçakaya et al. 2007). These theories stimulated considerable attention on the size, arrangement and isolation of islands (or by extension habitat patches), with metapopulation theory adding a focus on connectivity among patches (or subpopulations) as key to community stability in terrestrial systems (Hansson 1991; Hanski 1999). Further developments of both theories added more complexity to the models, considering the rescue effect, and other mechanisms that reduces the isolation and increases immigration to forest patches (i.e., corridors) (Brown and Kodric-brown 1977; Simberloff and Cox 1987; Saunders and Hobbs 1991; Perault and Lomolino 2000) as well as the mainland-island system (Boorman and Levitt 1972; Harrison et al. 1988), and the idea of source-sink metapopulations (Pulliam 1988; Pulliam and Danielson 1991). However, theoretical models assume equilibrium conditions whereas human modified landscapes are likely to be in non-equilibrium states (Brown 1971; Thomas and Hanski 2004), which introduces the concept of extinction debt, an irreversible loss of species that follows a prolonged transient or delay after the habitat destruction (Loehle and Li 1996; Hanski and Ovaskainen 2002). Given that a loss of biodiversity might alter ecosystem processes and change the resilience of ecosystems to environmental change (Chapin III et al. 2000), identifying thresholds in habitat amount or connectivity that support species richness, abundance or functional diversity (Andrén 1994; Michalski and Peres 2005; Pardini et al. 2010; Estavillo et al. 2013; Magioli et al. 2015; Ochoa-Quintero et al. 2015; Muylaert et al. 2016) may be crucial for conservation planning.

The creation and adequate management of protected areas is one way to increase the persistence of animal populations in fragmented landscapes. Protected areas have diverse origins, but many of them are being now managed to maintain or enhance biodiversity value (Jepson et al. 2011). However, some species, such as large mammals, require large home ranges, and often protected areas are not big enough for protecting populations of those species (Newmark 1993; Hilty et al. 2006). Connectivity, which is defined by the degree to which the landscape impedes or facilitates movement among resource patches (Taylor et al. 1993), plays an important role in maintaining viable populations for many wide-ranging species (Carroll 2006; Crooks and Sanjavan 2006; Paul C. Paquet et al. 2006). There are primarily two components of connectivity: structural, which represents the spatial arrangement of different types of habitats or other elements in the landscape, and functional, representing the behavior responses of individuals, species or ecological processes to the landscape structure (Crooks and Sanjavan 2006). Also, functional connectivity might be separated into potential connectivity, based on the organism's dispersal ability, and actual connectivity, when the movement of individuals through a landscape is quantified (Fagan and Calabrese 2006).
The identification of biodiversity hotspots is another alternative for setting priorities for conservation (Reid 1998; Myers et al. 2000). The Neotropical region has seven out of the 25 biodiversity hotspots, which concentrate nearly 35% of all vertebrate endemic species and

exceptional undergoing loss of habitat (Myers et al. 2000). Brazil's Atlantic Forest is among the five richer hotspots in number of endemic plants and vertebrates (Myers et al. 2000), and it is one of the most threatened tropical forests in the world, with around 12% of its original extent left and more than 80% of the fragments smaller than 50 ha (Ribeiro et al. 2009). This fragmentation scenario over the entire biome poses additional threats to many vertebrate species, and based on allometric theory which predicts that larger species require larger amounts of habitat (Jetz et al. 2004), any assessment of habitat function and connectivity involving communities require consideration and integration over multiple spatial scales.

Many studies focused on landscape connectivity analysis for single species, usually building a model for wide-ranging and often large-bodied species, assuming that conservation of these umbrella species – species with large area requirements, which if given sufficient protected habitat area, will bring many other species under protection (Noss 1990) – will also facilitate conservation of small and less mobile species (Castilho et al. 2015; Pitman et al. 2017). An application of a multispecies landscape connectivity analysis showed that building separate scenarios for carnivore and herbivore mammals could be an effective alternative for considering more species (Brodie et al. 2015). However, there are few attempts in empirically evaluating the effectiveness of areas indicated as corridors for wide-ranging species (e.g., large carnivores) to other species (e.g., smaller carnivores and herbivores). For instance, what may be a corridor for some species, might be a filter – dispersal route more restrictive than a corridor – for others, such that many species or functional groups might be present in both sides of a filter, while others are absent on either side (Lomolino et al. 2017).

Altered species interactions might further degrade natural systems in fragmented landscapes (Valiente-Banuet et al. 2015), although a species impact on ecosystem function might be compensated for by other species in the community. An ecological guild is a group of species that exploits the same class of environmental resources in a similar way (Root 1967), which provides a useful framework for assessing redundancies in ecological function among species and elucidate potential changes in ecosystem impacts from changes in species diversity. Although many different classifications of species guilds exist (Simberloff and Dayan 1991), the use of the original concept might indicate whether species interactions are being lost. For instance, the extinction of top predators may destabilize ecosystems and initiate trophic cascades (Ripple and Beschta 2006; Beschta and Ripple 2009; Wallach et al. 2015), as has been exemplified with the case of wolf-deer-vegetation interaction in Yellowstone National Park (Smith et al. 2003; Ripple and Beschta 2012; William J. Ripple et al. 2014). Similarly, it has been pointed out that seed dispersal interactions involving large-sized fruits and birds have been lost in fragments smaller than 10,000 ha in the Brazilian Atlantic Forest (Emer et al. 2018). Considering that more than 65% (reaching more than 80% in some regions) of the wood species are endozoochorous in tropical rainforests such as the Atlantic Forest (Almeida-Neto et al. 2008), the loss of frugivores might represent a decline in dispersal and gene flow for many plant species. Therefore, evaluating how each guild (e.g., trophic guild) is affected in fragmented landscapes is a complementary approach to assessing the habitat use by each individual species.

In human-dominated landscapes factors such as hunting, logging, fires, pollution, and presence of domestic/feral dogs can interact synergistically with habitat loss and fragmentation to reduce habitat quality, animal fitness, and species diversity (Laurance 2008; Zapata-Ríos and Branch 2016). Anthropogenic activities might impact medium and large-mammal populations direct or indirectly (Redford 1992). Direct persecution is often an important threat to many carnivore species, often occurring in retaliation for real or perceived threats to livestock (Jedrzejewski et al. 2017). Carnivore mammals might also be impacted from indirect effects, such as human hunting pressure on their prey species, considering that the availability of suitable prey is a key determinant of carnivore occurrence and abundance (Karanth et al. 2004; Henschel et al. 2011). At the same time, frugivore populations might be impacted by legal or illegal exploitation of forest resources, such as fruits, nuts (Redford 1992), and palm-heart, a common illegal activity in some regions as the Brazilian Atlantic Forest (Galetti and Fernandez 1998). Obtaining a quantitative measure of hunting pressure is often challenging; for this reason, many studies used proxies to poaching pressure, such as number of occasional encounters with poachers, traps, or hunting dogs during fieldwork (Chiarello 2000; Cullen et al. 2000; Cullen Jr et al. 2001) or by park rangers and other researchers (Galetti et al. 2009; Xavier da Silva et al. 2018), interviews (Michalski and Peres 2005; Sampaio et al. 2010), and poacher seizure records (Ghoddousi et al. 2017). As poaching and hunting rates usually increase in areas closer to roads, and settlements (Lyon and Burcham 1998; Gratson and Whitman 2000; Burton et al. 2012), showing a markedly decrease in bird and mammal abundances (Benítez-López et al. 2017) another possible approach is to consider these variables as proxies to poaching pressure. The use of camera traps might also bring another possibility of using the detections of people as a proxy to the ease of access of the area, which might correlate with poaching pressure. If this is true, hunted species might show behavioral and population differences in areas accessed or not by humans.

Domestic or feral dogs – the latter considered as individuals not associated with people or human settlements – also have been shown to negatively influence the presence of herbivore and carnivore mammals in native habitats (Silva-Rodríguez and Sieving 2012; Zapata-Ríos and Branch 2016). In many regions, and especially in tropical regions, it is common that dogs engage in some form of free-ranging behavior regardless of being owned (Vanak and Gompper 2009). Free-ranging dogs usually interact with wildlife (Hughes and Macdonald 2013), including as predator (Campos et al. 2007; Young et al. 2011), prey (Edgaonkar and Chellam 2002; Butler et al. 2004), competitor (Vanak and Gompper 2010), and disease reservoir and vector (Cleaveland et al. 2000; Funk et al. 2001; Fiorello et al. 2004). For this reason, addressing the degree to which native mammals interact with domestic dogs (e.g., avoiding or not) is a relevant aspect to be addressed in human-dominated landscapes to consider management options in the case of negative impact of domestic dogs on wildlife.

Numerous studies have focused on medium and large mammal populations inside protected areas (Martins et al. 2008; Wearn et al. 2013; Ferreira et al. 2017; M. Galetti et al. 2017; Mariana B. Nagy-Reis et al. 2017), but understanding how landscape and disturbance factors in protected areas affect mammals across fragmented landscapes is needed to direct policy efforts towards their conservation. For this reason, this dissertation focused on studying forest remnants inside and among protected areas, encompassing a landscape with varying levels of amount of forest in different regions, and human disturbances. Moreover, many previous studies addressing the relationship between landscape factors (e.g., forest amount, patch size, and isolation) and biological variables (e.g., species richness) or the interactions of disturbance factors and native species habitat use did not consider the problem of imperfect detection, which is often less than one, and might bias parameter estimates (MacKenzie et al. 2002; Guillera-Arroita et al. 2014). The probability of detecting an individual can vary among species, observers, survey methods, and sites (Iknayan et al. 2014; MacKenzie et al. 2018). Hierarchical multispecies occupancy models that incorporate both the detection process and the occurrence state provide a promising way forward, because they lead to a process-driven estimate of diversity through the delineation of the biological and sampling processes (Iknayan et al. 2014)

This dissertation evaluates different drivers of mammalian communities in a highly fragmented Atlantic Forest landscape, where forest amount has remained fairly stable since at least 1985.

Mammals' taxonomic classification follows the document elaborated by the Brazilian Mastozoology Society (Abreu et al. 2021). In chapter 2, "Domestic dogs and humans in Atlantic Forest remnants: spatial and temporal implications for native mammals", I test whether domestic dogs and/or humans influence spatial or temporal use of habitat by mammals of distinct trophic guilds (frugivores, omnivores, carnivores, insectivores, and herbivores). By using dynamic two-species occupancy models it was possible to infer that a few mammal species showed spatial changes in terms of their probability of use of forest remnants when domestic dogs and or/humans were present compared when one or both species were absent. Other species, however, showed a temporal change in their habitat use (cases when the detection probability decreased when domestic dogs and/or humans were detected in a certain occasion). No species showed changes in their activity patterns (temporal change) but this could be due to the wide use by domestic dogs and humans in the studied landscape (a situation that is very likely to expand to most of the Atlantic Forest biome).

In chapter 3, "Scale affects how forest cover influences apparent community shifts in Atlantic Forest mammals in Southeastern Brazil", I used multispecies occupancy models to test how forest proportion in landscapes with different areas (multiscale approach) influenced medium and large mammal community habitat use, while controlling for non-target variables that had a large variation across the studied landscape (e.g., elevation, and human footprint). This multiscale approach made it possible to detect that the shift in habitat use by forest-dependent versus generalist species is highly dependent upon scale of observation, so selecting the best scale for the studied community is paramount for a more accurate assessment of how forest amount in landscapes influence these two groups of mammal species. In this study a proportion of forest much higher than what the literature reports (studies that usually do not evaluate different scales or use a limited number of scales) was found, which is relevant for the mammal community conservation planning in anthropogenic landscapes.

In chapter 4, “Evaluating multispecies connectivity in a human-dominated landscape in Atlantic Forest, Southeastern Brazil”, I evaluated whether forest remnants important for the connectivity of multiple mammal species (frugivores and carnivores) were already included in the protected areas across the studied landscape. Using graph theory I identified the most important forest patches for connectivity for the forest-dependent mammals and found observed considerable variation of areas important for connectivity for different species. This distinction was larger when we compared species of one trophic guild to another, which indicates the benefit of including multiple species, specially of different trophic guilds, when evaluating the most important areas for connectivity when conservation of the medium and large-mammal community is the aim. Although many areas important for connectivity are already protected (i.e., inside protected areas), a large proportion of these areas still can be managed, and important forest patches could be lost considering that more than half of the area is inside private properties. Therefore, planning of landscapes outside protected areas is paramount for the conservation of forest-dependent mammal species in the long term.

CHAPTER 2 – DOMESTIC DOGS AND HUMANS IN ATLANTIC FOREST REMNANTS: SPATIAL AND TEMPORAL IMPLICATIONS FOR NATIVE MAMMALS

ABSTRACT

Since human-dominated landscapes have become widespread worldwide, species have not only to deal with the consequences of both habitat loss and fragmentation but also must face the spread of invasive species as well as the presence of human beings in many forest remnants. In this chapter I aimed to evaluate how Atlantic Forest native mammal species are spatial or temporally influenced by the presence of domestic dogs or humans in forest remnants. I sampled 112 camera trap sites across an Atlantic Forest landscape in Southeastern Brazil between September 2018 and May 2019 and selected the mammals most detected (N>90) for this study. Dynamic two-species occupancy models were applied to each pair of species being a native mammal species and domestic dogs or humans as the closure assumption was not met. The coefficient of overlapping was used to investigate the overlap of activity patterns between pairs of species (domestic dogs or humans and each native mammal species). Housing density was the most important covariate for almost all species pairs. Some species such as ocelots and oncillas showed the predicted patterns of avoiding domestic dogs or humans, while others had a positive co-occurrence with dogs: crab-eating fox, paca, and deer or humans: crab-eating fox, paca, oncilla, and deer. These species except for deer had a very low activity overlap with dogs or humans, which could indicate a temporal avoidance. Deer was the only species to have a positive co-occurrence and high activity overlap with dogs and humans, which could be due to the avoidance of its main predator in the area of study, the puma (*Puma concolor*), which respond responded negatively to the housing density covariate.

INTRODUCTION

Human activities have modified more than 75% of the Earth's land surface (Vitousek et al. 1997; Ellis and Ramankutty 2008; Ellis et al. 2010). Human-dominated ecosystems are increasingly common (Romero-Lankao and Dodman 2011; Fragkias et al. 2013; Jacobson et al. 2019), with lands transformed to better accommodate humans contributing to ongoing habitat loss and fragmentation —two of the primary forces driving the biological diversity crisis worldwide (Wilcove et al. 1986; Vitousek et al. 1997; Brooks et al. 2002; Pimm et al. 2014; Haddad et al. 2015). Domestic dogs (*Canis familiaris*) have followed human population trends in terms of increasing their numbers in human-dominated regions (Butler and Bingham 2000; Espartosa 2009). The global dog population is estimated to be larger than 700 million individuals (Hughes and Macdonald 2013). In many parts of the world, domestic dogs are essentially free-ranging animals (Wandeler et al. 1993; Boitani and Ciucci 1995; Slater 2001; Vanak and Gompper 2009), whose presence may interact synergistically with habitat loss and fragmentation to further degrade habitat quality, animal fitness, and species diversity (Laurance 2008; Zapata-Ríos and Branch 2016).

Many vertebrates are negatively impacted by the presence of dogs. Direct predation is the most common threat posed by dogs to vertebrates, and mammals are the taxonomic group most threatened by dogs (Silva-Rodríguez and Sieving 2012; Lessa et al. 2016; Doherty et al. 2017). Native mammals may adjust their behavior in time or space to reduce encounters with people or dogs (Berger 2010; Darimont et al. 2015), such as increasing time spent in secure refuge habitats. Such behavioral adjustments to perceived risk may come at a cost in terms of reductions in daily foraging time (Ripple and Beshta 2004; Stephens et al. 2007; Creel and Christianson 2008; Berger 2010; Benítez-López 2018; Gaynor et al. 2018). For medium- to large-bodied carnivores, the presence of free-ranging dogs may pose less of a direct predation risk than a force of competition that could reduce prey encounter rates (Vanak and Gompper 2009), constrain habitat selection (Vanak and Gompper 2010), or limit their spatial distribution (Ritchie and Johnson 2009). Importantly, the behavioral adjustments wild animals make in response to people or dogs, whether in space or time (Berger 2010; Zapata-Ríos and Branch 2016), may decouple apparent habitat quality from realized habitat use, especially given the lack of reliable information on the drivers of space use by dogs in different landscape contexts.

Assessment of species co-occurrence may reveal the degree to which inter-specific interactions help shape species distributions (Schoener 1974a; Rosenzweig 1995; Davis et al. 2018; MacKenzie et al. 2018)—from predator effects on prey distribution (Weterings et al. 2019; Smith et al. 2020), to competitive suppression (Cruz et al. 2018; Davis et al. 2018), and even facilitative interactions, in which at least one of the species is benefited and cause no harm to neither (Kowalczyk et al. 2008; Goyert et al. 2014; Crego et al. 2016). The majority of research on free-ranging dogs has focused on the direct risk of predation in natural areas (Young et al. 2011; Hughes and Macdonald 2013). Co-occurrence models indicate that many native mammals tend to use areas where dogs occur less often than expected (Soultan et al. 2021), with dogs replacing native species (i.e., carnivores) in forest remnants closer to villages (Lacerda et al. 2009; Farris et al. 2016; Farris et al. 2017). Many of these studies, however, have focused on reserves only (Srbek-Araujo and Chiarello 2008; Lacerda et al. 2009; Lessa et al. 2016; Massara et al. 2016; Paschoal et al. 2018; Coronel-Arellano et al. 2021), and information is needed both in protected and unprotected landscapes, as well as alternative ecological (e.g., tropical versus temperate forests) and cultural (e.g., variation in dog-keeping practices) contexts, to understand the role of free-ranging dogs in structuring species distributions. Importantly, whether evaluating spatial avoidance or numerical suppression, methods should account for the imperfect detection of both dogs and the target mammal species (MacKenzie et al. 2018). Moreover, studies evaluating species responses to dogs should evaluate temporal changes in behavior as an alternative mechanism to spatial avoidance as a means of evading the threats posed by dogs (Lima and Dill 1990; Werner and Anholttt 1993; Lima 1998a).

Free-ranging dogs have long been a concern within Brazil's Atlantic Forest (Paschoal et al. 2016), which is among the five richest hotspots with respect to endemic plants and vertebrates (Myers et al. 2000) while also being one of the most threatened tropical forests in the world. Only ~12% of the original extent of Atlantic Forest remains, and more than 80% of the forest fragments are smaller than 50 ha (Ribeiro et al. 2009)—making patches of Atlantic Forest especially vulnerable to the external pressures posed from dogs and other non-native mammals, including people. Among the world's biodiversity hotspots in 2000, the Atlantic Forest hosted the highest proportion of urban area with an expected 200% increase in urban extent by 2030 (Seto et al. 2012). Although the direct "urban" footprint within the Atlantic Forest remains concentrated and rather small, the effect of urban areas is compounded by associated infrastructure connecting urban settings and contributing to additional habitat loss and fragmentation throughout the region (Seto et al. 2012). The effect of free-ranging dogs, despite being the most abundant carnivore in several natural areas (Paschoal et al. 2012; Hughes and Macdonald 2013), has not been fully evaluated within the Atlantic Forest and other regions. Dogs are among the most detected mammal species in Atlantic Forest remnants (Paschoal et al. 2012; Paschoal et al. 2018; Ribeiro et al. 2018), where they are commonly observed to exert negative effects on wild carnivores, yet information for other groups of species (e.g., frugivores or herbivores), in both space and time, require further investigation.

Herein, I evaluated how a suite of medium and large-bodied native mammals responded spatially or temporally to the presence of humans and free-ranging dogs in forest remnants across the Atlantic Forest in southeastern Brazil. Fundamentally, I expected that mammals persecuted by dogs or humans (e.g., pacas, armadillos) may be unable to avoid these threats spatially and instead would exhibit patterns of temporal avoidance. However, I expected those patterns to vary among species such that meso-predators and dogs may exhibit spatial avoidance instead. Overall, I expected native mammals to exhibit increasing nocturnal patterns of activity in areas predicted to have a high probability of use by dogs or humans (Gaynor et al. 2018).

METHODS

STUDY AREA

My 66,870 km^2 study area was situated in the Atlantic Forest biome of southeastern Brazil, in São Paulo and Minas Gerais states (Figure 1). The study area encompassed 5 major metropolitan areas: São Paulo, Baixada Santista, Campinas, Vale do Paraíba and Litoral Norte, and Sorocaba metropolitan regions, where human populations ranged from 1.7 to more than 20 million (IBGE 2010). The landscape also included part of the largest remaining Atlantic Forest remnant, Serra do Mar, situated close to the coast.

This biome has a long history of deforestation, with urban areas being identified as early as the eighteenth century (Ellis et al. 2010), and experienced a massive agricultural expansion since the sixteenth century, followed by industrialization and urban expansion starting in the nineteenth century (Dean 1995). Although urban areas are expected to cover an additional 2-3.3% of the biome by 2030 (Seto et al. 2012), for the most part I consider this landscape an “after-math” forest. Massive deforestation halted ~1985 (Souza et al. 2020). Since then, forest changes have been relatively minor in my study area compared to elsewhere in the Atlantic Forest, and minor forest gains (via restoration) have been greater than forest loss (Lira et al., 2012; Souza et al., 2020; Silva Junior et al., 2020), and since ~1985, the average yearly rate of change in forest cover has been negligible to slightly positive, +0.05 (Souza et al., 2020). As a result, I consider the extent of existing forest patches and their landscape context to have remained fairly stable over the past 30+ years – making this area a useful model system for considering the long-term behavioral and spatial responses of wildlife to forest fragmentation.

Six climates occur across the studied landscape following Köppen's classification: Cfb (36.21% of the landscape), Cfa (26.97%), Cwb (22.42%), Cwa (6.71%), Af (6.27%), and Am (1.40%), where Cf stands for humid subtropical, oceanic climate without dry season, Cw stands for humid subtropical climate with dry winter, and with hot summer (a) or with temperate summer (b), and A indicates tropical climate without dry season (f) or monsoon (m) (Alvares et al., 2013). Across ~92% of the area of study, the average temperature in the hottest month is above 22°C and the average temperature in the coldest month is between -3°C and 18°C. The average precipitation in the driest month varies from 25 mm to 60 mm across the whole area. The average annual precipitation is about 1,300-1,400 mm, with seasonal variations, between April and August being the driest months (Alvares et al. 2013).

DATA COLLECTION

I documented habitat use and activity patterns by native wildlife, dogs, and humans using passive infrared trail cameras. I selected 30 x 30 km sample units that varied in the proportional coverage of forest: (1) <20%, (2) 20-40%, (3) 40-60%, (4) 60-80%, and (5) >80%, housing density (0 – 729 houses/km^2), and road density (0 – 0.78 road km/km^2). Density calculations were conducted within a circular radius of 2000 m centered in each potential sample unit. A total of 112 sample units were selected, each having 1 camera trap deployed from September 2018 to May 2019 (4 traps ultimately were stolen so their duration was truncated). Within each survey unit, the camera was placed as centrally as possible, within a forest remnant (minimum size = 17 ha), and more often on a trail (59%) than off trail (41%).

Four camera brands were deployed: Bushnell Trophy Cam (models 119636, 199537, 119736, 119774, 119776), Moultrie (MCG13183, 990i, 1100i), Browning Dark OPS HD, and Spypoint Solar, with the largest number of cameras of the same model being Browning Dark OPS HD (N=25), and Bushnell 119537 (N=23). The other models used varied from two cameras (Spypoint solar) to 13 cameras (Moutrie 1100i). All camera trap models used were infrared models with video trigger speed of less than 3 seconds. Four models had trigger speed faster than 1 second (Spypoint Solar, Browning Dark OPS HD, Bushnell 119774, and 119776), with the others having slower trigger speeds for videos. The choice of deploying a slow versus fast trigger camera traps was random across the gradient of forest amount (Appendix 1). All cameras were fixed at 30-40 cm above ground and were not baited. Cameras were set to take videos with the fastest recovery time available for each model (usually up to a few seconds).

I retained for analysis all species having ≥ 59 total detections (considering the maximum of one detection by one-week occasion by site). Number of detections varied from 59 simultaneous detections of dogs and humans (when both species were detected on one occasion) to 214 detections of humans. Native mammal detections fell between 92 (*L. pardalis*) and 158 (*Dasypus* spp.). In this region there were two species each of armadillo (*Dasypus novemcinctus*, and *D. septencinctus*) and deer (*Mazama gouazoubira* and *M. americana*) that could not be reliably classified to species by visual appearance alone (Reis et al. 2010; Duarte et al. 2012; Grotta-Neto et al. 2019), which were classified to genus level only. This process yielded for analysis 1 insectivore (*Dasypus* spp.), 1 herbivore (*Mazama* spp.), 1 frugivore (paca, *Cuniculus paca*), 1 omnivore (crab-eating fox, *Cerdocyon thous*), and 2 carnivores (ocelot, *Leopardus pardalis* and oncilla, *Leopardus guttulus*). Records of domestic dogs (N = 209 detections) and humans (N = 214 detections) were also retained (Table 1).

DATA ANALYSIS

Collectively, I interpreted spatial occupancy patterns and temporal activity patterns as indications of whether and how native mammals responded to the risks imposed by people and dogs – anticipating either no behavioral response, movement to avoid risk, or adaptation in place by shifting temporal activity patterns to avoid risk (Table 2).

HABITAT USE PATTERNS

I quantified spatial patterns of animal occurrence, and the interactive influences of dogs and humans on space use by native mammals, using occupancy models. Given the 9-month survey duration, which crossed both the wet and dry seasons, I employed multi-season occupancy models. These models employed a robust design where seasons (year) represented the primary sampling periods and survey intervals (week; see below) represented the secondary sampling periods (MacKenzie et al., 2018, 2003). As I could not ensure closure to changes in occupancy for the duration of the study, I interpreted the estimated probability of occupancy (ψ) as the initial probability of use within time t, i.e., the probability of occupancy of one species in one time interval does not depend upon its occupancy status in the previous time interval (Mackenzie and Royle 2005). Models were fit using the packages RMark (Laake and Rexstad 2017) and RPresence (Hines 2006) for R (R Core Team 2019). Akaike's Information Criterion (AIC) was used to rank and compare alternative models (Burnham and Anderson 2002).

Initially, I fit single species models using alternative durations (i.e., 1 day to 2 weeks) for the secondary survey intervals, and, lacking a better tool, used the estimate of over-dispersion ($\hat{c}$) to choose the optimal sampling interval across species (Burnham and Anderson, 2002; MacKenzie et al., 2018). I ultimately selected a 1-week sampling interval, which yielded $\hat{c} \approx$

1.0 for domestic dogs and humans while indicating under-dispersion for all native mammals ($-1.7 < \hat{c} < 0.1$). Finer sampling intervals tended to yield overdispersion for native mammals, e.g., 1-day sampling intervals yielded $\hat{c} \geq 3.7$. In contrast, intervals longer than 1 week yielded under-dispersion for all species including dogs and humans. As overdispersion is more common, several approaches for addressing it have been developed, e.g., negative binomial distribution, or quasi-likelihood in frequentist analyses (Burnham and Anderson 2002; Kéry and Royle 2016; MacKenzie et al. 2018). However, the usual advice to under-dispersion is to ignore it, although it is known that the uncertainty assessments will be too pessimistic, e.g., SEs become too wide (Kéry and Royle, 2016).

Using the 1-week sampling interval, I initially explored single species models to determine whether camera placement (on trail=1 or off trail=0), or camera functionality (fully functional=0, periods of malfunction=1) or camera trigger speed (slow=0, fast=1) affected a species' probability of detection. Only a few cameras intermittently malfunctioned (mainly in the infrared, preventing the record of nocturnal records). Preliminary analyses indicated that on/off trail should be retained as a covariate informing detection probability, but camera functionality, and trigger speed should not (ΔAIC > 7 when camera functionality compared to the global occupancy model lacking this variable). In the case of trigger speed, although one species (ocelot) had its detection probability decreased when using slower trigger cameras, the relationships of the variables with occupancy probability kept the same, and this covariate was no further included.

Next, I fit dynamic, two-species models to investigate whether the presence of domestic dogs, humans or both (when both species were detected in the same one-week occasion) influenced the probability of detection (p) or site use (ψ) of native mammals. Employing the conditional

(ψBa/rBa) formulation of Richmond et al. (2010), the parameters estimated for occupancy probability under this model include:

- ψA = probability that the area is initially (time t) occupied by the dominant species,
- ψBa = probability that the area is initially occupied by the subordinate species when the dominant species is absent, and
- ψBA = probability that the area is initially occupied by the subordinate species when the dominant species is present.

Parameters representing colonization (γ) and extinction (ε) probabilities were also estimated:

- γBA = probability that the site was colonized by species B in the interval t to t+1 given species A was present in survey t,
- γBa = probability that the site is colonized by species B in the interval t to t+1, given species A is absent in survey t,
- εBA = probability that species B failed to re-use a site in the interval t to t+1 when species A was present, and
- εBa = probability that species B failed to re-use a site in the interval t to t+1 when species A was absent.

Importantly, γ and ε were considered nuisance parameters (i.e., artifacts from the need for a dynamic model given the long-time survey duration) rather than biologically meaningful parameters of interest. Estimates for detection probability included:

- rA = probability of dominant species being detected when the subordinate species is present,
- pA = probability of dominant species being detected when the subordinate species is not present,

- *p*B = probability of subordinate species being detected when the dominant species is not present,
- *r*BA = probability of subordinate species being detected when the dominant species is present and detected, and
- *r*Ba = probability of subordinate species being detected when the dominant species is present but not detected.

I tested the effects of three landscape covariates on ψ, γ, and ε: proportion of forest, housing density, and road density (Table 2), as described next. Observed responses of organisms to their environment, and interactions among species, depend fundamentally on the scale of animal perception (Boscolo and Metzger 2009; Lyra-Jorge et al. 2010; Lesmeister et al. 2015; Nagy-Reis et al. 2017). For this reason, I considered alternative measurement scales (i.e., extents) that were, for each species, roughly equivalent to: (1) minimum home range size, (2) half the minimum range size, and (3) double the minimum home range size (Wiens 1976; Turner and Gardner 2015). For armadillo, deer, paca, and domestic dogs, I used radii of 0.25, 0.5, and 1 km, while for crab-eating fox, ocelot, and oncilla I used radii of 0.5, 1, and 2 km (Beck-King and von Helversen 1999; Beisiegel 1999; Meek 1999; Bond et al. 2000; Juarez and Marinho-Filho 2002; Di Bitetti et al. 2006; Black-Décima et al. 2010; de Oliveira et al. 2010; Kasper et al. 2013; Dürr and Ward 2014; Gutierrez et al. 2016). For humans, who easily moved throughout the landscape on roads, I used radii of 1, 2, and 4 km. Within buffers defined by each of these radii, centered on camera locations, I calculated the proportional coverage of forest from reclassified Landsat 7 images (ETM+ sensor, 30 m resolution; (MMA/PROBIO, 2007). Road layers were provided by the Brazilian Ministry of Environment, and density was calculated using the density tool in ArcGIS 10.6.1, yielding linear km of road per square km. Likewise, I used the density tool to calculate the number of houses per square km from the number of houses in each census sector within the national census data, acquired from Instituto Brasileiro de Geografia e Estatística (IBGE 2010).

To identify the best scale for each variable and species pair, I fit alternative candidate models and compared them using AIC. Candidate models included spatial covariates (percentage forest cover, housing density, and road density) on ψ, γ, and ε while controlling for the effects of on/off trail on *p*. At this stage, candidate models differed only in the scale at which each landscape covariate was measured. To guard against multi-collinearity, I did not include pairs of variables having Pearson $r > 0.7$ when $P < 0.05$; (Dormann et al., 2013). The only problematic pairing was housing density (1 km) and road density (2 km), which were not allowed within the same candidate model. After identifying the appropriate scale of analysis for each landscape variable, full model selection proceeded as described next.

Full models were built assuming either that occupancy, colonization, and extinction of the subordinate species was influenced by the dominant species (ψBA ≠ ψBa, γBA ≠ γBa, and εBA ≠ εBa) or remained independent of the dominant species (ψBA = ψBa, γBA = γBa, and εBA = εBa). Following the secondary candidate set strategy (Morin et al., 2020), model selection proceeded in four steps: modeling ψ, then γ, then ε, and, finally all parameters at once (overall modeling). Non-modeled parameters in the first three steps were set to null (not influenced by any covariate), and models for ψ, γ, or ε having ΔAIC < 5 were kept for the overall modeling step.

From the best overall model, I calculated the species interaction factor (SIF) for occupancy as:

$$\left(\nu = \frac{\dfrac{\psi^{\mathrm{BA}}}{(1 - \psi^{\mathrm{BA}})}}{\dfrac{\psi^{\mathrm{Ba}}}{(1 - \psi^{\mathrm{Ba}})}} \right)$$

which indicates whether the two species occurred at sites independently of each other (ν = 1), co-occurred less often than expected under independence (i.e., avoidance; ν < 1), or co-occurred more often than expected under independence (ν > 1). The same equation (substituting $\psi\mathrm{BA}$ and $\psi\mathrm{Ba}$ for *r*BA and *r*Ba) was applied to detection probability to calculate ρ, which indicates the level of dependence in the detection of the two species such that detections of the target species (B) may be independent from (ρ = 1), less likely (ρ < 1) or more likely (ρ > 1) when the dominant species (A) is present (MacKenzie et al. 2018).

TEMPORAL ACTIVITY PATTERNS

To quantify daily activity patterns, I recorded the time of day of each species detection. Given the long survey duration, I transformed clock time to sun time (Nouvellet et al. 2012). For this analysis, I further considered records separated by ≥60 min to be independent detections (Romero-Muñoz et al. 2010; Porfirio et al. 2016).

For each species, daily activity patterns were quantified using kernel density functions (Ridout and Linkie 2009). The overlap coefficient (Δ), ranging from 0 (no overlap) to 1 (identical activity patterns) (Ridout and Linkie, 2009), was used to compare activity patterns between either dogs or humans and each of the native mammal species. For species with large samples sizes (≥75 independent observations), I applied Δ_4 and a smoothing parameter of 1, else I applied Δ_1 and a smoothing parameter of 0.8 (Ridout and Linkie 2009; Meredith and Ridout 2018). The 95% confidence intervals for Δ_4 and Δ_1 were calculated using a smoothed bootstrap with 10,000 resamples.

In addition, I split camera sites into low versus high disturbance (based on the predicted probability of use by dogs or humans from the occupancy analysis) and applied a non-parametric Watson's two sample test (Pewsey et al. 2013) to evaluate whether species exhibited significantly different activity patterns under these differing levels of risk. These analyses were conducted in the R environment v. 3.6.0 (R Core Team, 2019) using the *overlap* package to calculate overlap coefficients (Meredith and Ridout, 2018), and the *circular* package to determine whether two activity patterns were statistically different (Agostinelli and Lund 2017). Ultimately, I interpreted a shift in activity patterns either spatially (high versus low disturbance) or temporally (dog or human versus native mammal) as evidence of species exhibiting a risk-sensitive behavioral adaptation (Table 2).

RESULTS

From the 112 camera trap locations, I analyzed 12,481 camera trap days and recorded 92-158 overall detections of six native mammals (Table 1). Single species occupancy models indicated that placement of camera traps on trails positively influenced detection probabilities for all species except deer (Table 1). Models further indicated that the estimated probabilities of site use were considerably higher for dogs and humans (61-92% of sites) than observed for any of the native forest mammals (26-55% of sites; Table 1). Whereas the estimated extinction probability was larger than colonization probability for nearly all species, this may simply reflect cyclical space use differences (e.g., seasonal range shifts) rather than long-term trends in space use.

Two species models indicated that, when factoring in the presence of dogs or humans, site use was driven by landscape patterns on a scale equivalent to or larger than a species home range (Figure 2; Appendix 2). Housing density was the most important covariate for almost all dominant-subdominant species pairs (Figure 3; Appendix 3), except for two pairings (humans with either crab-eating fox or armadillo) for which forest proportion had a larger impact than housing density (although housing density was still important). In all cases (except for the pair ocelot – dogs and humans) the direction of effect of the covariates assumed the dominant species' responses (dogs or humans), being negative for forest proportion, and positive for housing density (Appendix 4). As it is possible to formally test the interaction between dominant and subordinate species in co-occurrence models, notably the overall species interaction factor was lowest between either dogs or humans and crab-eating fox or armadillo. Considering the top models (those with ΔAIC < 2), only paca, deer, and ocelot models indicated the species interaction as important in most or all models of co-occurrence with humans or dogs (Figure 3; Appendix 3).

Co-occurrence models indicated spatial avoidance of dogs and humans (either individually or in combination) by oncillas, and ocelots (Figures 4 A, B, C). Armadillo and crab-eating fox generally exhibited occupancy patterns independent of dogs and humans (Figure 4 A), except that armadillo avoided sites where both dogs and humans occurred (Figure 4 C). Interestingly, site use by dogs appeared independent of the presence of humans (Figure 4 B), indicating a free-ranging pattern by dogs in the region. Site use was also independent of the presence of humans for oncilla and paca (Figure 4 B). However, like armadillo, oncilla avoided sites where both dogs and humans occurred (Figure 4 C). Contrary to expectations, paca and deer exhibited a strong and positive spatial association with dogs (Figure 4 A), with deer further exhibiting a strong, positive association with dogs and humans collectively (Figure 4 C).

Armadillo, crab-eating fox, and deer proved less detectable, while paca and oncilla proved more detectable, in areas where dogs occurred (Figure 4 D). Moreover, all species except for deer (and dogs) became less detectable when humans were also detected at the same occasion (Figure 4 E). When both dogs and humans were detected at a given occasion, deer, ocelot, and oncilla became more detectable than when only humans or dogs were present (Figure 4 F). However, I note that some species, like deer, had higher detection probabilities in the absence of humans altogether (*p*B > *r*BA > *r*Ba, Table 3). Nevertheless, differential detectabilities conditional on the presence of a dominant species may reflect that some species take refuge while others get moving to avoid risk.

Like humans, dogs exhibited a largely diurnal, although less peaked, pattern of activity (Figures 5 and 6). And except for deer, most species exhibited a crepuscular to nocturnal activity pattern that led to little overlap with humans (Δ = 0.09-0.43). Native mammals exhibited moderate-high overlap in activity with dogs (Δ = 0.33-0.84), greater than that observed for humans (Δ = 0.09-0.60). For some species showing positive co-occurrence with dogs or humans, e.g., crab-eating fox and paca, I observed low temporal activity overlap (paca-dog, 33% overlap, Figure 5; crab-eating fox-human, 20% overlap, Figure 6) compared to other species. Deer, on the other hand, showed both a positive co-occurrence with dogs and humans as well as a high activity overlap (dogs 84%, Figure 5; humans 60%, Figure 6). When comparing a given species activity patterns between having low (ψ<0.55) versus high (ψ>0.55) predicted probabilities of use by dogs or humans, the only species exhibiting a significant shift in activity pattern was paca with respect to dogs (Watson's statistic = 0.49, p-value < 0.001), although that shift in activity still corresponded with a strongly nocturnal pattern of behavior (Appendices 4, 5) so was unlikely to be driven by dog activity (Figure 5).

DISCUSSION

Assessing how predators, competitors and landscape variables influence the distribution, habitat use, and activity of species has long held attention in Ecology (Schoener 1974b; Crowell and Pimm 1976; Gilpin and Diamond 1982; Connor and Simberloff 1983; Lima 1998b; Gotelli 2000; Ripple and Beschta 2004). Much interest has focused on interactions among wild species, although an increasing volume of studies documents domestic, free-ranging dogs as a concerning pressure affecting wild mammal populations especially across South America. I documented differential responses among six mammals native to Brazil's Atlantic Forest to the presence of dogs, humans, or both—observing a high degree of spatial and temporal exposure to what are effectively free-ranging dogs whose patterns of space use were independent of that of humans. Space use by dogs strongly reflected housing density, while space use by humans was predicted most strongly by road density. Therefore, the overwhelming focus on roads as a concentrator of human activities in most studies around the world (Fahrig and Rytwinski 2009; Benítez-López et al. 2010; Rytwinski and Fahrig 2012) is not a good representation of the potential impacts caused by dogs in areas lacking strict dog-keeping standards. Yet, as observed in the Ecuadorian Andes (Zapata-Ríos and Branch 2018), the amount of forest cover proved immaterial to dog habitat use—a disappointing result that indicates few Atlantic Forest remnants in my study area to be free from the risk posed by dogs.

Domestic dogs have been reported among the most detected mammal species in forests across Chile, Ecuador, and Brazil (Srbek-Araujo and Chiarello 2008; Silva-Rodríguez and Sieving 2012; Cassano et al. 2014; Zapata-Ríos and Branch 2018), including this present study, indicating that dog incursions into natural habitats is a widespread conservation concern. While I expected humans and domestic dogs to be common across the region (Torres and Prado 2010), I did not anticipate dogs to be far more common (in terms of the frequency of their detections) than any native mammal in this study. Nor did I anticipate dogs to be so widespread, including being detected within the largest contiguous and best protected forest remnants remaining in the Atlantic Forest biome. Although other studies referred to dogs in forest remnants as free-ranging (Belo et al. 2015; Paschoal et al. 2016; Montecino-Latorre and San Martín 2019), in this study co-occurrence models verified that dogs use space in a manner statistically independent of humans, despite being highly associated with housing density. Ultimately, dogs were predicted to occur in about 92% of the studied landscape (humans in about 61% of the area), with a minimum predicted probability of use of 41% among the sampled sites.

The native mammals in this study were inconsistent in their avoidance, either spatially or temporally, of dogs and humans. The expectation that armadillos and pacas would be unable to avoid dogs and/or humans spatially but instead would exhibit temporal avoidance was overall confirmed (except in the pair pacas and dogs). Similarly, as predicted, the felids (ocelots and oncillas) avoided dogs and both dogs and humans spatially. Ocelot was the only species to spatially avoid all situations when paired with dogs only, humans only or both dogs and humans detected at the same occasion.

Importantly, the mammals in this study generally perceived and responded to landscape and anthropogenic variables at extents equal or greater than the minimum home range size, suggesting the impacts of humans or dogs often extended further than species' home ranges. Crab-eating fox, armadillo, oncilla, and deer each exhibited higher habitat use and activity levels in more developed landscapes, although some (armadillo, ocelot, and oncilla) showed lower use when humans or dogs were present, while others (crab-eating fox, armadillo) were less detectable when one of those species were present. Two factors, food subsidies and predation refugia, likely underlie the pattern of attraction to human-modified environments by these species. For example, crab-eating fox and armadillo are opportunistic feeders known to use non-forested areas throughout their geographic range (Dotta and Verdade 2007; Beisiegel et al. 2013), and likely make ready use of anthropogenic food sources in human-dominated landscapes. Prey species have also been shown to use human activities or infrastructure as shields against predators (Terborgh 2000; Berger 2007), a pattern that has been observed with ungulates (Hebblewhite et al. 2005). In the current study, deer exhibited the highest amount of activity overlap with humans (Δ=0.6) and dogs (Δ=0.84) and did not shift their activity pattern between areas having higher or lower probability of use by dogs or humans. The main natural predator of deer in this region is cougar (*Puma concolor*), a species whose space use is inversely related to developed areas (Beier et al., 2010; Moss et al., 2016; Wang et al., 2015).

Whereas the other potential prey for cougars in this study, armadillo and paca, can find refuge in burrows (Beck-King and von Helversen 1999; McDonough et al. 2000; Ebensperger and Blumstein 2006; Figueroa-de León et al. 2016), deer may find greater refuge in areas of higher human activity—although that exposes them to likely higher rates of encounters with domestic dogs. As dogs in this region commonly travel in packs (my records showed groups between 2 to 6 dogs), it is very likely free-ranging dogs will chase deer. In fact, I have observed dogs chasing different animals in the field and recorded packs chasing deer at least twice in camera traps. This might be the case for other human-dominated landscapes as well.

With the growing human footprint across the world (Sanderson et al. 2002), animals actively trying to avoid humans or dogs are running out of space (Benítez-López et al. 2010). Lacking physical refuges left to move to, animals may adaptively create temporal refuges (Benítez-López 2018)—shifting from daytime activities to twilight or night hours (Benítez-López 2018; Gaynor et al. 2018). Except for deer, the mammals in this study exhibited largely crepuscular or nocturnal activity which is consistent to the known biology of the species (Reis et al. 2010). Therefore, the mammals' pattern of activity corresponded to a relatively low overlap with humans. For my study species, the observed activity patterns were similar to those reported elsewhere, including more pristine landscapes or larger forest remnants (Di Bitetti et al. 2006; Norris et al. 2010; Michalski and Norris 2011; Oliveira-Santos et al. 2013; Ferreguetti et al. 2015; Cruz et al. 2018). Combined with this observation, the fact that I failed to detect differences in activity patterns between areas with relatively higher versus lower probability of use by dogs and/ or humans (but see paca and dogs) could be do to the large probability of use of the landscape shown by dogs and humans. This fact decreases the amount of areas with no use by those species across the landscape to test the hypothesis of increase of nocturnal activity by native mammals. Anyway, the fact that all native mammals included in this study (except for deer) have a natural nocturnal activity pattern, could indicate this general behavior could enable these species to coexist with dogs and humans. Like humans, dogs exhibited a diurnal pattern of activity (George and Crooks, 2006; Moreira-Arce et al., 2015), but with a less pronounced mid-day peak in my study that resulted in moderate-high levels of overlap in activity with native mammals.

Domestic dogs are considered a threat to the persistence of many species worldwide, and have contributed to the extinction of at least 11 vertebrates (Doherty et al. 2017). Consider too that in the highly fragmented tropical forests, a largely unregulated harvest of wild species may act synergistically with threats posed by dogs to further imperil biodiversity (Schipper et al. 2008). This study documented that free-ranging dogs are widespread throughout the studied landscape, including strictly protected areas which are created as a tool for biodiversity conservation. Also, the indication of which species might fare better or worse given the threat posed by dogs suggests that management intervention might be needed to effectively create dog-free refuges for wildlife. For example, the oncilla *L. guttulus*, a threatened species, was showed to be negatively affected by the presence of dogs. Given the widespread occurrence of dogs, and the independent activity of dogs separate from humans, management of biodiversity in this human-dominated landscape should focus not only on reinforcement against illegal hunting, but also should engage creatively in the challenge of establishing dog-free areas.

Table 1. Number of detections (#) and naïve occupancy (N.O.) for native mammals, domestic dogs, and humans within an Atlantic Forest landscape, Brazil, along with the results of single-species, dynamic occupancy models including the probability of use ($\hat{\psi}$), colonization ($\hat{\gamma}$), extinction ($\hat{\varepsilon}$), and detection ($\hat{p}$); One occasion = seven days, SE shown in parentheses.

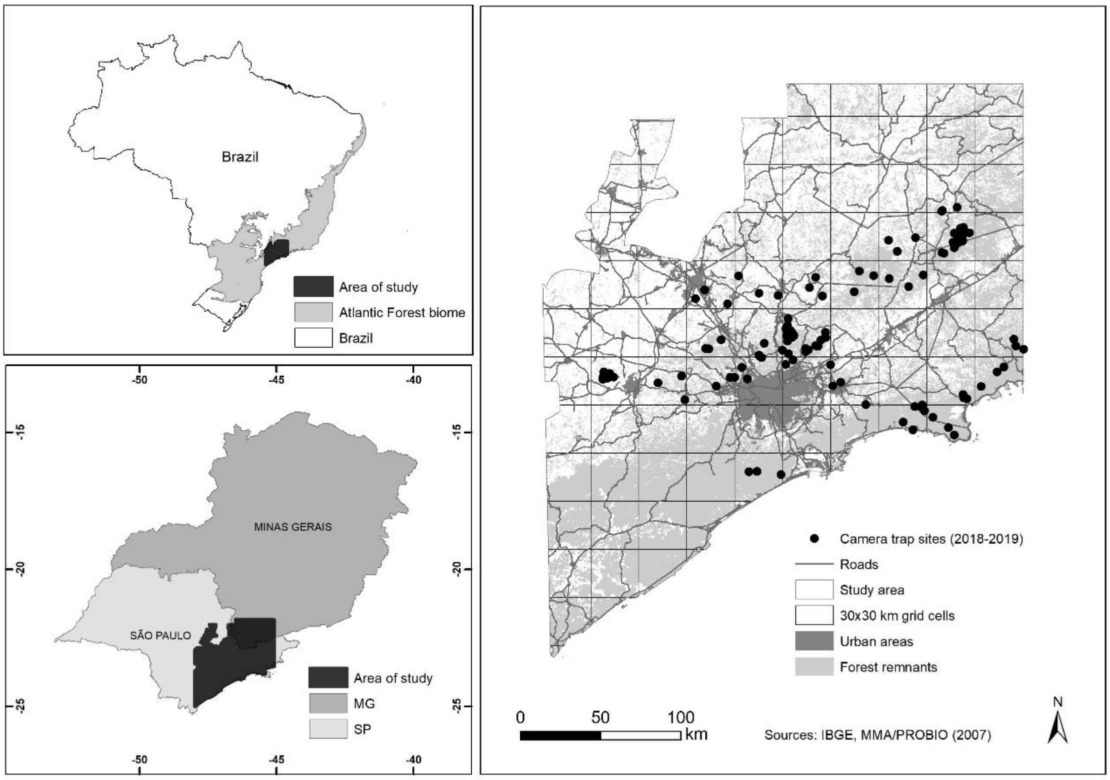
						$\hat{p}$	
Species	#	N.O.	$\hat{\psi}$	$\hat{\gamma}$	$\hat{\varepsilon}$	On trail	Off trail
Deer	117	0.26	0.26 (0.05)	0.07 (0.10)	0.55 (1.04)	0.25 (0.03)	0.36 (0.04)
Armadillo	158	0.37	0.32 (0.06)	0.13 (0.08)	0.41 (0.19)	0.29 (0.03)	0.23 (0.02)
Paca	136	0.25	0.31 (0.25)	0.07 (0.05)	0.17 (0.19)	0.35 (0.03)	0.20 (0.03)
Crab-eating fox	131	0.34	0.40 (0.07)	0.04 (0.06)	0.18 (1.65)	0.27 (0.02)	0.09 (0.02)
Ocelot	92	0.37	0.44 (0.09)	0.05 (0.09)	0.04 (0.15)	0.15 (0.02)	0.10 (0.02)
Oncilla	93	0.38	0.55 (0.14)	0.03 (0.10)	0.39 (0.18)	0.13 (0.02)	0.08 (0.01)
Domestic dog	209	0.54	0.92 (0.31)	0.83 (1.12)	0.17(1.58)	0.27 (0.02)	0.07 (0.02)
Humans	214	0.36	0.61 (0.07)	-	-	0.40 (0.02)	0.01 (0.01)
Domestic dog and humans	59	0.19	0.36 (0.07)	-	-	0.16 (0.02)	0.02 (0.01)

Table 2. Hypotheses and a priori predictions about the influence of dogs or humans, or features related to their occurrence, on temporal activity overlap with or space use patterns of native mammal species (armadillo, deer, paca, crab-eating fox, ocelot, oncilla) within the Atlantic Forest of Brazil. For the probability of use (ψ), colonization (γ), and extinction (ε), species interaction factor (SIF) on either ψ or detection (p), and the percent temporal activity overlap, hypothesized effects of covariates include a positive association (+), negative association (–), or indifference ("none").

			Statistical Expectation					
Outcome	**Covariate**	**Expectation**	ψ	γ	ε	**SIF (ψ)**	**SIF (p)**	**Activity overlap**
None	Increasing dog or human occupancy	Animals may not be insensitive to competition or predation by dogs or humans or may benefit from their presence.	None	None	None	1 (or >1)	1 (or >1)	None
Move (spatial avoidance)	Increasing percentage of area forested	Dogs occur predominantly in disturbed areas, such as small forest fragments or edges.	+	+	–	<1	<1	None
	Increasing road density	Human and dog activity is concentrated in areas near roads.	–	–	+	<1	<1	None
	Increasing housing density	Human and dog activity is concentrated near houses.	–	–	+	<1	<1	None
Adapt (temporal avoidance)	Dog or human presence	Vulnerable animals might adjust their activity to avoid competition or predation	None	None	None	1	1	–

Table 3. Dynamic, two-species occupancy model results indicating the probability of site use ($\hat{\psi}$) and detection probability when the dominant species is present ($\hat{r}$) or absent ($\hat{p}$) estimated for six native mammals with respect to either domestic dogs or humans in an Atlantic Forest landscape, Brazil. Target species, i.e., native mammals, are indicated by B while the presence or absence of dogs and humans, the dominant species, are indicated by A and a, respectively.

Target species (B)	ψBA	ψBa	rBA	rBa	pB
Dogs as dominant species (A = present, a = absent)					
Armadillo	0.39 (0.06)	0.37 (0.07)	0.11 (0.04)	0.23 (0.03)	0.11 (0.04)
Paca	0.39 (0.05)	0.06 (0.04)	0.26 (0.04)	0.18 (0.03)	0.15 (0.03)
Deer	0.44 (0.05)	0.15 (0.07)	0.15 (0.03)	0.23 (0.03)	0.10 (0.03)
Crab-eating fox	0.49 (0.07)	0.45 (0.12)	0.07 (0.02)	0.09 (0.02)	0.03 (0.01)
Ocelot	0.59 (0.06)	0.87 (-)	0.06 (0.02)	0.06 (0.01)	0.02 (0.01)
Oncilla	0.54 (0.06)	0.66 (0.17)	0.11 (0.02)	0.05 (0.01)	0.05 (0.01)
Humans as dominant species (A = present, a = absent)					
Armadillo	0.35 (0.05)	0.35 (0.06)	0.11 (0.04)	0.23 (0.03)	0.11 (0.03)
Paca	0.30 (0.04)	0.29 (0.06)	0.08 (0.03)	0.25 (0.06)	0.06 (0.02)
Deer	0.33 (0.05)	0.25 (0.07)	0.24 (0.05)	0.20 (0.05)	0.26 (0.04)
Crab-eating fox	0.42 (0.07)	0.40 (0.08)	0.03 (0.01)	0.05 (0.01)	0.04 (0.01)
Ocelot	0.45 (0.05)	0.77 (-)	0.13 (0.04)	0.16 (0.04)	0.04 (0.01)
Oncilla	0.43 (0.07)	0.41 (0.10)	0.03 (0.01)	0.05 (0.01)	0.05 (0.01)
Dog	0.55 (0.05)	0.55 (0.06)	0.10 (0.03)	0.04 (0.01)	0.06 (0.01)



Sources: IBGE, MMA/PROBIO (2007)

Figure 1. Area of study and sampling sites (camera traps) located at an Atlantic Forest human-modified landscape, São Paulo and Minas Gerais states, Southeastern Brazil.

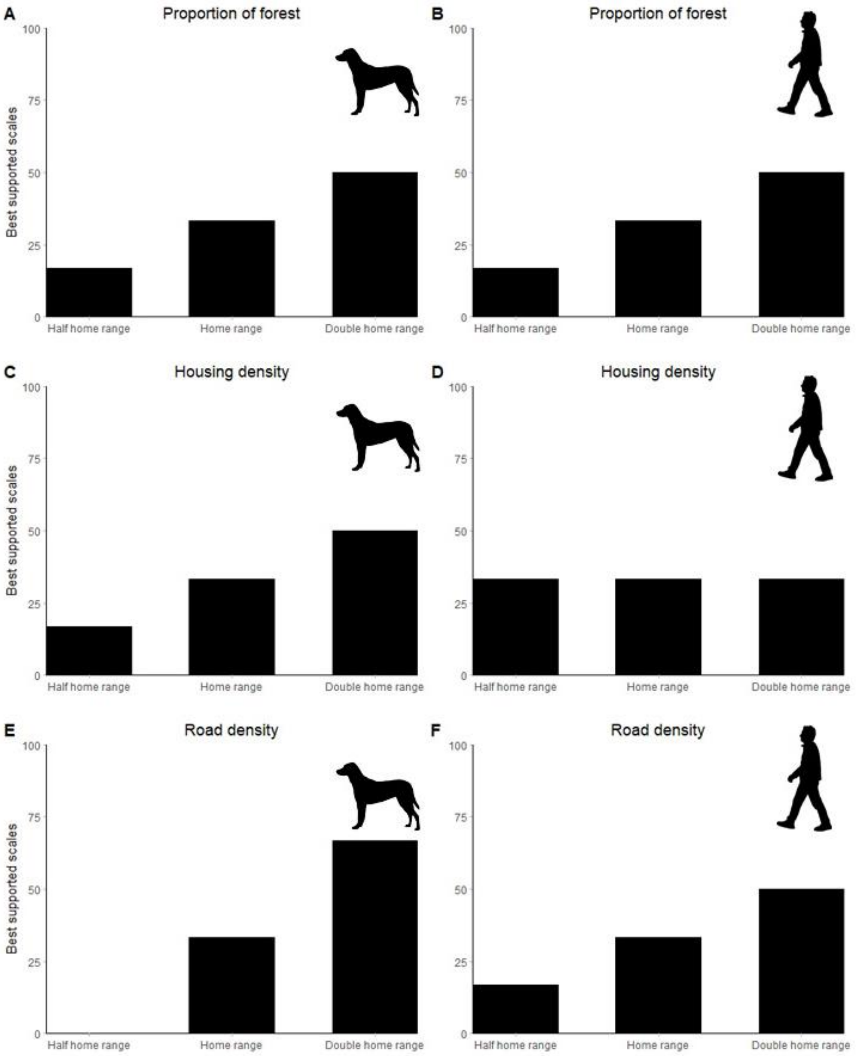


Figure 2. Number of top models, across six target mammal species, in which a given scale was indicated as best based on Akaike's Information Criterion (models with AIC<2) for the effects of the proportion of forest (A, B), housing density (C, D), or road density (E, F) on the probability of site use (ψ) parameter for the target species when either dogs (A, C, E) or humans (B, D, F) were indicated as the dominant species. Tested scales included an area equivalent to the minimum home range size for each native mammal species (estimated from published literature) along with half and double that estimated range size.

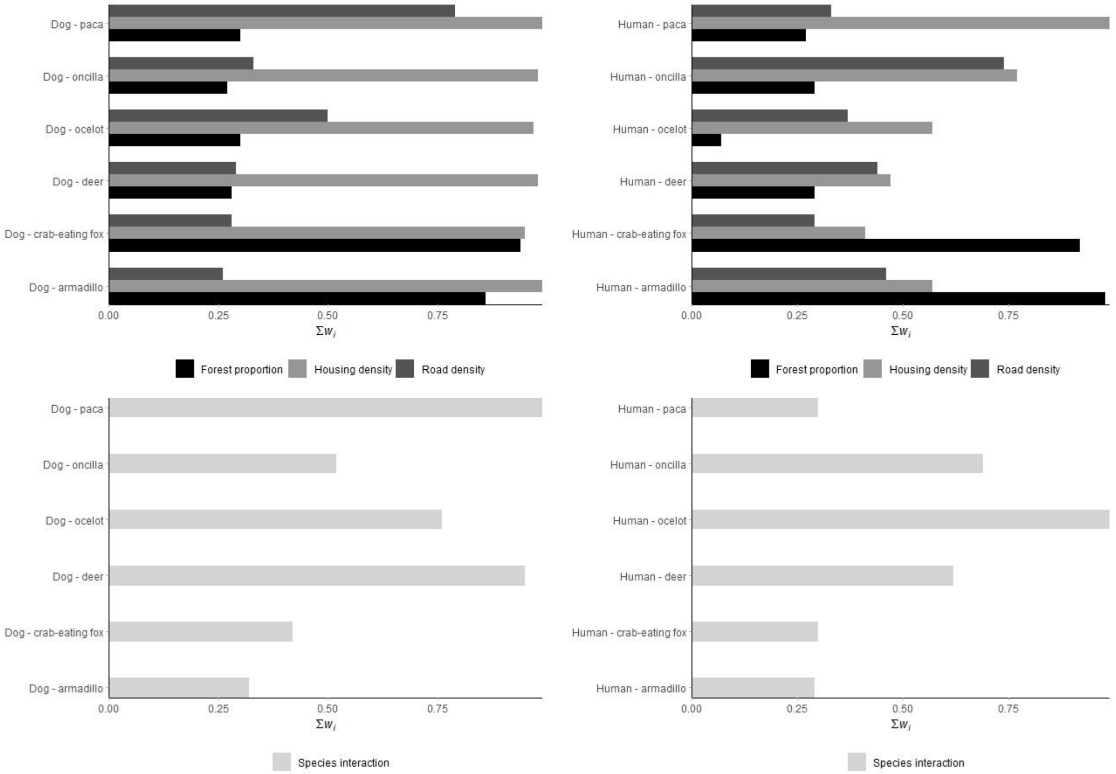


Figure 3. Sum of Akaike weights (w_i) indicating the level of support for the effect of each covariate—forest proportion, housing density, or road density—on the probability of use (ψ) by six native mammals within an Atlantic Forest landscape when either domestic dogs (*Canis familiaris*; top left) or humans (*Homo sapiens*; top right) were identified as the dominant competitor in dynamic, two-species models. Null models (those lacking site covariates) were not plotted as they rarely ranked among the top models and contributed little (<0.2) to the sum of Akaike weights. Bottom panels indicate the estimated species interaction factors, which illustrates the relative, overall effect of the dominant species on the site use patterns of the target species.

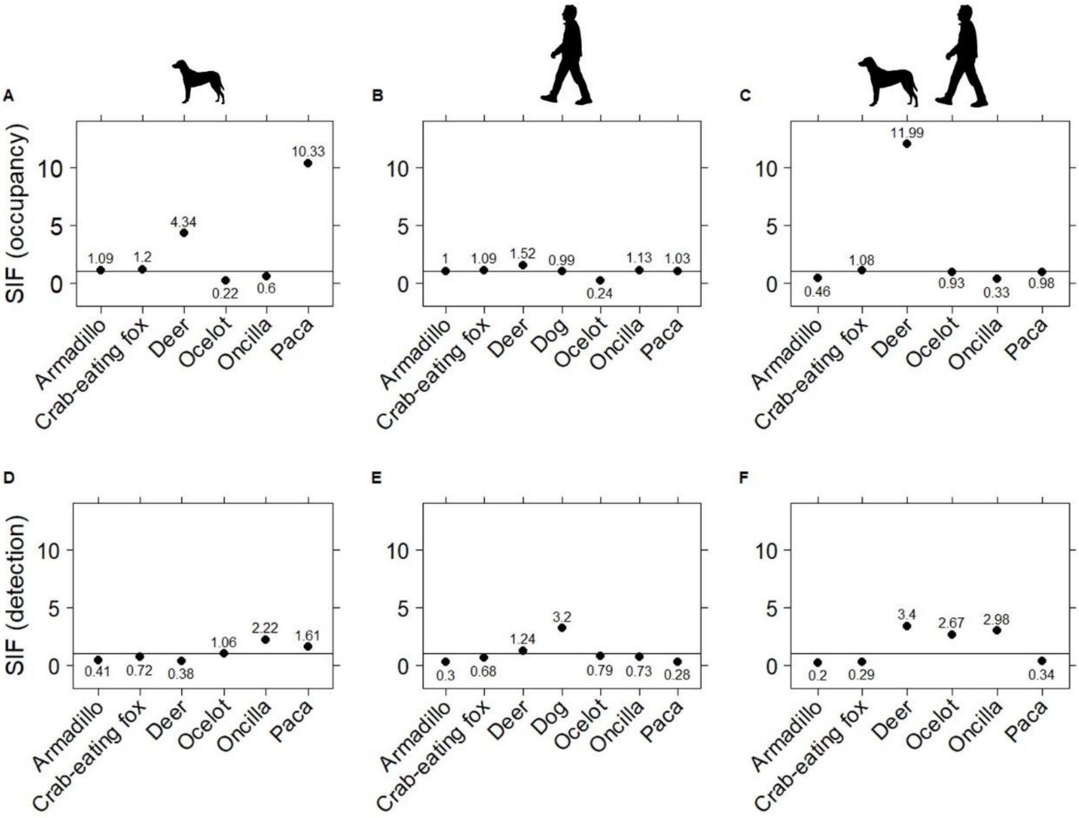


Figure 4. Species interaction factor (SIF) from dynamic co-occurrence models for native mammals and domestic dogs (A and D), humans (B and E), or both domestic dogs and humans detected at the same occasion (C and F). The horizontal line at 1.0 indicates independence between the target and dominant species, whereas SIF<1 indicates spatial avoidance and SIF>1 represents aggregation. Top panels indicate the SIF for the probability of site use while bottom panelse indicated SIF for detection probability.

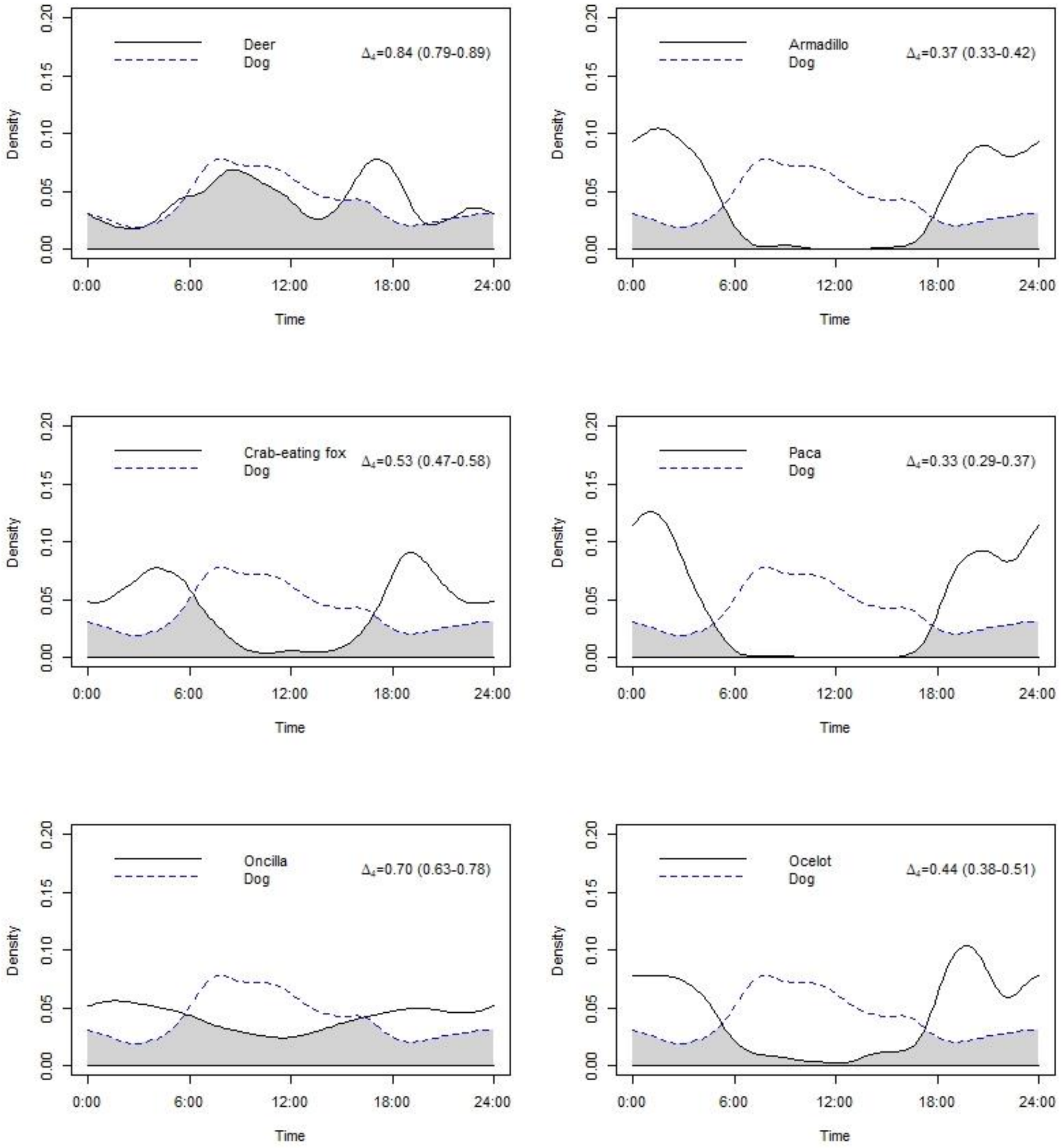


Figure 5. Daily activity patterns of native mammals and dogs within an Atlantic Forest landscape, Brazil. Grey shading indicates activity overlap between each target mammal species and dogs, with the overlap coefficient (Δ) ranging from 0 (no overlap) to 1 (identical activity patterns).

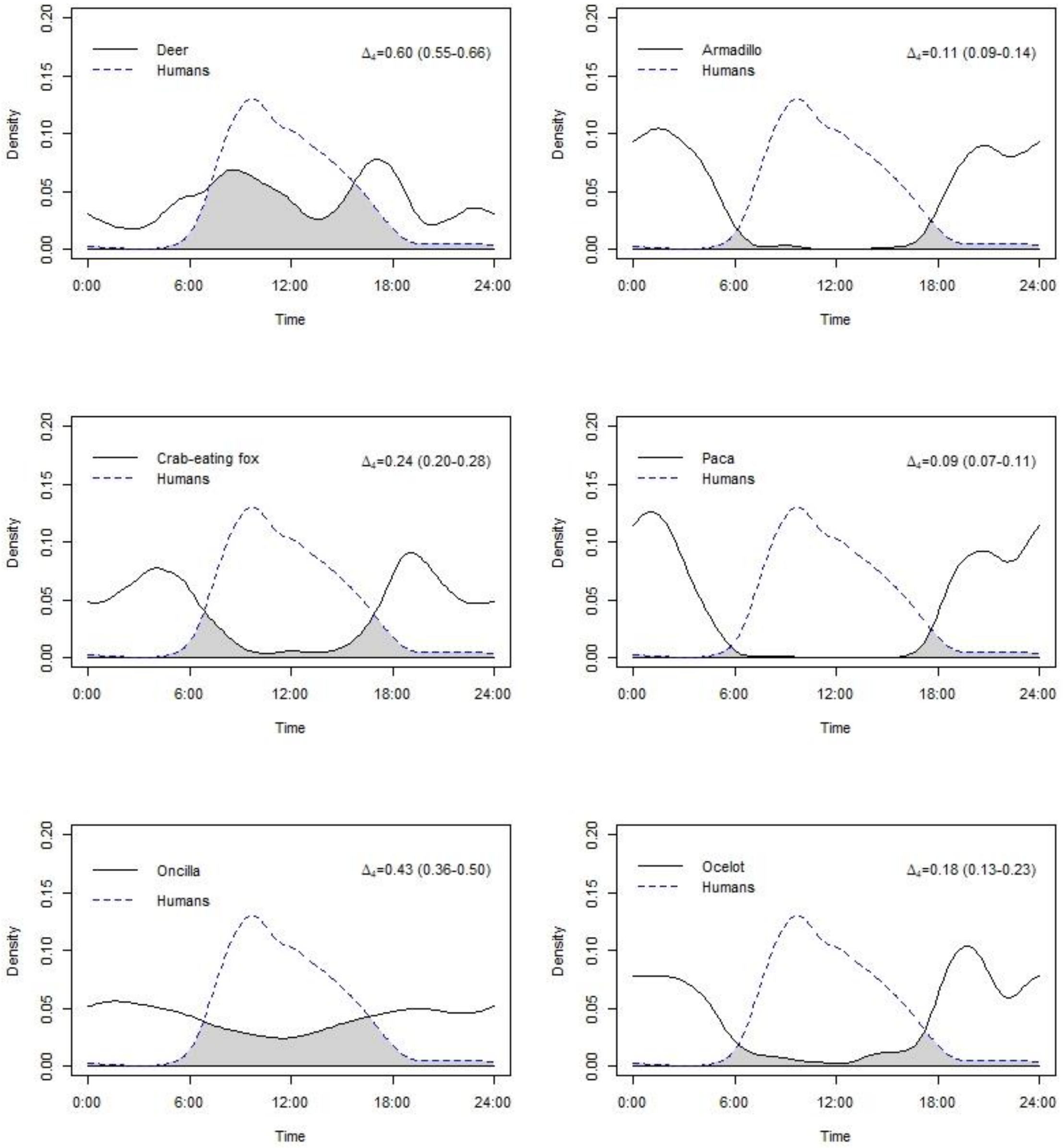
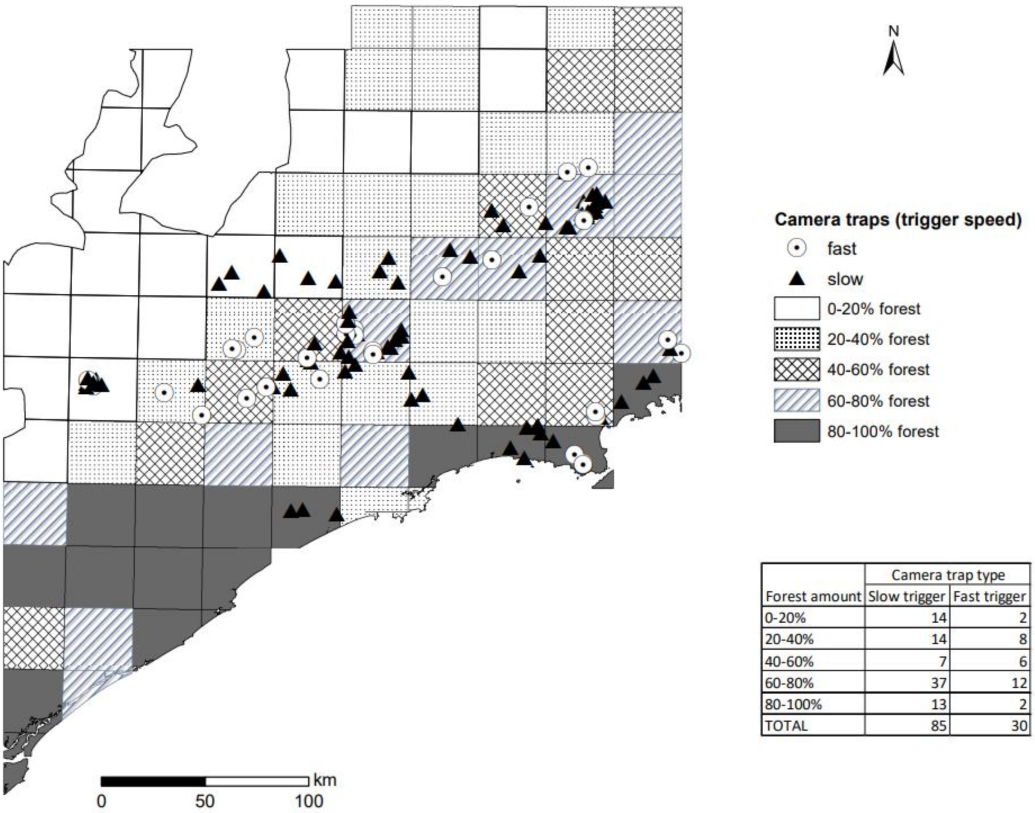


Figure 6. Daily activity patterns of native mammals and humans within an Atlantic Forest landscape, Brazil. Grey shading indicates activity overlap between each target mammal species and humans, with the overlap coefficient (Δ) ranging from 0 (no overlap) to 1 (identical activity patterns).

Appendix 1. Spatial distribution of camera trap models regarding trigger speed across a gradient of forest amount in the area of study.



	Camera trap type	
Forest amount	Slow trigger	Fast trigger
0-20%	14	2
20-40%	14	8
40-60%	7	6
60-80%	37	12
80-100%	13	2
TOTAL	85	30

Appendix 2. Model selection for occupancy, colonization, and extinction probability covariates (percentage forest cover, housing, and road density) at three scales: home range, half, and double the home range size for native mammals and domestic dogs or humans. The covariates included for p, referred as p(global), were trail, a term to indicate species effect on detection (SP), a detection-level interaction where the occurrence of one species changes the detection probability of the other species (INTo), a second detection-level interaction where the detection of one species changes the detection probability of the other species in the same survey (INTd), and an interaction effect of occupancy and detection on detection (SP:INTd).

Armadillo - dog			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor500) γ (.) ε (.) p (global)	0.00	0.53	10
ψ (PFor1000) γ (.) ε (.) p (global)	0.92	0.34	10
ψ (PFor250) γ (.) ε (.) p (global)	2.71	0.14	10

Armadillo - dog			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor1000) ε (.) p (global)	0.00	0.59	10
ψ (.) γ (PFor500) ε (.) p (global)	1.02	0.35	10
ψ (.) γ (PFor250) ε (.) p (global)	4.79	0.05	10

Armadillo - dog			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor500) p (global)	0.00	0.46	10

ψ (.) γ (.) ε (PFor250) p (global)	0.11	0.43	10
ψ (.) γ (.) ε (PFor1000) p (global)	2.83	0.11	10
Armadillo - dog			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (HD1000) γ (.) ε (.) p (global)	0.00	0.75	10
ψ (HD500) γ (.) ε (.) p (global)	2.44	0.22	10
ψ (HD250) γ (.) ε (.) p (global)	6.50	0.03	10
Armadillo - dog			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD1000) ε (.) p (global)	0.00	0.75	10
ψ (.) γ (HD250) ε (.) p (global)	6.33	0.04	10
ψ (.) γ (HD500) ε (.) p (global)	6.47	0.04	10
Armadillo - dog			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.72	10
ψ (.) γ (.) ε (HD250) p (global)	2.69	0.19	10
ψ (.) γ (.) ε (HD500) p (global)	3.98	0.10	10
Armadillo - dog			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD1000) γ (.) ε (.) p (global)	0.00	0.49	10
ψ (RD500) γ (.) ε (.) p (global)	0.77	0.33	10

ψ (RD250) γ (.) ε (.) p (global)	6.50	0.18	10
Armadillo - dog			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD1000) ε (.) p (global)	0.00	0.40	10
ψ (.) γ (RD500) ε (.) p (global)	0.34	0.34	10
ψ (.) γ (RD250) ε (.) p (global)	0.87	0.26	10
Armadillo - dog			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD250) p (global)	0.00	0.54	10
ψ (.) γ (.) ε (HD1000) p (global)	1.69	0.23	10
ψ (.) γ (.) ε (HD500) p (global)	1.72	0.23	10
Paca - dog			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor250) γ (.) ε (.) p (global)	0.00	0.34	10
ψ (PFor500) γ (.) ε (.) p (global)	0.00	0.34	10
ψ (PFor1000) γ (.) ε (.) p (global)	0.10	0.32	10
Paca – dog			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor1000) ε (.) p (global)	0.00	0.55	10
ψ (.) γ (PFor500) ε (.) p (global)	1.10	0.32	10
ψ (.) γ (PFor250) ε (.) p (global)	2.82	0.13	10

Paca – dog

Proportion of forest (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor1000) p (global)	0.00	0.46	10
ψ (.) γ (.) ε (PFor500) p (global)	0.06	0.45	10
ψ (.) γ (.) ε (PFor250) p (global)	3.21	0.09	10

Paca – dog

Housing density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (HD250) γ (.) ε (.) p (global)	0.00	0.53	10
ψ (HD500) γ (.) ε (.) p (global)	0.36	0.44	10
ψ (HD1000) γ (.) ε (.) p (global)	6.36	0.02	10

Paca – dog

Housing density (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD250) ε (.) p (global)	0.00	0.86	10
ψ (.) γ (HD500) ε (.) p (global)	3.84	0.13	10
ψ (.) γ (HD1000) ε (.) p (global)	8.06	0.02	10

Paca – dog

Housing density (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.63	10
ψ (.) γ (.) ε (HD500) p (global)	2.25	0.20	10
ψ (.) γ (.) ε (HD250) p (global)	2.65	0.17	10

Paca - dog

Road density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (RD500) γ (.) ε (.) p (global)	0.00	0.57	10
ψ (RD250) γ (.) ε (.) p (global)	1.73	0.24	10
ψ (RD1000) γ (.) ε (.) p (global)	2.24	0.19	10

Paca – dog

Road density (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.55	10
ψ (.) γ (RD1000) ε (.) p (global)	1.03	0.33	10
ψ (.) γ (RD250) ε (.) p (global)	3.02	0.12	10

Paca – dog

Road density (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.54	10
ψ (.) γ (.) ε (HD250) p (global)	1.54	0.25	10
ψ (.) γ (.) ε (HD1000) p (global)	1.81	0.22	10

Deer - dog

Proportion of forest (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (PFor1000) γ (.) ε (.) p (global)	0.00	0.38	10
ψ (PFor250) γ (.) ε (.) p (global)	0.37	0.32	10
ψ (PFor500) γ (.) ε (.) p (global)	0.50	0.30	10

Deer– dog

Proportion of forest (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor500) ε (.) p (global)	0.00	0.34	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.03	0.33	10
ψ (.) γ (PFor250) ε (.) p (global)	0.09	0.32	10
Deer – dog			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor500) p (global)	0.00	0.38	10
ψ (.) γ (.) ε (PFor250) p (global)	0.20	0.34	10
ψ (.) γ (.) ε (PFor1000) p (global)	0.62	0.28	10
Deer – dog			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (HD1000) γ (.) ε (.) p (global)	0.00	0.94	10
ψ (HD500) γ (.) ε (.) p (global)	5.77	0.05	10
ψ (HD250) γ (.) ε (.) p (global)	10.51	0.01	10
Deer – dog			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD1000) ε (.) p (global)	0.00	0.61	10
ψ (.) γ (HD500) ε (.) p (global)	2.29	0.20	10
ψ (.) γ (HD250) ε (.) p (global)	2.38	0.19	10
Deer – dog			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar

ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.40	10
ψ (.) γ (.) ε (HD250) p (global)	0.34	0.33	10
ψ (.) γ (.) ε (HD500) p (global)	0.80	0.27	10
Deer - dog			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD1000) γ (.) ε (.) p (global)	0.00	0.62	10
ψ (RD500) γ (.) ε (.) p (global)	1.32	0.32	10
ψ (RD250) γ (.) ε (.) p (global)	4.94	0.05	10
Deer – dog			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.36	10
ψ (.) γ (RD250) ε (.) p (global)	0.17	0.33	10
ψ (.) γ (RD1000) ε (.) p (global)	0.32	0.31	10
Deer – dog			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (RD500) p (global)	0.00	0.85	10
ψ (.) γ (.) ε (RD250) p (global)	4.75	0.08	10
ψ (.) γ (.) ε (RD1000) p (global)	4.88	0.07	10
Crab-eating fox - dog			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor2000) γ (.) ε (.) p (global)	0.00	0.83	10

ψ (PFor1000) γ (.) ε (.) p (global)	4.00	0.11	10
ψ (PFor500) γ (.) ε (.) p (global)	5.24	0.06	10
Crab-eating fox– dog			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor500) ε (.) p (global)	0.00	0.37	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.07	0.36	10
ψ (.) γ (PFor2000) ε (.) p (global)	0.66	0.27	10
Crab-eating fox – dog			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor2000) p (global)	0.00	0.57	10
ψ (.) γ (.) ε (PFor1000) p (global)	1.50	0.27	10
ψ (.) γ (.) ε (PFor500) p (global)	2.51	0.16	10
Crab-eating fox – dog			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (HD1000) γ (.) ε (.) p (global)	0.00	0.70	10
ψ (HD500) γ (.) ε (.) p (global)	2.17	0.23	10
ψ (HD2000) γ (.) ε (.) p (global)	4.64	0.07	10
Crab-eating fox – dog			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD1000) ε (.) p (global)	0.00	0.65	10
ψ (.) γ (HD500) ε (.) p (global)	1.63	0.29	10

ψ (.) γ (HD2000) ε (.) p (global)	4.70	0.06	10
Crab-eating fox – dog			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.55	10
ψ (.) γ (.) ε (HD2000) p (global)	0.74	0.38	10
ψ (.) γ (.) ε (HD500) p (global)	3.96	0.08	10
Crab-eating fox - dog			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD2000) γ (.) ε (.) p (global)	0.00	0.91	10
ψ (RD1000) γ (.) ε (.) p (global)	5.87	0.05	10
ψ (RD500) γ (.) ε (.) p (global)	6.17	0.04	10
Crab-eating fox – dog			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.37	10
ψ (.) γ (RD1000) ε (.) p (global)	0.02	0.33	10
ψ (.) γ (RD2000) ε (.) p (global)	0.05	0.30	10
Crab-eating fox – dog			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD2000) p (global)	0.00	0.37	10
ψ (.) γ (.) ε (HD1000) p (global)	0.22	0.33	10
ψ (.) γ (.) ε (HD500) p (global)	0.43	0.30	10

Oncilla - dog

Proportion of forest (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (PFor2000) γ (.) ε (.) p (global)	0.00	0.48	10
ψ (PFor1000) γ (.) ε (.) p (global)	1.11	0.27	10
ψ (PFor500) γ (.) ε (.) p (global)	1.33	0.25	10

Oncilla– dog

Proportion of forest (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor2000) ε (.) p (global)	0.00	0.40	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.33	0.34	10
ψ (.) γ (PFor500) ε (.) p (global)	0.91	0.26	10

Oncilla – dog

Proportion of forest (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor2000) p (global)	0.00	0.54	10
ψ (.) γ (.) ε (PFor500) p (global)	1.49	0.26	10
ψ (.) γ (.) ε (PFor1000) p (global)	1.99	0.20	10

Oncilla – dog

Housing density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (HD1000) γ (.) ε (.) p (global)	0.00	0.75	10
ψ (HD500) γ (.) ε (.) p (global)	2.76	0.19	10
ψ (HD2000) γ (.) ε (.) p (global)	4.97	0.06	10

Oncilla – dog

Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD1000) ε (.) p (global)	0.00	0.63	10
ψ (.) γ (HD500) ε (.) p (global)	1.68	0.27	10
ψ (.) γ (HD2000) ε (.) p (global)	3.59	0.10	10
Oncilla – dog			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD2000) p (global)	0.00	0.46	10
ψ (.) γ (.) ε (HD1000) p (global)	0.07	0.44	10
ψ (.) γ (.) ε (HD500) p (global)	3.06	0.10	10
Oncilla - dog			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD2000) γ (.) ε (.) p (global)	0.00	0.62	10
ψ (RD1000) γ (.) ε (.) p (global)	1.82	0.25	10
ψ (RD500) γ (.) ε (.) p (global)	3.10	0.13	10
Oncilla – dog			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD2000) ε (.) p (global)	0.00	0.39	10
ψ (.) γ (RD1000) ε (.) p (global)	0.34	0.33	10
ψ (.) γ (RD500) ε (.) p (global)	0.61	0.29	10
Oncilla – dog			
Road density (Epsilon)			

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.51	10
ψ (.) γ (.) ε (HD2000) p (global)	1.19	0.28	10
ψ (.) γ (.) ε (HD1000) p (global)	1.85	0.20	10
Ocelot - dog			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor1000) γ (.) ε (.) p (global)	0.00	0.37	10
ψ (PFor500) γ (.) ε (.) p (global)	0.24	0.33	10
ψ (PFor2000) γ (.) ε (.) p (global)	0.36	0.31	10
Ocelot– dog			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor2000) ε (.) p (global)	0.00	0.40	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.33	0.34	10
ψ (.) γ (PFor500) ε (.) p (global)	0.91	0.26	10
Ocelot – dog			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor500) p (global)	0.00	0.37	10
ψ (.) γ (.) ε (PFor1000) p (global)	0.26	0.33	10
ψ (.) γ (.) ε (PFor2000) p (global)	0.39	0.31	10
Ocelot – dog			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar

ψ (HD2000) γ (.) ε (.) p (global)	0.00	0.57	10
ψ (HD1000) γ (.) ε (.) p (global)	0.90	0.36	10
ψ (HD500) γ (.) ε (.) p (global)	4.04	0.08	10
Ocelot – dog			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD1000) ε (.) p (global)	0.00	0.68	10
ψ (.) γ (HD500) ε (.) p (global)	2.33	0.21	10
ψ (.) γ (HD2000) ε (.) p (global)	3.74	0.11	10
Ocelot – dog			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.48	10
ψ (.) γ (.) ε (HD2000) p (global)	0.77	0.33	10
ψ (.) γ (.) ε (HD500) p (global)	1.90	0.19	10
Ocelot – dog			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD1000) γ (.) ε (.) p (global)	0.00	0.41	10
ψ (RD500) γ (.) ε (.) p (global)	0.65	0.30	10
ψ (RD250) γ (.) ε (.) p (global)	0.74	0.29	10
Ocelot – dog			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.69	10

ψ (.) γ (RD1000) ε (.) p (global)	3.01	0.15	10
ψ (.) γ (RD2000) ε (.) p (global)	3.01	0.15	10
Ocelot – dog			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD2000) p (global)	0.00	0.43	10
ψ (.) γ (.) ε (HD1000) p (global)	0.72	0.30	10
ψ (.) γ (.) ε (HD500) p (global)	0.94	0.27	10
Armadillo - human			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor1000) γ (.) ε (.) p (global)	0.00	0.64	10
ψ (PFor500) γ (.) ε (.) p (global)	1.34	0.33	10
ψ (PFor250) γ (.) ε (.) p (global)	6.11	0.03	10
Armadillo– human			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor1000) ε (.) p (global)	0.00	0.52	10
ψ (.) γ (PFor500) ε (.) p (global)	0.89	0.33	10
ψ (.) γ (PFor250) ε (.) p (global)	2.61	0.14	10
Armadillo – human			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor500) p (global)	0.00	0.54	10
ψ (.) γ (.) ε (PFor250) p (global)	1.09	0.31	10

ψ (.) γ (.) ε (PFor1000) p (global)	2.50	0.15	10
Armadillo – human			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (HD500) γ (.) ε (.) p (global)	0.00	0.64	10
ψ (HD250) γ (.) ε (.) p (global)	1.49	0.31	10
ψ (HD1000) γ (.) ε (.) p (global)	5.06	0.05	10
Armadillo – human			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD250) ε (.) p (global)	0.00	0.41	10
ψ (.) γ (HD500) ε (.) p (global)	0.12	0.38	10
ψ (.) γ (HD1000) ε (.) p (global)	1.34	0.21	10
Armadillo – human			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD250) p (global)	0.00	0.80	10
ψ (.) γ (.) ε (HD500) p (global)	3.26	0.16	10
ψ (.) γ (.) ε (HD1000) p (global)	5.73	0.04	10
Armadillo - human			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD250) γ (.) ε (.) p (global)	0.00	0.54	10
ψ (RD1000) γ (.) ε (.) p (global)	1.46	0.26	10
ψ (RD500) γ (.) ε (.) p (global)	1.90	0.21	10

Armadillo – human

Road density (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD1000) ε (.) p (global)	0.00	0.51	10
ψ (.) γ (RD500) ε (.) p (global)	1.29	0.26	10
ψ (.) γ (RD250) ε (.) p (global)	1.59	0.23	10

Armadillo – human

Road density (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.48	10
ψ (.) γ (.) ε (HD1000) p (global)	0.63	0.35	10
ψ (.) γ (.) ε (HD250) p (global)	2.15	0.17	10

Paca - human

Proportion of forest (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (PFor500) γ (.) ε (.) p (global)	0.00	0.39	10
ψ (PFor250) γ (.) ε (.) p (global)	0.28	0.34	10
ψ (PFor1000) γ (.) ε (.) p (global)	0.71	0.27	10

Paca– human

Proportion of forest (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor1000) ε (.) p (global)	0.00	0.41	10
ψ (.) γ (PFor500) ε (.) p (global)	0.00	0.36	10
ψ (.) γ (PFor250) ε (.) p (global)	1.17	0.23	10

Paca – human

Proportion of forest (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor500) p (global)	0.00	0.38	10
ψ (.) γ (.) ε (PFor1000) p (global)	0.11	0.36	10
ψ (.) γ (.) ε (PFor250) p (global)	0.73	0.26	10

Paca – human

Housing density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (HD250) γ (.) ε (.) p (global)	0.00	0.80	10
ψ (HD500) γ (.) ε (.) p (global)	2.84	0.19	10
ψ (HD1000) γ (.) ε (.) p (global)	13.05	0.00	10

Paca – human

Housing density (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD250) ε (.) p (global)	0.00	0.69	10
ψ (.) γ (HD500) ε (.) p (global)	2.14	0.24	10
ψ (.) γ (HD1000) ε (.) p (global)	4.45	0.07	10

Paca – human

Housing density (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.36	10
ψ (.) γ (.) ε (HD250) p (global)	0.02	0.36	10
ψ (.) γ (.) ε (HD1000) p (global)	0.58	0.27	10

Paca - human

Road density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (RD500) γ (.) ε (.) p (global)	0.00	0.35	10
ψ (RD250) γ (.) ε (.) p (global)	0.05	0.34	10
ψ (RD1000) γ (.) ε (.) p (global)	0.24	0.31	10
Paca – human			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD1000) ε (.) p (global)	0.00	0.43	10
ψ (.) γ (RD500) ε (.) p (global)	0.27	0.38	10
ψ (.) γ (RD250) ε (.) p (global)	1.69	0.19	10
Paca – human			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.36	10
ψ (.) γ (.) ε (HD250) p (global)	0.06	0.35	10
ψ (.) γ (.) ε (HD1000) p (global)	0.49	0.28	10
Deer - human			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor250) γ (.) ε (.) p (global)	0.00	0.34	10
ψ (PFor1000) γ (.) ε (.) p (global)	0.04	0.33	10
ψ (PFor500) γ (.) ε (.) p (global)	0.08	0.33	10
Deer– human			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar

ψ (.) γ (PFor250) ε (.) p (global)	0.00	0.37	10
ψ (.) γ (PFor500) ε (.) p (global)	0.31	0.32	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.41	0.31	10
Deer – human			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor1000) p (global)	0.00	0.34	10
ψ (.) γ (.) ε (PFor250) p (global)	0.01	0.33	10
ψ (.) γ (.) ε (PFor500) p (global)	0.02	0.33	10
Deer – human			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (HD500) γ (.) ε (.) p (global)	0.00	0.42	10
ψ (HD1000) γ (.) ε (.) p (global)	0.57	0.32	10
ψ (HD250) γ (.) ε (.) p (global)	1.01	0.26	10
Deer – human			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD500) ε (.) p (global)	0.00	0.70	10
ψ (.) γ (HD1000) ε (.) p (global)	3.08	0.15	10
ψ (.) γ (HD250) ε (.) p (global)	3.11	0.15	10
Deer – human			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.37	10

ψ (.) γ (.) ε (HD500) p (global)	0.33	0.32	10
ψ (.) γ (.) ε (HD250) p (global)	0.35	0.31	10
Deer - human			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD1000) γ (.) ε (.) p (global)	0.00	0.42	10
ψ (RD250) γ (.) ε (.) p (global)	0.23	0.38	10
ψ (RD500) γ (.) ε (.) p (global)	1.53	0.20	10
Deer – human			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.39	10
ψ (.) γ (RD250) ε (.) p (global)	0.36	0.32	10
ψ (.) γ (RD1000) ε (.) p (global)	0.55	0.29	10
Deer – human			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (RD500) p (global)	0.00	0.43	10
ψ (.) γ (.) ε (RD1000) p (global)	0.80	0.29	10
ψ (.) γ (.) ε (RD250) p (global)	0.82	0.28	10
Crab-eating fox - human			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor1000) γ (.) ε (.) p (global)	0.00	0.44	10
ψ (PFor500) γ (.) ε (.) p (global)	0.37	0.36	10

ψ (PFor2000) γ (.) ε (.) p (global)	1.63	0.19	10

Crab-eating fox– human

Proportion of forest (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor500) ε (.) p (global)	0.00	0.51	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.60	0.37	10
ψ (.) γ (PFor2000) ε (.) p (global)	2.92	0.12	10

Crab-eating fox – human

Proportion of forest (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor1000) p (global)	0.00	0.42	10
ψ (.) γ (.) ε (PFor2000) p (global)	0.44	0.34	10
ψ (.) γ (.) ε (PFor500) p (global)	1.07	0.24	10

Crab-eating fox – human

Housing density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (HD500) γ (.) ε (.) p (global)	0.00	0.81	10
ψ (HD1000) γ (.) ε (.) p (global)	4.24	0.10	10
ψ (HD2000) γ (.) ε (.) p (global)	4.28	0.09	10

Crab-eating fox – human

Housing density (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD500) ε (.) p (global)	0.00	0.73	10
ψ (.) γ (HD2000) ε (.) p (global)	3.39	0.13	10
ψ (.) γ (HD1000) ε (.) p (global)	3.41	0.13	10

Crab-eating fox – human			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.43	10
ψ (.) γ (.) ε (HD500) p (global)	0.31	0.36	10
ψ (.) γ (.) ε (HD2000) p (global)	1.44	0.21	10
Crab-eating fox - human			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD2000) γ (.) ε (.) p (global)	0.00	0.49	10
ψ (RD1000) γ (.) ε (.) p (global)	1.25	0.26	10
ψ (RD500) γ (.) ε (.) p (global)	1.39	0.25	10
Crab-eating fox – human			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.34	10
ψ (.) γ (RD2000) ε (.) p (global)	0.02	0.33	10
ψ (.) γ (RD1000) ε (.) p (global)	0.04	0.33	10
Crab-eating fox – human			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (RD1000) p (global)	0.00	0.38	10
ψ (.) γ (.) ε (RD500) p (global)	0.17	0.35	10
ψ (.) γ (.) ε (RD2000) p (global)	0.68	0.27	10
Oncilla - human			

Proportion of forest (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (PFor500) γ (.) ε (.) p (global)	0.00	0.35	10
ψ (PFor1000) γ (.) ε (.) p (global)	0.04	0.34	10
ψ (PFor2000) γ (.) ε (.) p (global)	0.21	0.31	10

Oncilla– human

Proportion of forest (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor2000) ε (.) p (global)	0.00	0.45	10
ψ (.) γ (PFor500) ε (.) p (global)	0.97	0.28	10
ψ (.) γ (PFor1000) ε (.) p (global)	0.98	0.27	10

Oncilla – human

Proportion of forest (Epsilon)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor1000) p (global)	0.00	0.37	10
ψ (.) γ (.) ε (PFor500) p (global)	0.16	0.34	10
ψ (.) γ (.) ε (PFor2000) p (global)	0.55	0.28	10

Oncilla – human

Housing density (Psi)

Models	Δ AIC	AIC weight	NPar
ψ (HD2000) γ (.) ε (.) p (global)	0.00	0.36	10
ψ (HD500) γ (.) ε (.) p (global)	0.15	0.33	10
ψ (HD1000) γ (.) ε (.) p (global)	0.23	0.32	10

Oncilla – human

Housing density (Gamma)

Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD500) ε (.) p (global)	0.00	0.66	10
ψ (.) γ (HD2000) ε (.) p (global)	2.72	0.17	10
ψ (.) γ (HD1000) ε (.) p (global)	2.74	0.17	10
Oncilla – human			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.54	10
ψ (.) γ (.) ε (HD1000) p (global)	0.82	0.36	10
ψ (.) γ (.) ε (HD2000) p (global)	3.23	0.11	10
Oncilla - human			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD2000) γ (.) ε (.) p (global)	0.00	0.44	10
ψ (RD1000) γ (.) ε (.) p (global)	0.72	0.30	10
ψ (RD500) γ (.) ε (.) p (global)	1.05	0.26	10
Oncilla – human			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD2000) ε (.) p (global)	0.00	0.44	10
ψ (.) γ (RD500) ε (.) p (global)	0.78	0.30	10
ψ (.) γ (RD1000) ε (.) p (global)	1.03	0.26	10
Oncilla – human			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar

ψ (.) γ (.) ε (HD1000) p (global)	0.00	0.41	10
ψ (.) γ (.) ε (HD2000) p (global)	0.45	0.33	10
ψ (.) γ (.) ε (HD500) p (global)	0.96	0.26	10
Ocelot - human			
Proportion of forest (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (PFor1000) γ (.) ε (.) p (global)	0.00	0.41	10
ψ (PFor2000) γ (.) ε (.) p (global)	0.23	0.36	10
ψ (PFor500) γ (.) ε (.) p (global)	1.14	0.23	10
Ocelot– human			
Proportion of forest (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (PFor2000) ε (.) p (global)	0.00	0.49	10
ψ (.) γ (PFor500) ε (.) p (global)	1.00	0.30	10
ψ (.) γ (PFor1000) ε (.) p (global)	1.69	0.21	10
Ocelot – human			
Proportion of forest (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (PFor500) p (global)	0.00	0.38	10
ψ (.) γ (.) ε (PFor1000) p (global)	0.25	0.34	10
ψ (.) γ (.) ε (PFor2000) p (global)	0.62	0.28	10
Ocelot – human			
Housing density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (HD1000) γ (.) ε (.) p (global)	0.00	0.54	10

ψ (HD2000) γ (.) ε (.) p (global)	1.28	0.28	10
ψ (HD500) γ (.) ε (.) p (global)	2.21	0.18	10
Ocelot – human			
Housing density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (HD500) ε (.) p (global)	0.00	0.99	10
ψ (.) γ (HD1000) ε (.) p (global)	11.59	0.00	10
ψ (.) γ (HD2000) ε (.) p (global)	11.63	0.00	10
Ocelot – human			
Housing density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD2000) p (global)	0.00	0.37	10
ψ (.) γ (.) ε (HD500) p (global)	0.01	0.37	10
ψ (.) γ (.) ε (HD1000) p (global)	0.66	0.26	10
Ocelot - human			
Road density (Psi)			
Models	Δ AIC	AIC weight	NPar
ψ (RD1000) γ (.) ε (.) p (global)	0.00	0.36	10
ψ (RD500) γ (.) ε (.) p (global)	0.21	0.32	10
ψ (RD2000) γ (.) ε (.) p (global)	0.22	0.32	10
Ocelot – human			
Road density (Gamma)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (RD500) ε (.) p (global)	0.00	0.42	10
ψ (.) γ (RD2000) ε (.) p (global)	0.75	0.29	10

ψ (.) γ (RD1000) ε (.) p (global)	0.79	0.28	10
Ocelot – human			
Road density (Epsilon)			
Models	Δ AIC	AIC weight	NPar
ψ (.) γ (.) ε (HD500) p (global)	0.00	0.45	10
ψ (.) γ (.) ε (HD2000) p (global)	0.92	0.28	10
ψ (.) γ (.) ε (HD1000) p (global)	1.09	0.26	10

Covariates: PFor: Proportion of forest within buffers around camera traps; HD: housing density within buffers around camera traps; RD: road density within buffers around camera traps. The buffer radius varied from 250 m to 2000 m depending on the species pair. ψ = probability that the area is initially occupied by the species; γ = colonization probability or probability that the species occupy the area between time t and t+1 when it did not in time t; ε = extinction probability or probability that the species do not occupy the area between time t and t+1 when it did in time t; p(global) = trail + SP + INTo + INTd + SP:INT. SP = species effect on detection (pB,rBa or rBA ≠ pA,rA); INTo = interaction effect of occupancy on detection (pBa or pBA ≠ rBa or rBA); INTd = interaction effect of detection on detection (rBa or rBA ≠ rA); SP:INTd = interaction effect of occupancy and detection on detection (rBa ≠ rBA).

Appendix 3. Top models and untransformed coefficient of covariates in dynamic co-occurrence models between domestic dogs (Canis familiaris) or humans and native mammals (armadillo, paca, deer, crab-eating fox, oncilla, and ocelot). Only models with delta AIC < 2 were included.

Armadillo - dog

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψ A	Intercept ψ Ba	Forest proportion	HD	RD
1	0.00	0.03	14	0.54 (0.32)		-0.69 (0.31)	1.31 (0.98)	
2	0.26	0.02	13	0.47 (0.33)		-0.70 (0.31)	1.34 (0.98)	
3	0.56	0.02	13	0.62 (0.32)		-0.65 (0.30)	1.33 (0.98)	
4	1.06	0.02	15	0.53 (0.32)		-0.64 (0.30)	1.38 (0.99)	
5	1.18	0.01	14	0.52 (0.32)	-0.68 (0.66)	-0.64 (0.28)	1.27 (0.94)	
6	1.24	0.01	14	0.47 (0.32)		-0.68 (0.30)	1.36 (0.98)	
7	1.41	0.01	12	0.58 (0.32)		-0.67 (0.30)	1.33 (0.97)	
8	1.42	0.01	14	0.61 (0.32)		-0.59 (0.29)	1.41 (0.99)	
9	1.44	0.01	15	0.55 (0.33)		-0.68 (0.31)	1.31 (1.00)	
10	1.50	0.01	15	0.54 (0.32)		-0.75 (0.31)	1.23 (0.96)	
11	1.51	0.01	15	0.52 (0.32)		-0.69(0.31)	1.31 (0.98)	
12	1.63	0.01	15	0.55 (0.32)	-0.45 (0.73)	-0.65 (0.29)	1.28 (0.95)	
13	1.74	0.01	14	0.46 (0.32)		-0.71 (0.31)	1.34 (0.98)	
14	1.87	0.01	14	0.63 (0.33)		-0.63 (0.32)	1.33 (1.01)	
15	1.92	0.01	15	0.54 (0.32)		-0.69 (0.30)	1.36 (0.97)	
16	1.94	0.01	14	0.47 (0.33)		-0.68 (0.31)	1.36 (1.00)	
17	1.97	0.01	14	0.63 (0.32)		-0.72 (0.31)	1.23 (0.95)	

18	1.98	0.01	15	0.52 (0.34)		-0.69 (0.31)	1.30 (0.98)	-0.06 (0.38)

Paca - dog

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψ A	Intercept ψ Ba	Forest proportion	HD	RD
1	0.00	0.04	16	0.01 (0.21)	-2.35 (0.74)		1.34 (0.54)	
2	0.24	0.03	15	-0.01 (0.21)	-2.39 (0.75)		1.30 (0.51)	
3	0.31	0.03	15	0.01 (0.21)	-2.39 (0.82)		1.34 (0.54)	
4	0.38	0.03	14	0.02 (0.22)	-2.38 (0.79)		1.42 (0.59)	
5	0.55	0.03	14	-0.01 (0.21)	-2.42 (0.82)		1.30 (0.51)	
6	0.61	0.03	13	0.01 (0.22)	-2.40 (0.80)		1.38 (0.56)	
7	0.66	0.03	15	0.02 (0.22)	-2.36 (0.74)		1.43 (0.59)	
8	0.77	0.02	16	-0.02 (0.22)	-2.26 (0.75)		1.39 (0.57)	
9	0.90	0.02	14	-0.00 (0.22)	-2.38 (0.75)		1.38 (0.56)	
10	1.08	0.02	14	0.00 (0.23)	-2.34 (0.80)		1.46 (0.59)	
11	1.08	0.02	15	0.02 (0.23)	-2.34 (0.77)		1.45 (0.63)	
12	1.08	0.02	17	0.00 (0.22)	-2.23 (0.74)		1.45 (0.59)	
13	1.19	0.02	15	-0.00 (0.23)	-2.30 (0.75)		1.47 (0.59)	
14	1.24	0.02	15	-0.01 (0.22)	-2.31 (0.82)		1.38 (0.56)	
15	1.25	0.02	17	0.00 (0.21)	-2.34 (0.74)		1.35 (0.54)	
16	1.25	0.02	16	0.01 (0.21)	-2.34 (0.80)		1.34 (0.54)	
17	1.38	0.02	14	-0.00 (0.22)	-2.37 (0.77)		1.39 (0.56)	
18	1.44	0.02	15	0.02 (0.23)	-2.31 (0.79)		1.50 (0.62)	
19	1.51	0.02	16	0.10 (0.24)	-2.38 (0.76)		1.65 (0.67)	
20	1.52	0.02	16	-0.02 (0.21)	-2.37 (0.75)		1.30 (0.51)	

21	1.54	0.02	16	0.01 (0.22)	-2.27 (0.81)		1.42 (0.60)	
22	1.54	0.02	15	-0.01 (0.21)	-2.38 (0.80)		1.30 (0.51)	
23	1.56	0.02	16	0.02 (0.23)	-2.27 (0.74)		1.52 (0.61)	
24	1.62	0.02	16	0.02 (0.22)	-2.33 (0.73)		1.45 (0.60)	
25	1.62	0.02	16	-0.00 (0.21)	-2.39 (0.75)		1.32 (0.52)	
26	1.65	0.02	17	0.02 (0.22)	-2.36 (0.75)		1.37 (0.56)	
27	1.75	0.02	14	0.02 (0.22)	-2.41 (0.79)		1.41 (0.57)	
28	1.81	0.01	15	0.04 (0.23)	-2.38 (0.79)		1.46 (0.61)	
29	1.91	0.01	15	0.01 (0.21)	-2.43 (0.82)		1.32 (0.52)	
30	1.91	0.01	15	-0.00 (0.22)	-2.36 (0.74)		1.39 (0.56)	
31	1.93	0.01	16	0.02 (0.21)	-2.39 (0.82)		1.36 (0.56)	
32	1.95	0.01	15	-0.00 (0.23)	-2.30 (0.78)		1.47 (0.60)	

Deer - dog

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψ A	Intercept ψ Ba	Forest proportion	HD	RD
1	0.00	0.05	13	-0.04 (0.18)	-1.57 (0.58)		0.65 (0.29)	
2	0.71	0.03	14	-0.07 (0.19)	-1.48 (0.59)		0.65 (0.29)	
3	1.13	0.03	14	-0.05 (0.18)	-1.40 (0.620		0.65 (0.29)	
4	1.50	0.02	14	-0.04 (0.18)	-1.56 (0.58)		0.64 (0.28)	
5	1.82	0.02	14	-0.04 (0.18)	-1.57 (0.58)		0.65 (0.29)	
6	1.85	0.02	14	-0.02 (0.19)	-1.58 (0.58)		0.61 (0.31)	
7	1.90	0.02	14	-0.04(0.18)	-1.58 (0.58)		0.65 (0.29)	
8	1.96	0.02	14	-0.05 (0.19)	-1.57 (0.58)	-0.03 (0.16)	0.64 (0.30)	
9	2.00	0.02	14	-0.04 (0.19)	-1.57 (0.58)		0.66 (0.31)	

Crab-eating fox - dog

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψ A	Intercept ψ Ba	Forest proportion	HD	RD
1	0.00	0.03	14	0.54 (0.32)		-0.69 (0.31)	1.31 (0.98)	
2	0.26	0.02	13	0.47 (0.33)		-0.70 (0.31)	1.34 (0.98)	
3	0.56	0.02	13	0.62 (0.32)		-0.65 (0.30)	1.33 (0.98)	
4	1.06	0.02	15	0.53 (0.32)		-0.64 (0.30)	1.38 (0.99)	
5	1.18	0.01	14	0.52 (0.32)	-0.68 (0.66)	-0.64 (0.28)	1.27 (0.94)	
6	1.24	0.01	14	0.47 (0.32)		-0.68 (0.30)	1.36 (0.98)	
7	1.41	0.01	12	0.58 (0.32)		-0.67 (0.30)	1.33 (0.97)	
8	1.42	0.01	14	0.61 (0.32)		-0.59 (0.29)	1.41 (0.99)	
9	1.44	0.01	15	0.55 (0.33)		-0.68 (0.31)	1.31 (1.00)	
10	1.50	0.01	15	0.54 (0.32)		-0.75 (0.31)	1.23 (0.96)	
11	1.51	0.01	15	0.52 (0.32)		-0.69(0.31)	1.31 (0.98)	
12	1.63	0.01	15	0.55 (0.32)	-0.45 (0.73)	-0.65 (0.29)	1.28 (0.95)	
13	1.74	0.01	14	0.46 (0.32)		-0.71 (0.31)	1.34 (0.98)	
14	1.87	0.01	14	0.63 (0.33)		-0.63 (0.32)	1.33 (1.01)	
15	1.92	0.01	15	0.54 (0.32)		-0.69 (0.30)	1.36 (0.97)	
16	1.94	0.01	14	0.47 (0.33)		-0.68 (0.31)	1.36 (1.00)	
17	1.97	0.01	14	0.63 (0.32)		-0.72 (0.31)	1.23 (0.95)	
18	1.98	0.01	15	0.52 (0.34)		-0.69 (0.31)	1.30 (0.98)	-0.06 (0.38)
19	2.08	0.01	15	0.52 (0.32)	-0.70 (0.65)	-0.62 (0.28)	1.28 (0.93)	

Oncilla - dog

Untransformed coefficients of covariates (SE)

Models	Δ AIC	AIC weight	NPar	Intercept ψ A	Intercept ψ Ba	Forest proportion	HD	RD
1	0.00	0.04	11	0.52 (0.26)			1.11 (0.64)	
2	0.13	0.04	12	0.49 (0.26)	1.00 (0.92)		1.21 (0.65)	
3	1.09	0.02	13	0.49 (0.25)	1.07 (0.90)		1.23 (0.68)	
4	1.28	0.02	15	0.54 (0.24)	1.16 (0.94)		1.17 (0.62)	
5	1.34	0.02	12	0.54 (0.26)			1.12 (0.67)	
6	1.65	0.02	12	0.52 (0.26)			1.11 (0.64)	
7	1.75	0.02	12	0.52 (0.26)			1.11 (0.64)	
8	1.78	0.02	13	0.49 (0.26)	1.01 (0.93)		1.20 (0.65)	
9	1.83	0.02	13	0.49 (0.26)	1.01 (0.91)		1.21 (0.65)	
10	1.87	0.02	12	0.53 (0.27)			1.11 (0.67)	
11	1.91	0.02	12	0.52 (0.26)			1.13 (0.64)	
12	1.95	0.02	13	0.48 (0.27)	0.98 (0.86)		1.20 (0.65)	
13	1.97	0.02	13	0.50 (0.27)	1.01 (0.91)		1.19 (0.67)	
14	1.97	0.02	12	0.52 (0.26)			1.10 (0.65)	
15	1.99	0.02	12	0.52 (0.26)			1.11 (0.64)	

Ocelot - dog

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.03	13	2.10 (0.78)			5.35 (2.42)	
2	0.45	0.03	13	2.09 (7.83)			5.23 (2.42)	
3	1.02	0.02	17	2.57 (0.96)			6.92 (2.94)	
4	1.02	0.02	17	2.57 (0.96)			6.92 (2.94)	

5	1.55	0.02	15	2.12 (0.79)			5.53 (2.44)	
6	1.55	0.02	15	2.12 (0.79)			5.53 (2.44)	
7	1.55	0.02	15	2.12 (0.79)			5.53 (2.44)	
8	1.55	0.02	15	2.12 (0.79)			5.53 (2.44)	
9	1.78	0.01	17	2.57 (0.96)			6.89 (2.94)	
10	1.79	0.01	17	2.57 (0.95)			6.91 (2.92)	
11	1.96	0.01	14	2.08 (0.78)			5.25 (2.42)	

Armadillo - human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.02	15	-0.38 (0.19)		-0.45 (0.17)	0.38 (0.26)	
2	0.46	0.02	14	-0.42 (0.18)		-0.52 (0.16)		
3	0.94	0.02	16	-0.40 (0.19)		-0.43 (0.17)	0.36 (0.26)	
4	0.96	0.01	14	-0.39 (0.19)		-0.45 (0.16)	0.36 (0.25)	
5	1.15	0.01	15	-0.45 (0.19)		-0.50 (0.160		
6	1.16	0.01	16	-0.37 (0.19)		-0.44 (0.17)	0.39 (0.27)	
7	1.29	0.01	13	-0.42 (0.18)		-0.52 (0.16)		
8	1.51	0.01	17	-0.39 (0.19)		-0.42 (0.17)	0.37 (0.27)	
9	1.67	0.01	15	-0.42 (0.18)		-0.51 (0.16)		
10	1.68	0.01	15	-0.44 (0.18)		-0.49 (0.16)		
11	1.75	0.01	16	-0.44 (0.18)		-0.49 (0.16)		
12	1.81	0.01	13	-0.37 (0.20)		-0.45 (0.17)	0.43 (0.29)	
13	1.85	0.01	15	-0.41 (0.19)		-0.44 (0.17)	0.34 (0.25)	
14	1.92	0.01	16	-0.42 (0.24)	0.13 (0.45)	-0.46 (0.17)	0.38 (0.26)	

15	1.94	0.01	14	-0.44 (0.18)		-0.50 (0.16)		
16	2.00	0.01	16	-0.38 (0.19)		-0.45 (0.17)	0.39 (0.28)	

Paca - human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.04	16	0.01 (0.21)	-2.35 (0.74)		1.34 (0.54)	
2	0.24	0.03	15	-0.01 (0.21)	-2.39 (0.75)		1.30 (0.51)	
3	0.31	0.03	15	0.01 (0.21)	-2.39 (0.82)		1.34 (0.54)	
4	0.38	0.03	14	0.02 (0.22)	-2.38 (0.79)		1.42 (0.59)	
5	0.55	0.03	14	-0.01 (0.21)	-2.42 (0.82)		1.30 (0.51)	
6	0.61	0.03	13	0.01 (0.22)	-2.40 (0.80)		1.38 (0.56)	
7	0.66	0.03	15	0.02 (0.22)	-2.36 (0.74)		1.43 (0.59)	
8	0.77	0.02	16	-0.02 (0.22)	-2.26 (0.75)		1.39 (0.57)	
9	0.90	0.02	14	-0.00 (0.22)	-2.38 (0.75)		1.38 (0.56)	
10	1.08	0.02	14	0.00 (0.23)	-2.34 (0.80)		1.46 (0.59)	
11	1.08	0.02	15	0.02 (0.23)	-2.34 (0.77)		1.45 (0.63)	
12	1.08	0.02	17	0.00 (0.22)	-2.23 (0.74)		1.45 (0.59)	
13	1.19	0.02	15	-0.00 (0.23)	-2.30 (0.75)		1.47 (0.59)	
14	1.24	0.02	15	-0.01 (0.22)	-2.31 (0.82)		1.38 (0.56)	
15	1.25	0.02	17	0.00 (0.21)	-2.34 (0.74)		1.35 (0.54)	
16	1.25	0.02	16	0.01 (0.21)	-2.34 (0.80)		1.34 (0.54)	
17	1.38	0.02	14	-0.00 (0.22)	-2.37 (0.77)		1.39 (0.56)	
18	1.44	0.02	15	0.02 (0.23)	-2.31 (0.79)		1.50 (0.62)	
19	1.51	0.02	16	0.10 (0.24)	-2.38 (0.76)		1.65 (0.67)	

20	1.52	0.02	16	-0.02 (0.21)	-2.37 (0.75)		1.30 (0.51)	
21	1.54	0.02	16	0.01 (0.22)	-2.27 (0.81)		1.42 (0.60)	
22	1.54	0.02	15	-0.01 (0.21)	-2.38 (0.80)		1.30 (0.51)	
23	1.56	0.02	16	0.02 (0.23)	-2.27 (0.74)		1.52 (0.61)	
24	1.62	0.02	16	0.02 (0.22)	-2.33 (0.73)		1.45 (0.60)	
25	1.62	0.02	16	-0.00 (0.21)	-2.39 (0.75)		1.32 (0.52)	
26	1.65	0.02	17	0.02 (0.22)	-2.36 (0.75)		1.37 (0.56)	
27	1.75	0.02	14	0.02 (0.22)	-2.41 (0.79)		1.41 (0.57)	
28	1.81	0.01	15	0.04 (0.23)	-2.38 (0.79)		1.46 (0.61)	
29	1.91	0.01	15	0.01 (0.21)	-2.43 (0.82)		1.32 (0.52)	
30	1.91	0.01	15	-0.00 (0.22)	-2.36 (0.74)		1.39 (0.56)	
31	1.93	0.01	16	0.02 (0.21)	-2.39 (0.82)		1.36 (0.56)	
32	1.95	0.01	15	-0.00 (0.23)	-2.30 (0.78)		1.47 (0.60)	

Deer - human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.03	12	-0.55 (0.20)	-0.64 (0.39)		0.36 (0.22)	
2	0.88	0.02	11	-0.73 (0.17)			0.34 (0.22)	
3	0.97	0.02	11	-0.56 (0.19)	-0.62 (0.38)			
4	1.06	0.02	13	-0.55 (0.20)	-0.64 (0.39)		0.37 90.230	
5	1.21	0.02	13	-0.51 (0.21)	-0.65 (0.39)		0.32 (0.23)	0.20 (0.23)
6	1.38	0.01	12	-0.51 (020)	-0.63 (0.39)		0.27 (0.21)	
7	1.48	0.01	13	-0.55 (0.20)	-0.64 (0.39)		0.36 (0.22)	
8	1.74	0.01	13	-0.56 (0.20)	-0.63 (0.39)		0.36 (0.23)	

9	1.76	0.01	13	-0.56 (0.20)	-0.63 (0.39)		0.36 (0.22)	
10	1.77	0.01	10	-0.73 (0.16)				
11	1.86	0.01	11	-0.56 (0.20)	-0.66 (0.40)		0.31 (0.23)	
12	1.87	0.01	13	-0.55 (0.20)	-0.63 (0.39)		0.35 (0.23)	
13	1.95	0.01	10	-0.57 (0.20)	-0.66 (0.39)			
14	1.95	0.01	12	-0.73 (0.17)			0.35 (0.22)	
15	1.96	0.01	13	-0.55 (0.20)	-.64 (0.39)	-0.03 (0.15)	0.35 (0.23)	
16	2.00	0.01	13	-0.55 (0.20)	-0.64 (0.39)		0.36 (0.23)	

Crab-eating fox - human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0	0.03	12	-0.14 (0.22)		-0.54 (0.20)		
2	0.4145	0.03	12	-0.16 (0.22)		-0.57 (0.21)		
3	0.4356	0.03	12	-0.12 (0.22)		-0.49 (0.22)	0.21 (0.28)	
4	0.6639	0.02	12	-0.15 (0.22)		-0.55 (0.21)		
5	0.6842	0.02	12	-0.07 (0.25)	-0.29 (0.50)	-0.55 (0.20)		
6	0.8993	0.02	12	-0.13 (0.22)		-0.53 (0.21)		0.07 (0.20)
7	0.9309	0.02	12	-0.15 (0.22)		-0.55 (0.21)		
8	1.0133	0.02	12	-0.15 (0.22)		-0.55 (0.21)		
9	1.3799	0.02	13	-0.15 (0.22)		-0.57 (0.21)		
10	1.3955	0.02	13	-0.11 (0.22)		-0.50 (0.21)	0.21 (0.28)	
11	1.7458	0.01	13	-0.07 (0.25)	-0.25 (0.51)	-0.55 (0.20)		
12	1.8283	0.01	13	-0.14 (0.22)		-0.52 (0.22)	0.20 (0.28)	
13	1.8792	0.01	13	-0.12 (0.22)		-0.53 (0.21)		0.07 (0.19)

14	1.8866	0.01	13	-0.14 (0.22)		-0.55 (0.21)		
15	1.961	0.01	13	-0.14 (0.22)		-0.55 (0.21)		

Oncilla - human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.06	13	-0.13 (0.20)			-0.65 (0.28)	0.59 (0.27)
2	1.17	0.03	13	-0.23 (0.22)	0.93 (0.54)		-0.64 (0.26)	0.55 (0.27)
3	1.18	0.03	14	-0.21 (0.22)	0.47 (0.53)		-0.65 (0.27)	0.59 (0.27)
4	1.39	0.03	14	-0.14 (0.20)			-0.65 (0.28)	0.60 (0.27)
5	1.47	0.03	14	-0.17 (0.20)			-0.64 (0.27)	0.60 (0.27)
6	1.58	0.03	14	-0.15 (0.20)			-0.65 (0.27)	0.60 (0.27)
7	1.70	0.02	14	-0.14 (0.20)			-0.64 (0.27)	0.59 (0.27)
8	1.98	0.02	14	-0.13 (0.21)		0.02 (0.17)	-0.65 (0.28)	0.60 (0.28)

Ocelot - human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	1.00	13	-0.37 (0.20)	1.43 (0.89)		-0.69 (0.43)	
2	0.48	0.79	15	-0.45 (0.21)	1.26 (0.76)		-0.72 (0.44)	
3	1.13	0.57	14	-0.37 (0.20)	1.44 (0.97)		-0.70 (0.44)	
4	1.40	0.50	14	-0.33 (0.21)	1.41 (0.87)		-0.76 (0.44)	0.23 (0.30)
5	1.48	0.48	16	-0.45 (0.21)	1.26 (0.81)		-0.72 (0.44)	
6	1.68	0.43	16	-0.40 (0.22)	1.25 (0.75)		-0.81 (0.45)	0.27 (0.31)
7	1.97	0.37	14	-0.37 (0.20)	1.47 (0.92)		-0.71 (0.44)	

8	1.99	0.37	14	-0.37 (0.20)	1.43 (0.89)		-0.69 (0.43)	

Armadillo – dog and human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.35	19	-0.86 (0.25)	0.76 (0.40)	-0.41 (0.16)	0.33 (0.24)	
2	1.03	0.21	18	-0.82 (0.24)	0.73 (0.40)	-0.40 (0.16)	0.33 (0.24)	
3	1.67	0.15	17	-0.86 (0.25)	0.74 (0.40)	-0.44 (0.17)	0.33 (0.24)	

Paca – dog and human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.08	16	-0.92 (0.20)			1.16 (0.34)	
2	0.19	0.07	15	-0.92 (0.20)			1.15 (0.34)	
3	0.51	0.06	14	-0.93 (0.20)			1.17 (0.35)	
4	0.60	0.06	14	-0.93 (0.20)			1.19 (0.35)	
5	0.86	0.05	15	-0.93 (0.20)			1.18 (0.35)	
6	0.92	0.05	17	-0.88 (0.20)			1.17 (0.34)	0.26 (0.24)
7	1.09	0.04	16	-0.88 (0.20)			1.17 (0.34)	0.26 (0.24)
8	1.29	0.04	15	-0.89 (0.20)			1.19 (0.35)	0.28 (0.24)
9	1.35	0.04	15	-0.91 (0.20)			1.16 (0.34)	
10	1.37	0.04	17	-0.92 (0.20)			1.17 (0.35)	
11	1.46	0.04	15	-0.89 (0.20)			1.20 (0.35)	0.27 (0.24)
12	1.49	0.04	15	-0.94 (0.20)			1.19 (0.35)	
13	1.53	0.04	14	-0.91 (0.20)			1.15 (0.34)	

14	1.63	0.03	15	-0.93 (0.20)			1.20 (0.36)	
15	1.65	0.03	17	-0.89 (0.20)			1.20 (0.35)	0.28 (0.24)
16	1.68	0.03	17	-0.89 (0.20)		0.11 (0.18)	1.21 (0.37)	
17	1.74	0.03	15	-0.93 (0.20)			1.20 (0.36)	
18	1.75	0.03	16	-0.93 (0.20)			1.16 (0.35)	
19	1.85	0.03	16	-0.93 (0.20)			1.20 (0.35)	
20	1.86	0.03	13	-0.93 (0.20)			1.17 (0.35)	
21	1.91	0.03	16	-0.89 (0.20)		0.10 (0.18)	1.20 (0.37)	
22	1.92	0.03	16	-0.99 (0.25)	0.20 (0.39)		1.17 (0.34)	
23	1.95	0.03	17	-0.96 (0.25)	0.11 (0.39)		1.16 (0.34)	

Deer – dog and human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0	0.08	16	0.11 (0.25)	-2.43 (0.59)		0.65 (0.37)	0.55 (0.39)
2	0.23	0.07	17	0.10 (0.25)	-2.43 (0.59)	-0.21 (0.21)	0.55 (0.34)	0.61 (0.41)
3	0.82	0.05	16	0.15 (0.26)	-2.54 (0.65)		0.58 (0.37)	0.58 (0.40)
4	0.82	0.05	17	0.11 (0.25)	-2.52 (0.57)	-0.20 (0.20)	0.58 (0.35)	0.60 (0.40)
5	1.29	0.04	17	0.12 (0.25)	-2.52 (0.57)	-0.20 (0.20)	0.58 (0.35)	0.60 (0.40)
6	1.29	0.04	16	0.14 (0.25)	-2.56 (0.58)		0.65 (0.37)	0.55 (0.38)

Crab-eating fox – dog and human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0	0.04	14	-0.24 (0.22)		-0.53 (0.21)		

2	0.0	0.04	14	-0.23 (0.22)		-0.50 (0.21)		
3	0.29	0.03	13	-0.20 (0.24)		-0.66 (0.20)		
4	0.46	0.03	13	-0.19 (0.24)		-0.64 (0.20)		
5	0.53	0.0	14	-0.22 (0.21)		-0.56 (0.21)		
6	0.78	0.03	14	-0.18 (0.22)		-0.55 (0.21)	0.34 (0.29)	
7	0.88	0.02	14	-0.21 (0.22)	-0.55 (0.21)			
8	1.03	0.02	14	-0.26 (0.22)	-0.52 (0.21)			
9	1.11	0.02	14	-0.25 (0.22)	-0.49 (0.21)			
10	1.12	0.02	15	-0.22 (0.22)		-0.48 (0.21)	0.26 (0.31)	
11	1.23	0.02	15	-0.21 (0.22)		-0.62 (0.20)		
12	1.25	0.02	15	-0.23 (0.21)		-0.51 (0.21)		
13	1.52	0.02	14	-0.18 (0.25)	-0.21 (0.52)	0.53 (0.21)		
14	1.77	0.02	15	-0.19 (0.26)	-0.15 (0.52)	-0.50 (0.21)		

Oncilla – dog and human

				Untransformed coefficients of covariates (SE)				
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.07	12	-0.95 (0.25)	1.14 (0.38)			
2	0.00	0.07	12	-0.95 (0.25)	1.14 (0.39)			
3	0.06	0.07	16	-0.97 (0.24)	1.04 (0.39)		0.35 (0.22)	
4	0.07	0.07	13	-0.95 (0.25)	1.16 (0.39)			
5	0.07	0.07	13	-0.95 (0.25)	1.16 (0.39)			
6	1.08	0.04	17	-0.89 (0.27)	1.08 (0.39)		0.39 (0.25)	0.36 (0.41)

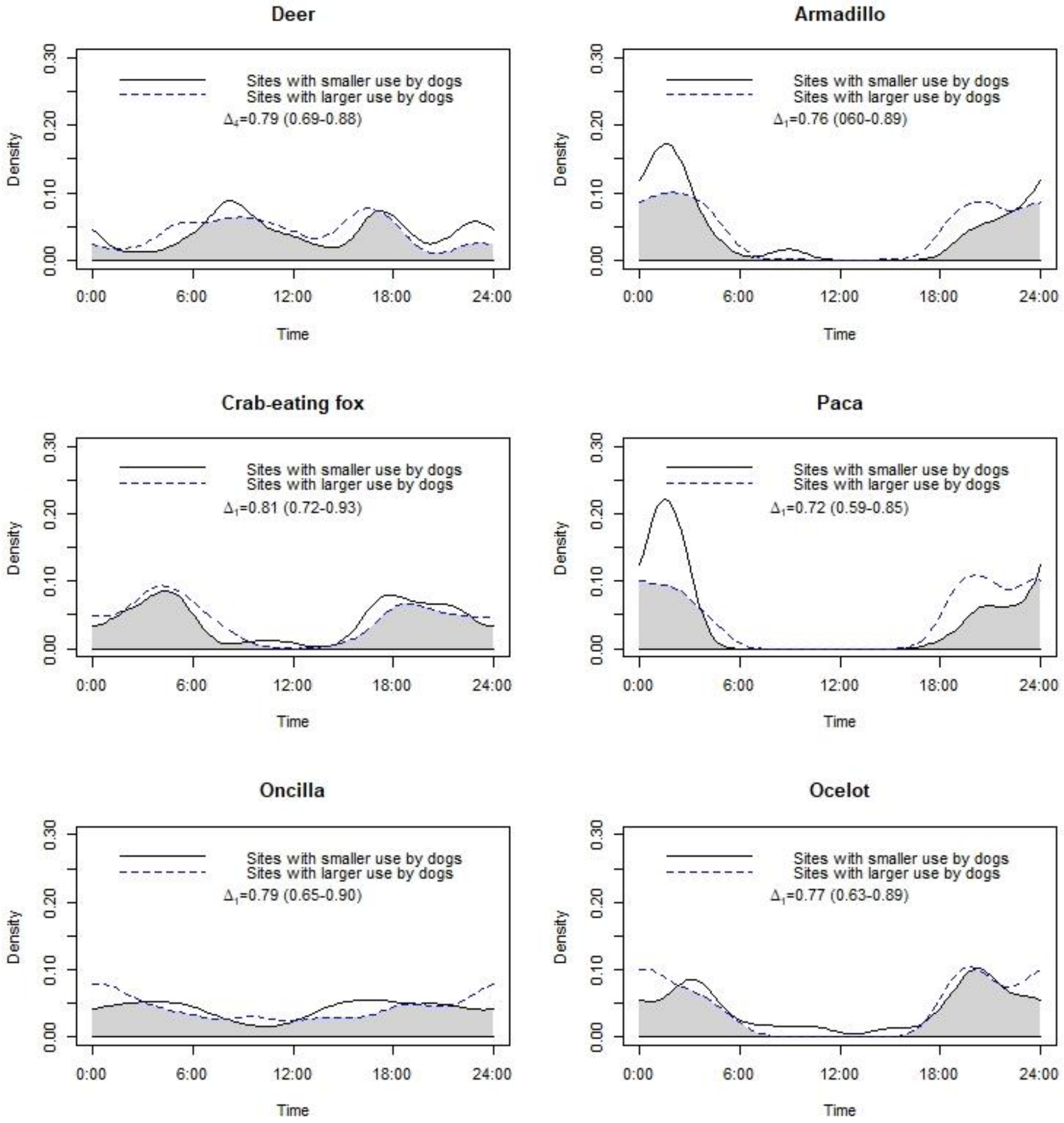
Ocelot – dog and human

Untransformed coefficients of covariates (SE)

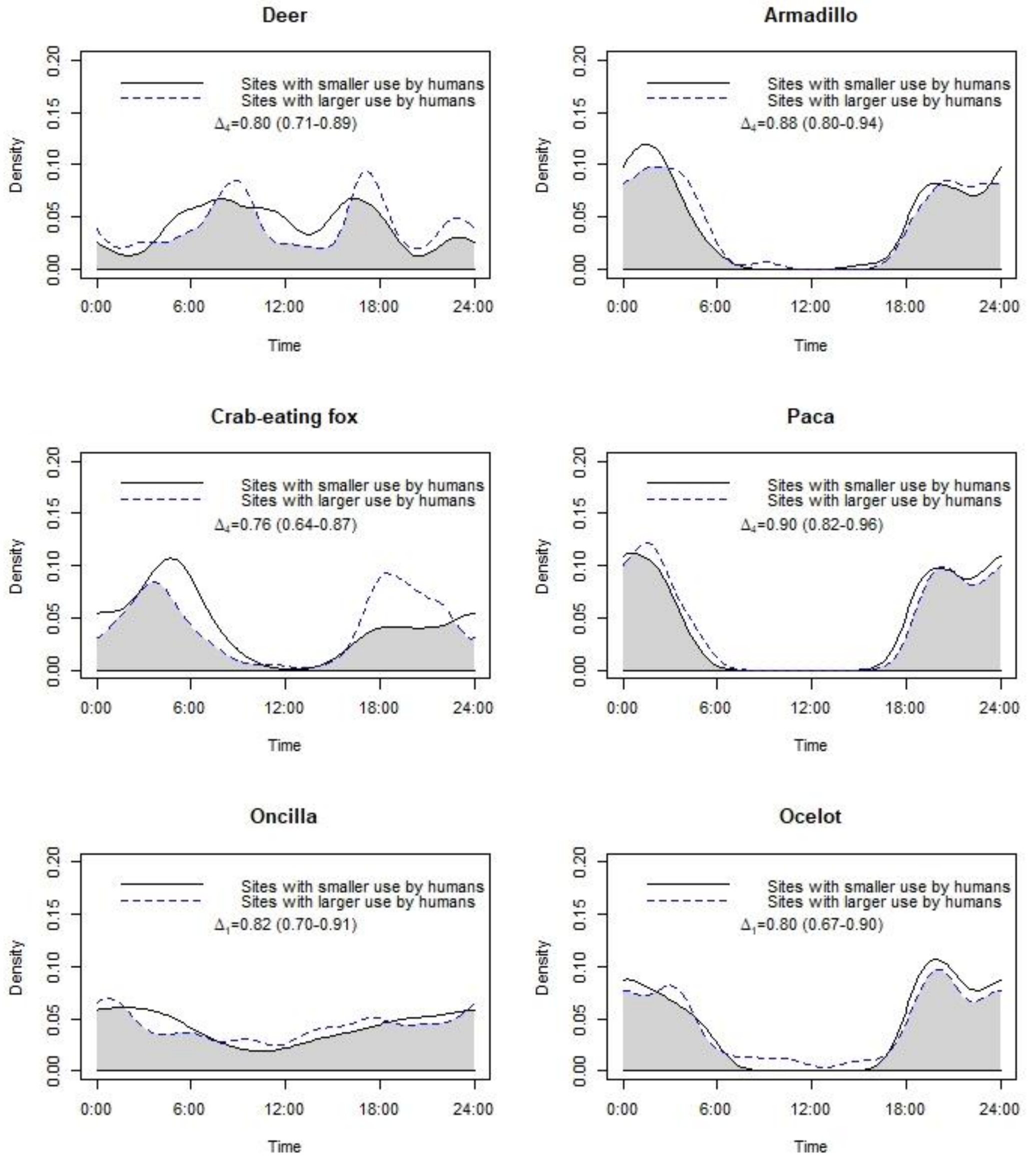
Models	Δ AIC	AIC weight	NPar	Intercept ψA	Intercept ψBa	Forest proportion	HD	RD
1	0.00	0.06	15	-0.75 (0.20)		0.39 (0.20)	-0.41 (0.31)	
2	0.12	0.06	16	-0.77 (0.20)		0.38 (0.20)	-0.44 (0.33)	
3	0.71	0.04	15	-0.76 (0.20)		0.38 (0.20)	-0.44 (0.33)	
4	1.03	0.04	14	-0.72 (0.20)		0.42 (0.19)		
5	1.36	0.03	14	-0.73 (0.20)		0.39 (0.20)	-0.40 (0.32)	
6	1.66	0.03	15	-0.79 (0.21)		0.40 (0.19)	-0.34 (0.32)	
7	1.76	0.03	16	-0.83 (0.26)	0.21 (0.42)	0.39 (0.20)	-0.41 (0.31)	
8	1.80	0.03	16	-0.74 (0.20)		0.38 (0.20)	-0.41 (0.31)	
9	1.88	0.02	17	-0.76 (0.20)		0.38 (0.20)	-0.44 (0.33)	
10	1.89	0.02	17	-0.84 (0.26)	0.20 (0.42)	0.38 (0.20)	-0.44 (0.33)	
11	1.97	0.02	16	-0.76 (0.22)		0.38 (0.20)	-0.38 (0.33)	-0.07 (0.37)

Covariates: Proportion of forest within buffers around camera traps; HD: housing density within buffers around camera traps; RD: road density within buffers around camera traps. The buffer radius varied from 250 m to 2000 m depending on the species pair. ψA = probability that the area is initially occupied by the dominant species, ψBa = probability that the area is initially occupied by the subordinate species when the dominant species is absent. Beta coefficients for ψBa is calculated only when models included the INT parameter (interaction between species); otherwise, ψA = ψBa.

Appendix 4. Kernel density estimates representing diel activity curves and temporal activity overlap for six native mammals among sites with smaller (ψ<0.55), in black solid line, and larger probabilities of use (ψ>0.55) by dogs, in blue dashed line. Periods of activity overlap is represented by the overlap coefficient (Δ), where Δ=1 represents no activity shift by native mammals between sites with smaller or larger probability of use by dogs, whereas Δ=0 indicates complete activity shift. Δ_4 was used when the number of detections of the species at the two categories of sites (with higher or smaller probability of use by dogs) was larger than 75. Δ_1 was used otherwise.



Appendix 5. Kernel density estimates representing diel activity ucrves and temporal activity overlap for six native mammals among sites with smaller (ψ<0.58), in black solid line, and larger probabilities of use (ψ>0.58) by humans, in blue dashed line. Periods of activity overlap is represented by the overlap coefficient (Δ), where Δ=1 represents no activity shift by native mammals between sites with smaller or larger probability of use by humans, whereas Δ=0 indicates complete activity shift. Δ_4 was used when the number of detections of the species at the two categories of sites (with higher or smaller probability of se by humans) was larger than 75. Δ_1 was used otherwise.



CHAPTER 3 - SCALE AFFECTS HOW FOREST COVER INFLUENCES APPARENT COMMUNITY SHIFTS IN ATLANTIC FOREST MAMMALS IN SOUTHEASTERN BRAZIL

ABSTRACT

Habitat loss is reported as the major factor contributing to the biodiversity crisis. Following habitat destruction, there is often a time lag before species extinctions occur for many animal groups, including mammals. Additionally, species and trophic guilds might respond differently to habitat loss, with some species being harmed while others, more generalists, are benefited. In this chapter, I aimed to evaluate how medium and large mammal species respond in terms of habitat use to different proportions of forest left in Atlantic Forest landscapes in Southeast Brazil, while controlling for anthropogenic and environmental variables, as well as the influence of scale. I sampled a 66,870 km^2 area that has been relatively stable in terms of forest loss since at least 1985, using 275 camera trap sites distributed in four camera trap sessions: 2013 and 2014, 2017, 2018, and 2019. To account for the imperfect detection of species, we used a multi-species multi-session occupancy models in a Bayesian framework, with species and sessions as random effects. All terrestrial species (N=28) detected at least once during the 20,383 camera trap days were included in the analysis. After correcting the probability of use considering the imperfect detection, carnivores and omnivores such as *Didelphis aurita*, *Herpailurus yagouaroundi*, *Galictis cuja*, and *Eira barbara* were the most common species throughout the study area. On the other hand, frugivores were the rarest trophic guild, with at least three species having probability of use smaller than 10% in the entire area: *Dasyprocta iacki*, *Tayassu pecari*, and *Tapirus terrestris*. Species from other trophic guilds (carnivore, omnivore, and herbivores) were also rare in this landscape: *Panthera onca*, *Chrysocyon brachyurus*, *Hydrochoerus hydrochaeris*, and *Sylvilagus minensis.* At about 78% of forest amount, there was a shift between generalist species (i.e., *Cerdocyon thous*, *Dasypus*

spp., *Myrmecophaga tridactyla*, and *S. minensis*), and species that are more dependent on forest amount (*P. onca*, *D. iacki*, *D. tajacu*, *T. terrestris*, and *T. pecari*), with generalists decreasing their probability of use and forest specialists becoming more common across the landscape in regions with more than 78% of forest cover (on 2 X 2 km landscape cells). Differently than has been suggested by other studies, the conservation of about 40% of forest within landscapes (about 50% in our study) would not guarantee the persistence of most forest species. As 72% of the studied landscape presents grid cells with less than 78% of forest cover, and this situation is commonly found in other regions within the Atlantic Forest biome, we might have already lost ecosystem services provided by medium and large frugivores in most of the biome. This situation implies that forest regeneration is already needed in order to create habitat suitable for the whole community of medium and large-sized mammals.

INTRODUCTION

Among the myriad threats affecting biodiversity, habitat loss remains paramount (Andrén 1994; Sala et al. 2000; Brooks et al. 2002; Pimm et al. 2014). Human uses of land have already modified up to 75% of the Earth's surface (Ellis and Ramankutty 2008), with accelerated changes in land use anticipated in many regions, i.e., tropical forests, savannas, warm mixed forests (Vitousek et al., 1997). To enable effective triage, scientists have long sought ecological thresholds, critical points where small additional losses of habitat could lead to abrupt declines in population abundance or species richness (Swift and Hannon 2010), and tipping points, situations where accelerating changes drives the system to a new state (van Nes et al. 2016). The concept of a habitat threshold is predicated on a nonlinear relationship between habitat amount and an ecological response (i.e., species richness, abundance, occurrence; (Bascompte and Solé, 1996; Fahrig, 2003, 2001; Hill and Caswell, 1999). Knowledge of critical thresholds should aid biodiversity conservation, e.g., by more effectively guiding the establishment of protected areas in otherwise human-modified landscapes (Banks-Leite et al. 2014; Arroyo-Rodríguez et al. 2020).

Identifying critical habitat thresholds remains challenging in part due to time lags between the onset of habitat loss and animal population responses, i.e., so called “extinction debt”. The time lag (debt) between reaching the critical threshold and observing population changes may span decades for birds, amphibians, reptiles, and mammals (Tilman et al. 1994; Cowlishaw 1999; Metzger et al. 2009; Halley et al. 2016; Chen and Peng 2017; Semper-Pascual et al. 2018)—during which time habitat loss may have continued unabated. There is some substantial support for critical thresholds occurring at ~10-30% of remaining habitat, below which ecological responses (e.g., species richness) of different groups (i.e., small mammals, amphibians, birds, trees) showed a more pronounced decrease with additional loss of habitat in both empirical and theoretical studies (Andrén 1994; Gibbs 1998; Banks-Leite et al. 2014; Lima and Mariano-Neto 2014; Boesing et al. 2017; Leite et al. 2018). Yet, a lot of residual variation remains, and, for some species or regions, critical thresholds have been identified at higher habitat amounts (Bascompte and Solé 1996; Gibbs 1998; With et al. 1999; Schrott et al. 2005; Jager et al. 2006; Rigueira et al. 2013). In fact, critical thresholds are expected at higher habitat amounts in the tropics (Rigueira et al. 2013; Morante-filho et al. 2015), where species turnover among localities is high (Arroyo-Rodríguez et al. 2013; Solar et al. 2015). Moreover, higher threshold values are expected for species that occur at low densities (Gibbs 1998; Swift and Hannon 2010), have low reproductive rates (Vance et al. 2003; Holland et al. 2005), or occupy landscapes where the quality of the matrix (areas surrounding habitat patches) is low (Fahrig 2001; Swift and Hannon 2010; Boesing et al. 2017). However, most empirical studies failed to sample landscapes where habitat amounts exceeded 50% of the landscape, for either theoretical or logistic reasons (Swift and Hannon 2010), which may mask the occurrence of thresholds or bias estimates where they are detected due to truncation of the data range (Brennan et al. 2002; Boyce 2006; Eigenbrod et al. 2011; Frair and Bastille-Rousseau 2021).

In addition to being affected by extent of the study region under consideration, extinction thresholds likely vary with the local scale at which habitat proportion is measured (Banks-Leite et al. 2021). Yet, very few studies have tested measures on more than one scale when attempting to isolate critical thresholds (Homan et al. 2004; Lindenmayer et al. 2005). Moreover, despite the multi-scale nature of animal-habitat associations (Boscolo and Metzger 2009; Lyra-Jorge et al. 2010), most studies have included only fine-scale investigations, e.g., extents covering m^2 to not more than ~5 km^2 (Guerry and Hunter 2002; Imbeau and Desrochers 2002; Reunanen et al. 2004). The relative importance of fine- versus broad-scale influences on species distribution varies widely (Wiens 1989; Frair et al. 2005; Boscolo and Metzger 2009; Lyra-Jorge et al. 2010; Alvarenga et al. 2021), perhaps due to differing habitat requirements, biological traits (e.g., body size), and perception ranges (Gutzwiller 2002). Therefore, the choice of appropriate spatial scale – in terms of both extent and resolution – should be considered in relation to the organisms and processes of interest over a particular time frame (Freemark et al. 2002).

As habitats become even rarer, fragmented, or otherwise diminished in quality, we can expect differential responses within the mammalian community (Newbold et al. 2014; Dornelas et al. 2019). Whereas larger-bodied mammals may decrease in number or go locally extinct as habitat declines (Crooks and Soulé 1999; Crooks 2002; Peres and Palacios 2007; Pimm et al. 2014), other species, e.g., habitat generalists, may increase in abundance or distribution (Mouquet et al. 2011). Carnivores appear particularly sensitive to anthropogenic disturbances, yet omnivores and herbivores are often observed using disturbed landscapes and edge habitats (Michalski and Peres 2005; Storm et al. 2007; Erb et al. 2012; Young et al. 2016). As a result, shifts in community composition are expected across landscapes varying in the amount of residual habitat. Such community shifts, especially the loss of strongly interacting or keystone species, may drive cascading effects to ecosystem functions critical for both wildlife and human well-being (Dirzo et al. 2014; Malhi et al. 2016; Young et al. 2016). Among other services, medium and large-sized mammals are sources of top-down regulation of prey and seed dispersal (Terborgh et al. 1999; Terborgh et al. 2010; Estes et al. 2011; Ordiz et al. 2013; Ripple et al. 2015; Van Valkenburgh et al. 2015). The magnitude of change in ecosystem function due to altered biotic communities may depend on the degree to which differente trophic guilds respond to habitat loss. Consideration of ecological guilds, i.e., groups of species that exploit resources in a similar way (Root 1967; Simberloff and Dayan 1991), might better elucidate habitat thresholds and the resulting shift in community dominance compared to single species assessments (Bueno et al. 2013; Galetti and Dirzo 2013; Jorge et al. 2013; Dirzo et al. 2014; Genes et al. 2017).

Herein, I applied multi-scale, multi-species occupancy models to investigate critical habitat thresholds for mid- to large-bodied terrestrial mammals within the Atlantic Forest of Brazil. Deforestation of the Atlantic Forest has a long history, beginning with the arrival of the first Europeans to the South American continent in the sixteenth century, which spurred massive agricultural expansion followed by industrialization and urbanization (Dean, 1995). Today the Atlantic Forest is one of the most endangered biodiversity hotspots in the world (Myers et al., 2000), with less than 12% of the original vegetation left and more than 80% of remaining forest remnants smaller than 50 ha (Ribeiro et al., 2009). In some regions, protected areas have retained abundant forest habitat along with the suite of forest mammals expected to occur across the Atlantic Forest. Importantly, since ~1985, the average yearly rate of change in forest cover has been negligible to slightly positive,+0.05% (Souza et al., 2020), with even higher rates of reforestation in some regions (Lira et al., 2012). Given relative stability in the pattern of forest cover over the past several decades, extant communities within the Atlantic Forest likely exist beyond the cycle of extinction debt that can muddy the detection of critical ecological thresholds. As such, my study within São Paulo state represents an ideal model system for investigating community responses to local forest amount. Using community-level occupancy models, I examined how apparent thresholds in habitat amount might vary among trophic guilds (e.g., frugivores, carnivores, omnivores, herbivores, and insectivores) as well as with the scale of observation.

METHODS

STUDY AREA

The 66,870 km^2 study area was situated in São Paulo and Minas Gerais states, Southeastern Brazil (Figure 1), and encompassed five major metropolitan regions (São Paulo, Baixada Santista, Campinas, Vale do Paraíba e Litoral Norte, and Sorocaba) ranging in size from 1.7 to more than 20 million people (IBGE 2010). Roughly 72% of the Brazilian population – more than 145 million people – live within the domain of the Atlantic Forest (IBGE 2014). Although the physical urban footprint remains relatively small (2-3.3% of biome extent), associated infrastructure connecting metropolitan areas, e.g., roads, extends human effects into surrounding landscapes including protected areas (Seto et al. 2012). The selected study area encompassed both highly fragmented forest as well as large tracts of contiguous forest, including the largest remaining Atlantic Forest remnant (Serra do Mar, situated close to the coast).

DATA COLLECTION

I deployed a series of camera traps across the study area (Figure 1), and organized deployments into four different sessions defined by year of deployment (Tobler et al. 2015). Cameras included four brands: Bushnell Trophy Cam (models 119636, 199537, 119636, 119736, 119774, 119776), Moultrie (MCG13183, 990i, 1100i), Browning Dark OPS HD, and Spypoint Solar. All cameras were fixed at 30-40 cm above ground. Cameras were set to take videos with the fastest recovery time available for each model (usually up to a few seconds). All native mammal species detected at least once were included in the analyses to follow (Burton et al., 2012; Rich et al., 2016; Tobler et al., 2015), except for primates (*Alouata guariba*, and *Sapajus nigritus*) and porcupines (*Coendou prehensilis*), which are primarily arboreal and not reliably detectable by my camera set ups. I note that *Tamandua tetradactyla* and *Guerlinguetus brasiliensis*, although also arboreal, yielded a considerable amount of detections (N=9 and 119, respectively using 1 week as the sampling occasion, see description later) and were thus included in this modeling effort. For indistinct pairs of species (*Mazama gouazoubira* vs. *Mazama americana*, *Dasypus novemcinctus* vs. *Dasypus septemcinctus*, and *Cabassous tatouay* vs. *Cabassous unicinctus*), I classified each to genus in lieu of species. Ultimately, data from 25 species and three genera were retained. These species further represented five trophic guilds: carnivores (N = 6), frugivores (N = 5), herbivores (N = 3), insectivores (N = 5), and omnivores (Paglia et al., 2012); Appendix 1). For species with diets that could be classified into more than one trophic guild, I assigned their guild based on dietary predominance (Paglia et al., 2012). For instance, paca (*Cuniculus paca*) was considered a frugivore given >50% of the items comprising its diet are fruits (Dubost and Henry, 2006).

To quantify forest cover, I chose a range of sampling extents anchored roughly by the home range sizes expected across this mammalian community. For example, smaller species, e.g., *S.*

minensis, *Didelphis aurita*, *Guerlinguetus brasiliensis*, and *C. paca*, have home ranges on the order of 0.5 x 0.5 km (Swihart 1986; Beck-King and von Helversen 1999; Bordignon and Monteiro-Filho 2000; Cáceres and Monteiro-Filho 2001; Cáceres 2003; Benavides et al. 2017) while larger species, e.g., *Panthera onca,* occupy home ranges on the order of 15 x 15 km (Cavalcanti and Gese 2009; Mazzolli 2010; Morato et al. 2016; Azevedo et al. 2020). Ultimately, I considered nine different square sampling extents having sides = 0.25, 0.5, 1, 2, 4, 8, 15, 30, or 60 km, and calculated the percentage of area covered by forest within each extent using ArcGIS. Forest cover was mapped using classified Landsat 7 images (30 m resolution; (MMA/PROBIO, 2007). Sample locations effectively captured variation in forest cover across the region, which ranged between 3-20% at the low end to 90-100% at the high end, depending upon the selected sampling extent (Table 1).

I included two additional site-specific metrics thought to influence species distribution across the region – human disturbance and elevation. For the former, I used the human footprint index (Venter et al., 2016), whose values range 0-100 and were derived from a combination of human population density, human land use and infrastructure, and human access (mapped at a 1 km resolution; Table 1). Lastly, the elevation of each camera site was recorded using Shuttle Radar Topography Mission (SRTM) data at 89 m resolution (Weber et al., 2004).

MODELING FRAMEWORK

I fit multi-species, multi-scale, and multi-session occupancy models using a Bayesian approach (MacKenzie et al. 2002; Tobler et al. 2015). In contrast to previous studies investigating forest cover thresholds, the multi-species modeling framework should improve parameter estimates, especially for species with sparse data, because species-level parameters are drawn from a common hyper-distribution for the community rather than being modeled independently (Kéry and Royle 2016).

For this analysis I first collapsed each session into 7-day sampling occasions (see Chapter 1). Since not all camera trap sites were repeated in all sessions, I modeled session as a random effect on occupancy and detection (Tobler et al., 2015). Species-level parameters were also assumed to be random effects drawn from a normal distribution governed by community-level hyperparameters (Zipkin et al. 2009; Petracca et al. 2019). Given that high abundance species were likely to have increased detection probabilities and caused strong, positive correlations between occupancy and detection (Royle and Nichols 2003), I modeled the correlation (ρ) between occurrence and detection by allowing their random intercepts to be jointly distributed (Zipkin et al. 2009; Kéry and Royle 2016; Rich et al. 2016). Ultimately, given the long-term nature of camera deployments, and assuming movements into and out of the sampled area (camera trap sites) to be random, I relaxed the closure assumption and interpreted the occupancy parameter as the probability of use (Mackenzie and Royle 2005).

I first denoted *z*(*i,j*) to be the site-specific occupancy (i.e., "true" presence/ absence) for species *i* = 1, 2, …, R at site *j* = 1, 2, …, S, such that *z*(*i,j*) = 1 if species *i* occurred at site *j* and zero otherwise. Occurrence probability was modelled as $z(i,j) \sim Bern(\psi_{i,j})$, where $\psi_{i,j}$ is the probability that species *i* occurred at site *j*. Models were organized to account for three hierarchical levels: (1) session-level *m* community (all species occurring at the study site within a session), (2) site-level community (occurrence process determining the species present in the vicinity of each camera trap location within a specified sampling extent), and (3) detection of a species given its occurrence at a site (Tobler et al., 2015). For detection probability, each model included $logit(p_{ijk}) = u_{im} + \beta 1_i effort_j + \beta 2_i trail_j$, where effort was the number of days each camera trap was operational and trail indicated whether the camera was placed on (y=1) or off (y=0) a trail.

Given no significant correlations among the three main covariates (r < |0.4|, Appendix 2), the base occupancy model was specified as:

$$logit(\psi_{ij}) = u_{im} + \beta 1_i\, forest_j + \beta 2_i\, elevation_j + \beta 3_i\, human\, footprint_j \qquad \textbf{Model 1}$$

where, u_{im} was the random intercept for species *i* and session *m*, which followed a normal distribution having mean and variance governed by community hyperparameters (i.e., $u_{im} \sim Normal(\mu_u, \sigma_u^2), \sigma_u \sim Uniform(0,10)$). For the forest variable, I substituted each of the nine sampling extents in turn to identify the most informative scales for each species. As these candidate models were structurally the same, I compared models using the deviance information criterion, DIC (Spiegelhalter et al. 2002; Royle et al. 2014; Kéry and Royle 2016).

A series of more complex models were compared to model 1 to determine whether (1) the effect of forest cover on ψ interacted with either elevation or the human footprint variable, (2) the effect of forest cover was non-linear (i.e., inclusion of $x + x^2$), or (3) a threshold response to forest cover was detectable. For the latter, following Jones et al. (2011), I specified the threshold model as:

$$logit(\psi_{ij}) = u_{im} + \beta 1_i\, forest_j + \beta 2_i (forest_j - t)_+ + \beta 3_i\, elevation_j$$
$$+ \beta 4_i\, human\, footprint_j \qquad \textbf{Model 2}$$

where, *t* represented an unknown threshold parameter, and $(forest_j - t)_+ = (forest_j - t)$ if $forest_j > t$, and was otherwise 0 (Jones et al. 2011). As these models were structurally different from Model 1, I compared models based on: (1) model convergence (non-converging models were not considered further), (2) credible intervals (i.e., 95% credible intervals excluding zero for the largest number of species retained), and (3) effect sizes.

Lastly, I evaluated a set of models that allowed forest cover to exert multi-scale effects on ψ either by (1) including the average amount of forest cover in the immediate 8-cell neighborhood surrounding each sampled unit, or (2) directly including both a fine-scale and broad-scale measure of forest cover (two different scales) in the same model, provided these two covariates were not correlated (i.e., $r < 0.7$, Appendix 2). These models were compared as described previously.

Prior to model fitting, all continuous covariates were centered and standardized so that the magnitude of their effects could be compared in the same model (Schielzeth 2010). I estimated posterior distributions of parameters using Markov chain Monte Carlo (MCMC) implemented in a Bayesian framework using the BUGS language and run in software JAGS (Plummer, 2003), using the package jagsUI in R 3.6.1 (Kellner 2019; R Core Team 2019). I specified three chains, 30000 iterations (burn-in of 5000 iterations), and a thinning rate of 20. For priors, I used a normal distribution having mean 0 and standard deviation 100 on the logit-scale for all covariate effects ($\beta_{1i}, \beta_{2i}, etc$) and a uniform distribution from 0 to 10 for σ parameters. I assessed convergence using the Gelman-Rubin statistic where values <1.1 indicated convergence (Kéry 2010).

COMMUNITY-LEVEL SUMMARIES

From the best model(s), I calculated relative species richness across the area of study by summing the predicted probabilities of use across species (Calabrese et al., 2014), such that theoretical maximum number of medium or large-sized mammal species at any given location (28) would be achieved should each be predicted to have probability of use = 1.00 within a given sampling extent.

Ultimately, I plotted the predicted probability of use for each species against proportion forest cover to search for a critical point at which community composition may shift away from being dominated by forest-dependent species. Such critical points were found as the intersections of the predicted probability of use of generalist species (those responding negatively to forest amount) and forest-dependent species (positive response to forest amount).

RESULTS

A total of 2,802 detections of 28 mammal species were recorded. The most detected species were the big-eared opossum *Didelphis aurita* (N=625) and crab-eating fox *Cerdocyon thous* (N=216; Figure 2), while the least detected species included the six-banded armadillo *Euphractus sexcinctus* (N=1) and striped hog-nose skunk *Conepatus semistriatus* (N=2). Both covariates included for detection probability proved informative for many species (12 species showed significant responses to the trail covariate, and 17 for the camera trap effort). Seven species exhibited greater detection probability when cameras were placed on trails (*T. pecari*, *P. concolor*, *L. pardalis*, *L. guttulus*, *C. thous*, *C. brachyurus*, and *S. minensis*), while five species exhibited greater detection probabilities off trail (*G. brasiliensis*, *D. tajacu*, *Eira barbara*, *Procyon cancrivorus*, and *Mazama* spp.; Appendix 3). When considering the sampling effort covariate, most species exhibited a result that might be counter-intuitive, they had reduced detection probability with increased sampling effort (*T. terrestris*, *C. paca*, *E. barbara*, *D. tajacu*, *T. pecari*, *L. guttulus*, *P. cancrivorus*, *Didelphis aurita*, *Nasua nasua*, *Dasypus* spp., *Cabassous* spp., *Mazama* spp., *S. minensis*, and *H. hydrochaeris*). Three species showed increased detection probabilities with increasing sampling effort: *P. concolor*, *L. pardalis*, and *C. thous* (Appendix 3). This could be related to the fact that a very large landscape was sampled (~66,870 km^2) following a gradient of forest cover, elevation, and the human footprint variable, where species might be heterogeneously distributed (Rosenzweig 1995), being more common in some parts of the sampled area than others, which could lead to a negative relationship between detection probability and sampling effort whether areas not used by the species are common among the sampled sites (Tobler et al. 2008).

The hyperparameter (community-level) means on coefficients for the effect of forest proportion, elevation, and human footprint on occupancy probability were very close to 0 due to the nearly equal number of species exhibiting opposite directionality (+/-) in their responses to these factors (Appendix 3). The threshold model (Model 2) failed to converge for many parameters and was not considered further. The simplest models, i.e., linear model, interaction models, and non-linear forest variable, each achieved convergence at all sampling extents. The simple linear model (Model 1) yielded informative parameter estimates, i.e., 95% credible intervals excluded zero, for 3 to 11 species depending on the sampling extent considered (Table 2; Appendix 3). Interaction terms proved uninformative (95% credible intervals overlapped zero) for all species and extents, with a few exceptions (*D. aurita*, 2 extents, *Mazama* spp. and agouti *D. iacki*, 1 extent each), and were not considered further. Likewise, adding a quadratic term for forest cover did not prove informative, so this model was also not considered further.

An 8-km sampling extent for forest amount yielded informative parameter estimates for the largest number of species (13 species), followed by the 2-, 15-, and 30-km extents (nine species each; Table 2). Notably, the extreme scales (0.25- and 60-km) yielded informative estimates for the fewest species. When comparing models using DIC, the 2-km extent was identified as the best fit overall for this mammal community (ΔDIC > 60 for all other extents; Table 3), coinciding with the largest effect sizes. In choosing a larger extent to include as a landscape context variable, the 30-km extent received more support than the 60-km extent (ΔDIC > 100).

In the neighborhood-based model, given a larger proportion of forest in the neighboring grid cells, locally some species increased their probability of use (*D. iacki*, *D. tajacu*, *T. terrestris*, *T. pecari*, *P. onca*, *L. pardalis*, and *P. concolor*) while others decreased their use (*Dasypus* spp., *C. thous*, and *Myrmecophaga tridactyla*). The alternative, multi-scale model included forest cover measured within both 2-km and 30-km sampling extents. This model converged for parameters at both extents and yielded informative parameter estimates for most species (except *Dasypus* spp. and *C. thous*). This multi-scale model yielded the largest number of informative parameters estimates at the 2-km extent (9). The direction of slopes was the same as the single scale (2-km extent) model, but effect sizes were lower than those obtained using Model 1. Additionally, comparing models using DIC, Model 1 appeared the best fit overall for this mammal community compared to the multi-scale models (ΔDIC > 110). Therefore, all results below are reported using Model 1 at the best extent for forest amount, i.e., 2x2 km.

COMMUNITY-LEVEL SUMMARIES

Carnivores such as jaguarundi *Herpailurus yagouaroundi* (mean probability of use = 0.59, 95% CI: 0.19-0.99), and omnivores such as opossum *D. aurita* (0.55, 0.44-0.66) and tayra *E. barbara* (0.50, 0.31-0.74), were predicted to be the most common species throughout the study area (Figure 2B). On the other hand, frugivores were the rarest trophic guild, with at least three species exhibiting probability of use smaller than 10% considering all sampled sites: *D.iacki* (mean probability of use = 0.04, 95% CI: 0.01-0.09), *T. pecari* (0.07, 0.03-0.13), and *T. terrestris* (0.09, 0.04-0.15). Some species across various trophic guilds (carnivore, omnivore, and herbivores) were also rare in this landscape: e.g., *P. onca* (mean probability of use = 0.02, 95% CI = 0.01-0.07), *C. brachyurus* (0.04, 0.01-0.10), *H. hydrochaeris* (0.10, 0.04-0.20), and *S. minensis* (0.09, 0.05-0.17).

Based on Model 1 fit at a 2-km sampling extent, the average number of species predicted at a site was 7 (Figure 3). Sites included 2-4 carnivores, 1-3 omnivores, and 1-2 insectivores on average, and generally lacked frugivores or herbivores (Figure 3). Overall, when considering the whole mammal community, there was an apparent increase in predicted species richness with increasing forest amount (Figure 4). However, the predicted richness of carnivores and frugivores suggested a positive relationship, while the richness of insectivores and herbivores a suggested a negative relationship with increasing forest amount. In general, survey units hosting the highest forest amount in the landscape were predicted to have the highest relative species richness (Figure 5). Similarly, most species (up to 17) exhibited increased occupancy probability in areas of high forest amount (Table 2).

The differential responses to forest cover between forest-dependent species (those exhibiting a significant positive association with forest cover) and more generalist species (those exhibiting either a negative or neutral response to forest cover revealed critical points at which community shifts might be expected (Figure 6). Importantly, the value for the critical forest amount declined as a non-linear function of the observation (Figure 7), increasing from 45% forest cover at the coarsest sampling extent (60-km) to 87% forest cover at the finest sampling extent (0.5-km). Given my selection of 2-km as the 'optimal' scale for quantifying forest responses in this mammalian community, prediction plots indicated a threshold amount of 78.26% forest (varying from 76.71 to 79.85% for species that yielded informative parameter estimates at this extent; Figures 7, Appendix 4) being required to maintain the suite of forest-dependent mammals in this area. The human footprint covariate was informative (and positive) only for *Mazama* spp. (Appendix 3), whereas more species presented meaningful relationships with elevation, either positive (*D. tajacu*, and *T. pecari*), or negative (*D. iacki*, *D. aurita*, and *Dasypus* spp.; Appendix 3).

DISCUSSION

This work clearly demonstrated the challenges of looking for ecological thresholds when considering community responses to habitat fragmentation. Species varied in their use of space with respect to forest amount, with different groups showing constrasting directional relationships with changes in forest cover, and with some species but not the overall community exhibiting statistically non-linear, interactive, or even multi-scale responses. Failing to statistically detect a community-level threshold in forest amount, I instead found individual species responses useful in identifying putative critical points beyond which forest specialists would become less likely (≤0.5 probability) than generalist or more open-habitat species (≥0.5 probability) to occur. Importantly, the amount of forest corresponding to that putative critical point variedly widely, from 45-87%, depending upon the scale of observation, or more specifically the extent within which the proportional coverage of forest was calculated. Ultimately, the best supported scale of observation for this Atlantic Forest mammalian community was a 2x2 km landscape cell, which corresponded to a critical point at ~78% forest cover. This indicated that even for landscape units largely dominated by forest we may expect a shift favoring generalists over forest specialists in this human-dominated region. Notably, this critical point is considerably higher than forest cover thresholds reported elsewhere, which more typically have been observed ~10-30% forest cover (Andrén 1994; Banks-Leite et al. 2014; Lima and Mariano-Neto 2014; Boesing et al. 2017; Leite et al. 2018). However, our observation is consistent with the higher forest cover thresholds estimated elsewhere in the tropics (up to 75%; (Arroyo-Rodríguez et al., 2020; Morante-filho et al., 2015; Rigueira et al., 2013; Saetersdal et al., 1993; Soulé and Sanjayan, 1998), possibly due to higher turnover rates among areas in the tropics (Solar et al. 2015; Arroyo-Rodríguez et al. 2020). As a result, considerably greater amounts of forest than previously considered may be needed to maintain forest-dependent mammals in this region.

A systematic shift in biodiversity has been observed worldwide in the so-called Anthropocene (Dornelas et al. 2014; Daskalova et al. 2020). My data indicate a decrease in both species richness (α diversity) at local sites (i.e., the maximum estimated number of species at a given site was 18 out of 28 species) and β diversity (species turnover) between landscapes with less or more than 78% forest cover (with generalist species having higher probability of use of areas with less than 78% forest and forest-dependent species using more commonly areas with more than 78% forest cover). Species turnover is defined as the rate or magnitude of change in species composition along predefined spatial or environmental gradients, meaning that turnover occurs when a species present at a given site is absent from another site, where it is replaced by another species that was absent from the first (Vellend 2001; Beca et al. 2017). Interpreting the potential for species turnover as differences in the probability of use by generalists versus forest specialists in this study, beta diversity provided a more sensitive indicator of potential community change than α diversity, providing a useful metric for conservation planning in the region, i.e., establishment of new protected areas (Dornelas et al., 2014; Magurran et al., 2018; Magurran and Henderson, 2010; Socolar et al., 2016).

Importantly, the great majority of studies seeking thresholds in animal responses to declining forest cover tend to have investigated those thresholds using a unique, study-specific observation scale rather than a consistent or standardized scale of observation (Guerry and Hunter 2002; Imbeau and Desrochers 2002; Reunanen et al. 2004; Swift and Hannon 2010), which muddies comparison of ecological thresholds across studies. My results point to a simple, single-observation scale to effectively capture community-level responses to forest cover. In particular, the 2 x 2 km scale determined as optimal for this community is the same scale adopted by the IUCN for species assessments (IUCN Standards and Petitions Committee 2019), indicating broad utility for considering changing animal occurrences, and by extension changing communities, in response to forest amount. With respect to the 2 x 2 km scale, the best-supported scale for this community, at least nine species (32% of the observed community) yielded informative estimates on the forest cover covariate at this scale, most exhibiting the largest effect sizes at this extent. Of these, three of the species were generalists, whereas five were forest-dependent species. The appropriate scale of observation may vary depending upon species (Wintle et al. 2005; Kennerley et al. 2019; Semper-Pascual et al. 2020), or species assemblage when looking at communities, and the general applicability of the 2x2 km scale will require additional multi-scale investigations like that conducted herein.

The long history of destruction of the Atlantic Forest combined with the concentration of over 70% of the Brazilian population within the limits of the biome (IBGE 2014) has led to a very fragmented forest, with most of the remaining fragments being small (<100 ha) and isolated, and with few contiguous forested areas (Ribeiro et al. 2009). The temporal lag between forest loss and population or assemblage-level shifts can extend up to 50 years depending on species' generation time (Daskalova et al. 2020). Given major forest deforestation in the early 20th century within my study area (Viana et al. 1997), I presume contemporary species patterns as observed in this study reflect the new equilibrium in this fragmented landscape. The most common species observed were big-eared opossum (*D. aurita*), grison (*G. cuja*), tayra (*E. barbara*), and jaguarundi (*H. yagouaroundi*) – the first two being generalist species (Emmons and Feer 1999; Cáceres 2004; Rodrigues et al. 2013). Notably, jaguarundi was known to occur in low densities and to rarely be more abundant than other felids (de Oliveira et al. 2010; Almeida et al. 2013). Several species proved very rare in this landscape, occurring in less than 15% of the study area, and representing four out of five trophic guilds: *P. onca* (carnivore), *D. iacki*, *T. terrestris*, and *T. pecari* (frugivores), *C. brachyurus* (omnivore), along with *H. hydrochaeris*, and *S. minensis* (herbivores). For many of those species (i.e., tapir, white-lipped peccary, and jaguar), rarity is the most common observation across the whole biome (Jorge et al. 2013; Bogoni et al. 2018). I found tapirs to be absent from 91% (85-96%) and white-lipped peccaries from 93% (87-97%) of the area of study, whereas the jaguar, the rarest species in this study, was absent from 98% (93-99%) of the landscape. Some rare species such as maned wolf and Brazilian cottontail prefer more open vegetation types while others such as capybara, which are common elsewhere in the biome but rare in this study area, require close proximity to water bodies (Ferraz et al. 2007; Ferraz et al. 2009; Queirolo et al. 2011; Bonvicino et al. 2015; de Paula 2016; Ferreguetti et al. 2017; Dias et al. 2019; Ruedas and Smith 2019).

Previous studies point to frugivores and carnivores as the trophic guilds most threatened by forest loss (Estes et al. 2011; W. J. Ripple et al. 2014; Ripple et al. 2015; Johnson et al. 2017; Magioli et al. 2021), as higher extinction risk is often related to larger body mass for mammals (Ripple et al. 2017). At 2x2 km landscape units containing <78% forest cover, I expect diminished probability of occurrence for three frugivores (tapir, collared-peccary, and white-lipped peccary), one omnivore (tayra), and two carnivores (puma and ocelot). The absence of frugivores is expected to have cascading ecological effects, since more than 80% of the trees in the Atlantic Forest are zoochoric, with 20-46% being dispersed by mammals (Almeida-Neto et al. 2008). Many large-seeded plants (i.e., palms) rely on a few, larger-bodied frugivores for seed dispersal—exactly those species that have already been eliminated from most parts of the landscape. In some cases, smaller species like squirrels *Guerlinguetus* sp. and spiny rats (Family Echimyidae) might act as dispersers in otherwise defaunated areas (Bonjorne de Almeida and Galetti 2007), but they cannot replace the long-distance dispersal provided by the larger frugivores, and even with their dispersal services the proportion of undispersed seeds remains very high with most seeds destroyed by insects (Galetti et al. 2006). Consequently, the distribution of many woody species is altered, and their gene flow compromised, following the loss of key frugivores. Likewise, the loss of the jaguar from a great part of the studied region also contributes to cascading effects throughout the community (Ripple and Beschta 2006; Bruno and Cardinale 2008; Beschta and Ripple 2009; Ripple and Beschta 2012). Pumas, being more tolerant of anthropogenic environments than jaguar, were predicted to occur across 28-59% of the study landscape and appear less likely to suffer local extinctions (Crawshaw and Quigley 2002; Foster et al. 2010; De Angelo et al. 2011; de la Torre et al. 2017). Despite the retention of a major predator across the region, puma use of habitats and food items differs from jaguar (Crawshaw and Quigley 2002), so they are not expected to compensate entirely for the loss of jaguars. It is important to note that the landscape conditions that support both apex predators, represented by areas with high proportion of forest (usually > 78%), are already rare in the landscape (~23.7% of the 2x2 km grid cells meet this condition).

With the predominance of small and isolated forest remnants across the Atlantic Forest biome (Ribeiro et al. 2009), an integration of scientists, policy makers, and stakeholders is urgently needed (Joly et al. 2019) to conserve the more threatened mammals in the biome, those important for different ecosystem services. One initiative that has been started in a few regions within the Atlantic Forest is payment for ecosystem services, which has yielded a small incremental increase in forest amount through forest regeneration on participating properties (Ruggiero et al. 2019). However, equally or more important as increasing forest amount is the conservation of existing old-growth forest fragments and increasing forest quality to satisfy many ecosystem services demands (Ferraz et al. 2014) and given their importance to many species, especially forest specialists (Acevedo-Charry and Aide 2019). Despite the importance of old growth forests, the tendency in the Atlantic Forest since 1990 is to lose old growth forests and gain younger native forest cover (Rosa et al. 2021). Even if restoring forest within a rather isolated 2x2 km landscape unit would not necessarily increase the amount of suitable habitat available for forest-dependent mammals, such as the jaguar or tapir, restored forest patches could serve as stepping stones facilitating dispersal for many species (Saura et al. 2014; Herrera et al. 2017), increasing connectivity among the largest habitat remnants in the landscape (many of them already in reserves), and benefiting gene flow for medium and large-sized mammals across this fragmented landscape.

Furthermore, as many mammal species have already been lost from Atlantic Forest landscapes, trophic rewilding may help regain ecological interactions and reverse defaunation and its cascading effects on ecosystem functioning (Svenning et al. 2016; Mauro Galetti, Pires, et al. 2017; Mauro Galetti, Root-Bernstein, et al. 2017; Root-Bernstein et al. 2017; Marjakangas et al. 2018). Indeed, some of the rarest species across the studied landscape and most of the Atlantic Forest biome (i.e., tapir, white-lipped peccary, and jaguar) appear to have more suitable habitats than they currently occupy within the biome, which could indicate potential areas that rewilding efforts could target (Jorge et al. 2013). So far, rewilding efforts have been made with the reintroduction of agoutis in Tijuca National Park, showing promising results for the restoration of ecological processes (Cid et al. 2014; Fernandez et al. 2017; Kenup et al. 2017). Trophic rewilding and landscape planning to increase areas suitable for forest-dependent mammals and connectivity across the landscape could have potential benefits in recovering many lost ecological functions in this biodiversity hotspot.

Table 1. Covariates’ range across the area of study.

Covariate	Resolution or grid cell size	Maximum range for covariate	Covariate range at sampled sites
Elevation (m)	89 m	0-2397	16-2051
Human footprint	1x1 km	0-100	15-71
Forest amount	0.25x0.25 km	0-100	20-100
Forest amount	0.5x0.5 km	0-100	3-100
Forest amount	1x1 km	0-100	15-100
Forest amount	2x2 km	0-100	7-100
Forest amount	4x4 km	0-100	3-100
Forest amount	8x8 km	0-100	5-100
Forest amount	15x15 km	0-100	6-99
Forest amount	30x30 km	0-100	14-95
Forest amount	60x60 km	0-100	8-90

Table 2. Beta coefficients (SE) for the forest amount covariate at different grid cell extents from Model 1 (linear effects for all covariate). Bold values indicate statistically significant results (credible intervals not overlapping zero).

Species by trophic guild	Beta coefficients (SE) for the forest amount covariate within each sampling extent								
	0.25 km	0.5 km	1 km	2 km	4 km	8 km	15 km	30 km	60 km
Frugivores									
Cuniculus paca	0.02 (0.15)	-0.01 (0.25)	0.12 (0.15)	0.09 (0.16)	-0.08 (0.15)	0.08 (0.15)	-0.07 (0.15)	-0.08 (0.15)	0.02 (0.35)
Dasyprocta iacki	0.27 (0.35)	0.51 (0.42)	0.33 (0.15)	0.58 (0.44)	0.36 (0.36)	**1.44 (0.58)**	0.56 (0.36)	**0.76 (0.37)**	**0.85 (0.34)**
Guerlinguetus brasiliensis	-0.06 (0.16)	-0.09 (0.16)	-0.05 (0.16)	0.03 (0.17)	-0.04 (0.17)	-0.07 (0.17)	-0.11 (0.17)	-0.15 (0.17)	-0.09 (0.17)
Dicotyles tajacu	0.45 (0.30)	**0.76 (0.35)**	**0.74 (0.31)**	**1.52 (0.49)**	**1.41 (0.43)**	**1.37 (0.38)**	**0.70 (0.25)**	**0.81 (0.27)**	**1.09 (0.29)**
Tapirus terrestris	0.40 (0.30)	**0.74 (0.37)**	**0.86 (0.35)**	**1.95 (0.61)**	**1.92 (0.57)**	**1.94 (0.51)**	**1.82 (0.40)**	**1.65 (0.39)**	**1.28 (0.27)**
Tayassu pecari	0.43 (0.34)	0.57 (0.36)	**0.95 (0.44)**	**1.29 (0.56)**	**1.34 (0.51)**	**1.81 (0.57)**	**1.11 (0.35)**	**0.71 (0.32)**	**1.16 (0.32)**
Carnivores									
Herpailurus yagouaroundi	0.36 (0.43)	0.56 (0.49)	0.49 (0.46)	0.81 (0.68)	0.31 (0.55)	0.11 (0.84)	0.04 (0.61)	-0.18 (0.54)	0.01 (0.51)
Leopardus guttulus	0.02 (0.17)	-0.19 (0.18)	**-0.36 (0.19)**	-0.26 (0.19)	-0.32 (0.19)	-0.33 (0.19)	-0.22 (0.18)	-0.19 (0.17)	-0.23 (0.18)
Leopardus pardalis	0.27 (0.17)	**0.49 (0.19)**	**0.36 (0.17)**	**0.46 (0.19)**	**0.49 (0.18)**	**0.36 (0.17)**	**0.40 (0.17)**	0.20 (0.17)	0.19 (0.18)
Leopardus wiedii	0.13 (0.41)	0.28 (0.53)	0.40 (0.55)	1.00 (0.86)	0.69 (0.73)	0.98 (0.82)	0.20 (0.60)	0.59 (0.63)	0.87 (0.65)

Panthera onca	0.21 (0.17)	0.42 (0.44)	0.54 (0.46)	1.07 (0.69)	1.02 (0.61)	**1.46 (0.73)**	**1.13 (0.52)**	**1.09 (0.52)**	0.33 (0.38)
Puma concolor	0.16 (0.18)	**0.61 (0.23)**	**0.41 (0.20)**	**0.58 (0.23)**	**0.41 (0.20)**	**0.42 (0.20)**	**0.54 (0.20)**	0.30 (0.19)	0.23 (0.20)
Omnivores									
Cerdocyon thous	**-0.53 (0.17)**	**-0.61 (0.16)**	**-0.74 (0.17)**	**-0.99 (0.20)**	**-0.75 (0.17)**	**-0.92 (0.18)**	**-0.60 (0.17)**	**-0.58 (0.17)**	**-0.73 (0.18)**
Conepatus semistriatus	0.09 (0.39)	0.20 (0.52)	0.18 (0.51)	0.57 (0.79)	0.14 (0.17)	0.15 (0.85)	-0.12 (0.63)	-0.04 (0.60)	0.17 (0.61)
Chrysocyon brachyurus	**-0.60 (0.23)**	-0.49 (0.25)	-0.47 (0.26)	-0.37 (0.31)	-0.51 (0.31)	-0.51 (0.36)	-0.50 (0.35)	-0.42 (0.35)	-0.11 (0.33)
Didelphis aurita	0.04 (0.13)	-0.12 (0.15)	-0.03 (0.14)	0.11 (0.13)	-0.02 (0.14)	-0.11 (0.15)	-0.27 (0.14)	-0.25 (0.15)	-0.07 (0.14)
Eira Barbara	-0.04 (0.22)	0.24 (0.24)	0.39 (0.24)	**0.57 (0.25)**	0.41 (0.26)	0.31 (0.25)	0.20 (0.18)	0.03 (0.25)	0.17 (0.23)
Galictis cuja	-0.16 (0.36)	-0.28 (0.44)	-0.29 (0.51)	-0.90 (0.76)	-1.05 (0.60)	**-1.41 (0.72)**	-0.69 (0.62)	-0.34 (0.59)	-0.32 (0.54)
Nasua nasua	-0.08 (0.15)	0.23 (0.18)	0.14 (0.17)	0.01 (0.17)	0.02 (0,17)	-0.19 (0.17)	-0.04 (0.17)	-0.13 (0.17)	0.03 (0.17)
Procyon cancrivorus	-0.04 (0.17)	0.14 (0.19)	-0.12 (0.18)	-0.17 (0.18)	-0.12 (0.18)	-0.32 (0.18)	-0.21 (0.19)	-0.20 (0.19)	-0.17 (0.18)
Insectivores									
Cabassous spp.	-0.17 (0.24)	-0.10 (0.25)	-0.04 (0.25)	-0.32 (0.28)	-0.18 (0.27)	-0.14 (0.28)	-0.02 (0.26)	0.10 (0.26)	0.02 (0.26)
Dasypus spp.	**-0.39 (0.15)**	**-0.73 (0.17)**	**-0.64 (0.16)**	**-0.79 (0.17)**	**-0.77 (0.16)**	**-0.63 (0.16)**	**-0.77 (0.17)**	**-0.52 (0.15)**	**-0.43 (0.15)**
Euphractus sexcinctus	0.05 (0.39)	0.21 (0.51)	0.18 (0.54)	0.49 (0.84)	0.22 (0.77)	0.06 (0.92)	-0.28 (0.69)	-0.16 (0.65)	0.06 (0.64)
Myrmecophaga tridactyla	-0.15 (0.36)	-0.37 (0.44)	-0.32 (0.48)	-0.73 (0.76)	-0.64 (0.64)	**-1.38 (0.70)**	-1.02 (0.64)	**-1.14 (0.57)**	**-1.36 (0.57)**

Tamandua tetradactyla	0.26 (0.36)	0.23 (0.40)	-0.01 (0.35)	0.30 (0.47)	0.27 (0.42)	0.42 (0.47)	0.01 (0.38)	0.14 (0.36)	0.02 (0.35)
Herbivores									
Hydrochoerus hydrochaeris	-0.08 (0.21)	0.07 (0.25)	-0.02 (0.24)	-0.37 (0.24)	-0.33 (0.23)	-0.41 (0.26)	**-0.70 (0.30)**	-0.43 (0.26)	-0.33 (0.26)
Mazama spp.	-0.15 (0.14)	-0.18 (0.15)	-0.16 (0.15)	**-0.41 (0.15)**	**-0.35 (0.16)**	-0.25 (0.16)	-0.06 (0.30)	-0.08 (0.17)	-0.24 (0.17)
Sylvilagus minensis	-0.22 (0.16)	-0.10 (0.19)	-0.08 (0.20)	-0.21 (0.20)	-0.10 (0.21)	-0.20 (0.21)	-0.11 (0.21)	**-0.44 (0.23)**	-0.39 (0.23)

Table 3. Deviance Information Criterion (DIC) considering Model 1 at nine grid cell extents for the forest amount covariate, multiscale Model 6 (neighborhood) at both fine- and broad-extents, and multiscale Model 7 including both a fine- (2x2 km) and broad-extent (30x30 km).

Model	Grid-cell extent for forest amount	DIC	ΔDIC
Model 1	2x2 km	16628.63	0
Model 1	8x8 km	16689.43	60.8
Model 6	2x2 km + neighboring forest index at 2x2 km	16738.76	110.13
Model 1	0.5x0.5 km	16746.05	117.42
Model 1	1x1 km	16753.75	125.12
Model 1	0.25x0.25 km	16758.82	130.19
Model 7	2x2 km + 30x30 km	16788.11	159.48
Model 1	30x30 km	16792.54	163.91
Model 1	4x4 km	16806.69	178.06
Model 6	30x30 km + neighboring forest index at 30x30km	16812.02	183.39
Model 1	15x15 km	16883.76	255.13
Model 1	60x60 km	16898.30	269.67

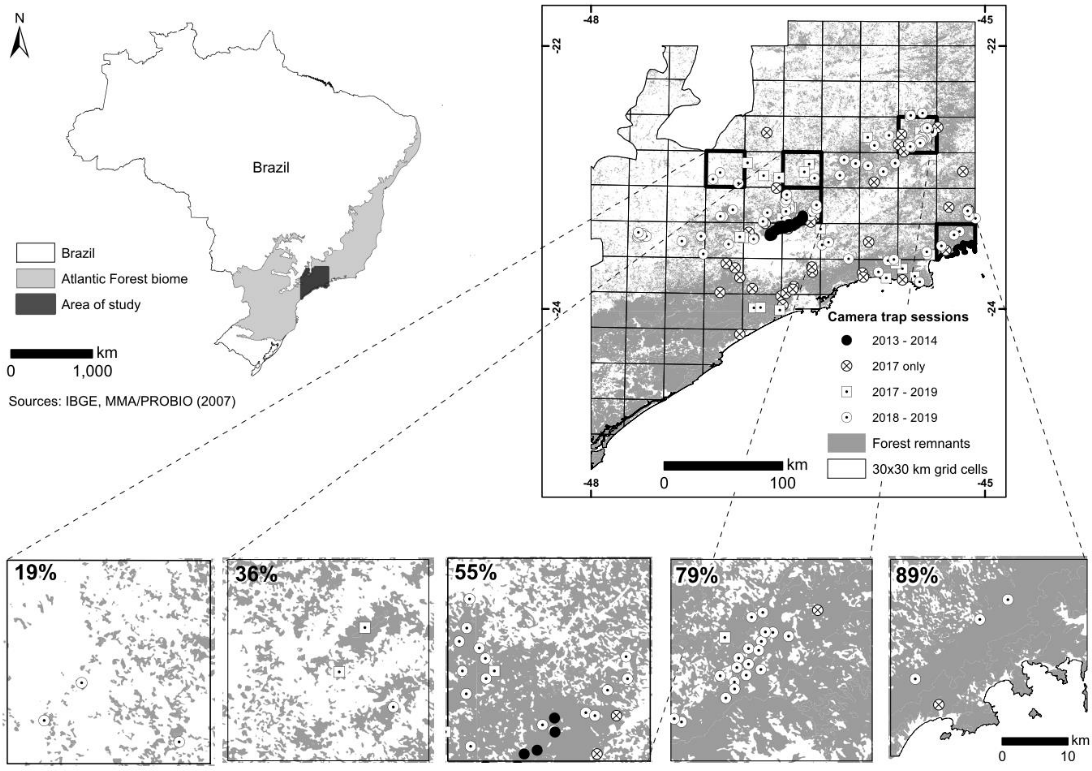


Figure 1. Location of study area in Brazil (top left), 30 by 30 km sampling units (top right), and camera traps (top right and insets). Different symbols represent different deployment windows for camera traps. Insets show variation in total amount of forest cover across sample units.

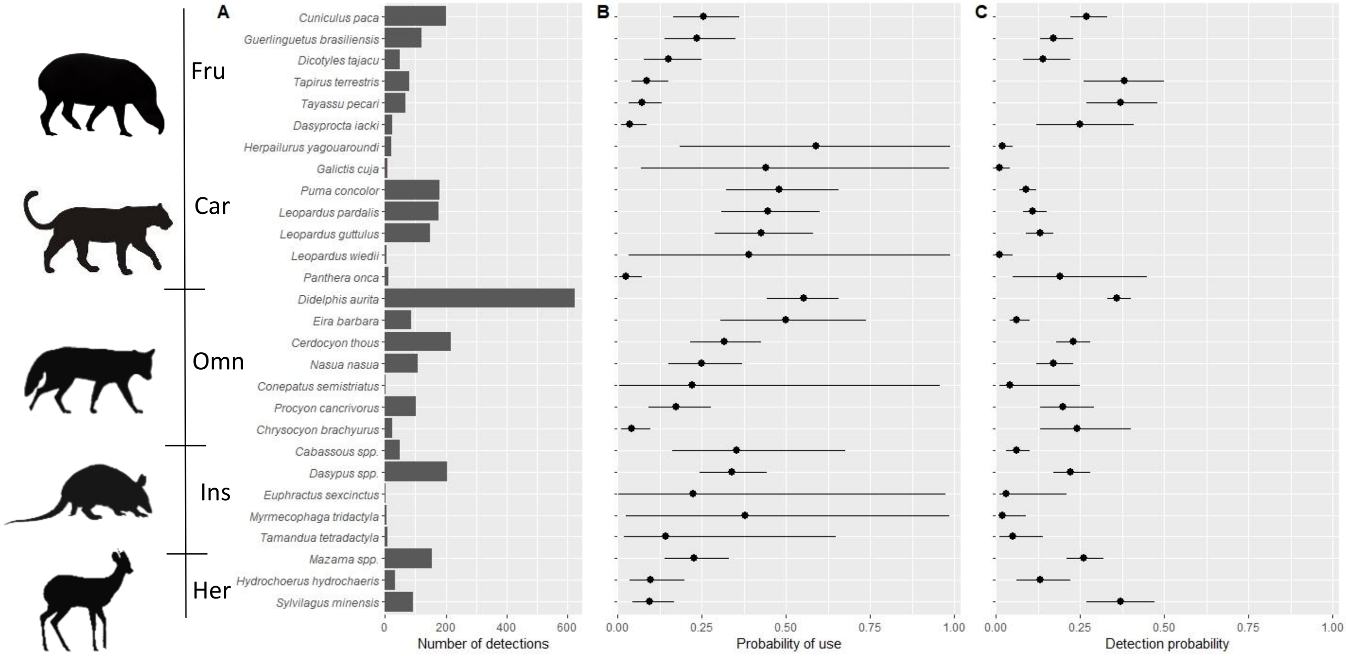


Figure 2. Number of detections by species (A) within the Atlantic Forest sites, along with the predicted mean probability of use in sampled sites (B) and detection probability (C). Fru = frugivore, Car = carnivore, Omn = omnivore, Ins = insectivore, and Her = herbivore. The results shown use Model 1 at the best overall extent for the forest amount covariate (i.e., 2x2 km).

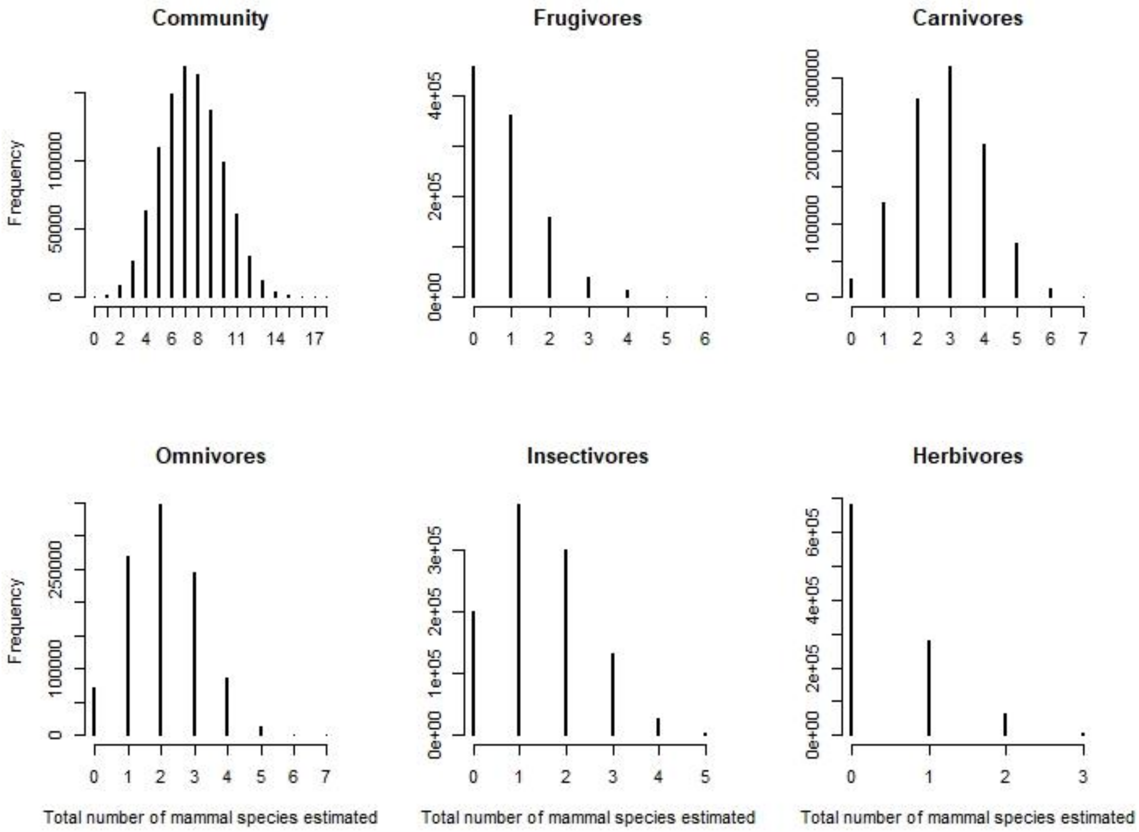


Figure 3. Frequency of predicted species richness observed within Atlantic Forest sites, considering a 2 x 2 km sampling extent. Results are shown for the entire mammal community (top left) as well as for individual trophic guilds.

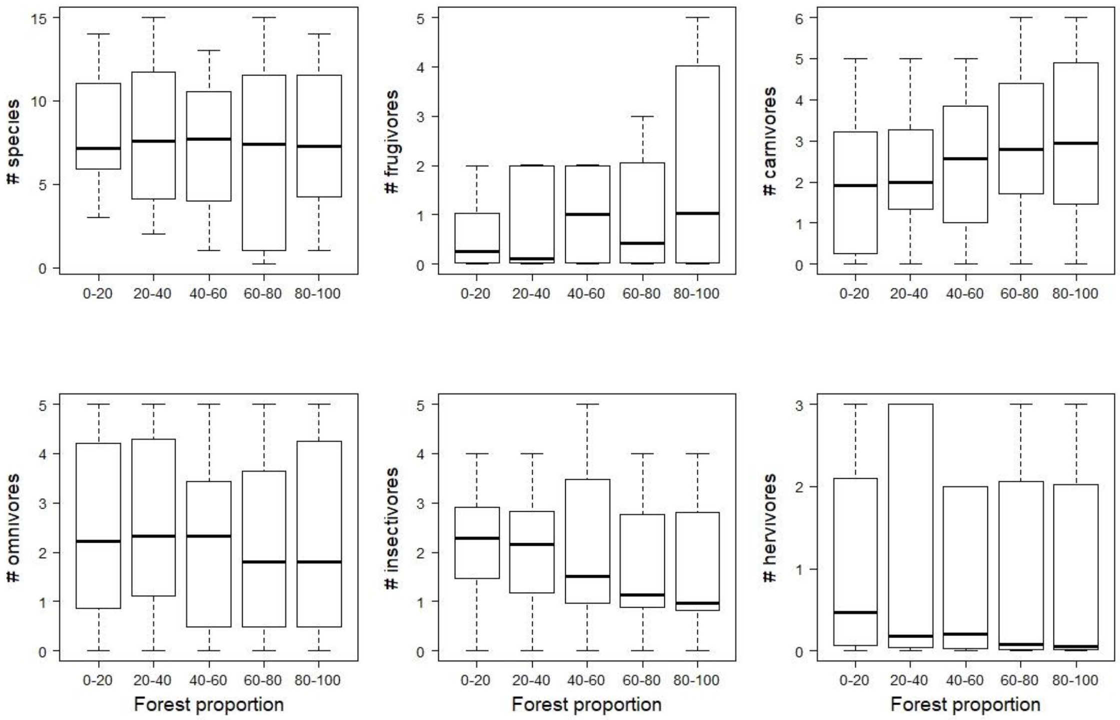


Figure 4. Estimated mammal species and trophic guild species richness across a gradient of forest amount at sampled sites. Box and whiskers-plot indicate median, lower and upper quantiles, minimum, and maximum values.

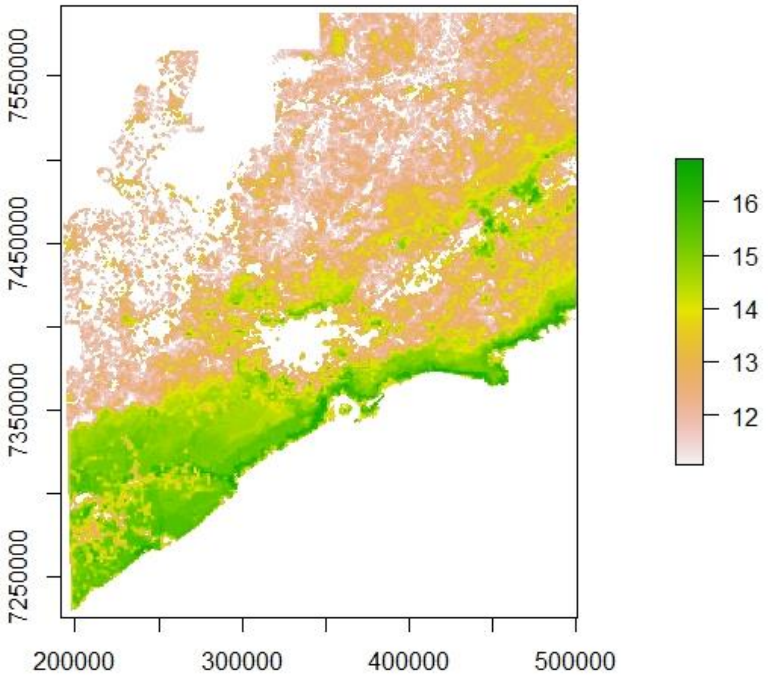


Figure 5. Relative species richness calculated by summing species' probabilities of use (Model 1) across the forest remnants in the study area at the best extent (2x2 km) for the medium and large-sized mammal community (28 species) in an Atlantic Forest human-dominated landscape.

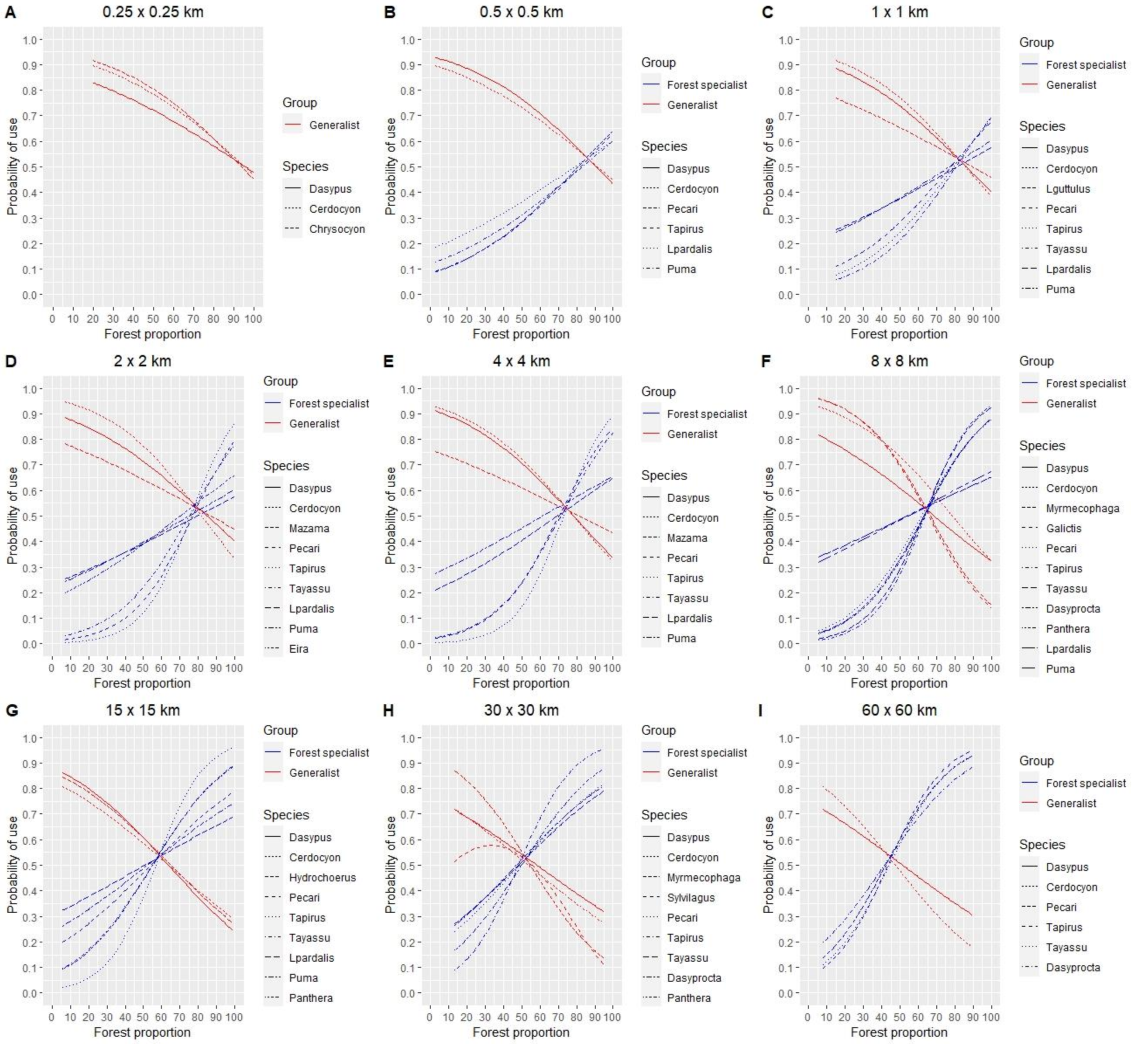


Figure 6. Prediction plots for the probability of use (ψ) for mammals showing significant positive and negative relationships with forest amount in the landscape. Each plot (A-I) depicts the partial slope for forest amount fit at different sampling extents (0.25x, 0.5, 1, 2, 4, 8, 15, 30, and 60 km). All plots were derived from the linear model (Model 1), except for *Sylvilagus minensis* at the 30 km extent, for which the nonlinear (quadratic) model (Model 2) was best. Critical points were identified where the probability of use was equal between forest-dependent (+ slopes) and generalist- or open-habitat species (- slopes).

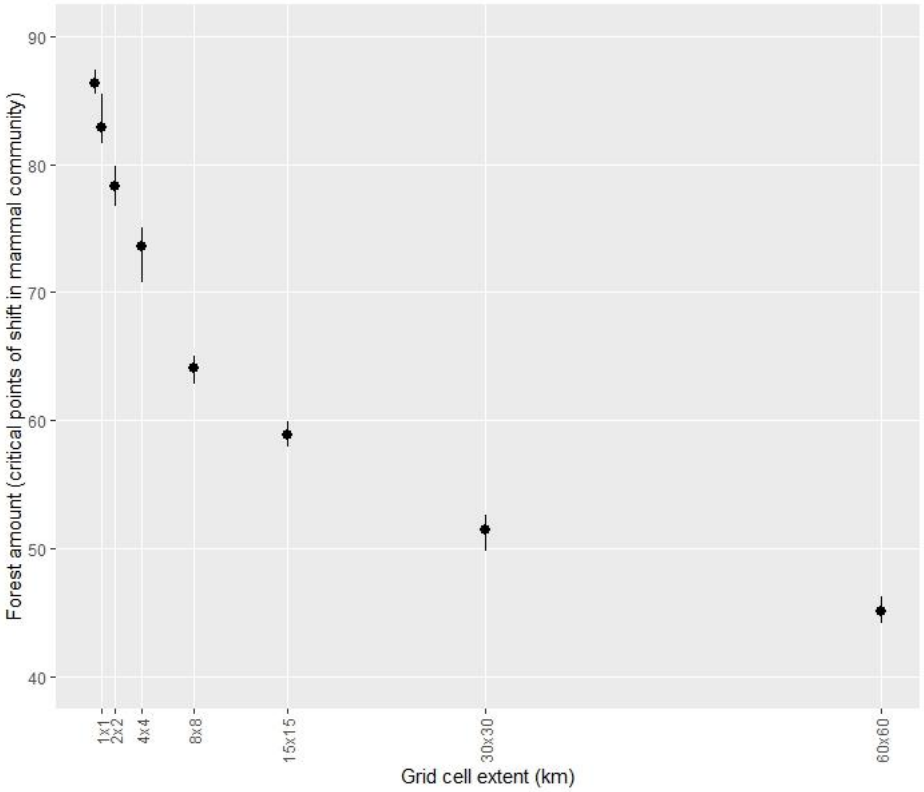


Figure 7. Critical (threshold) points at different grid cell extents for the forest amount covariate (from 0.5 km to 60 km) indicating the forest proportion at which a shift in the mammal community might be expected, i.e., where forest-dependent species have equally as high a probability of use as generalist- or open habitat-species.

Appendix 1. Species included in multi-species multi-session occupancy models, total number of detections for 7 days-pooled data, and naïve occupancy for four camera trap sessions (275 sites) in a human-dominated Atlantic Forest landscape in Southeastern Brazil. Car = carnivore, Fru = frugivore, Her = herbivore, Ins = insectivore, Omn = omnivore.

Species	Common name	Trophic guild	Detections (N)	Naïve Occupancy
Cabassous spp.	Naked-tailed armadillo	Ins	48	0.13
Cerdocyon thous	Crab-eating fox	Omn	216	0.25
Chrysocyon brachyurus	Maned wolf	Omn	24	0.03
Conepatus semistriatus	Striped Hog-nosed skunk	Omn	2	0.01
Cuniculus paca	Paca	Fru	201	0.23
Dasyprocta iacki	Agouti	Fru	25	0.03
Dasypus spp.	Nine-banded or seven-banded armadillo	Ins	205	0.30
Dicotyles tajacu	Collared peccary	Fru	50	0.11
Didelphis aurita	Big-eared opossum	Omn	625	0.52
Eira Barbara	Tayra	Omn	86	0.22
Euphractus sexcinctus	Six-banded armadillo	Ins	1	0.01
Herpailurus yaguaroundi	Jaguarundi	Car	22	0.08

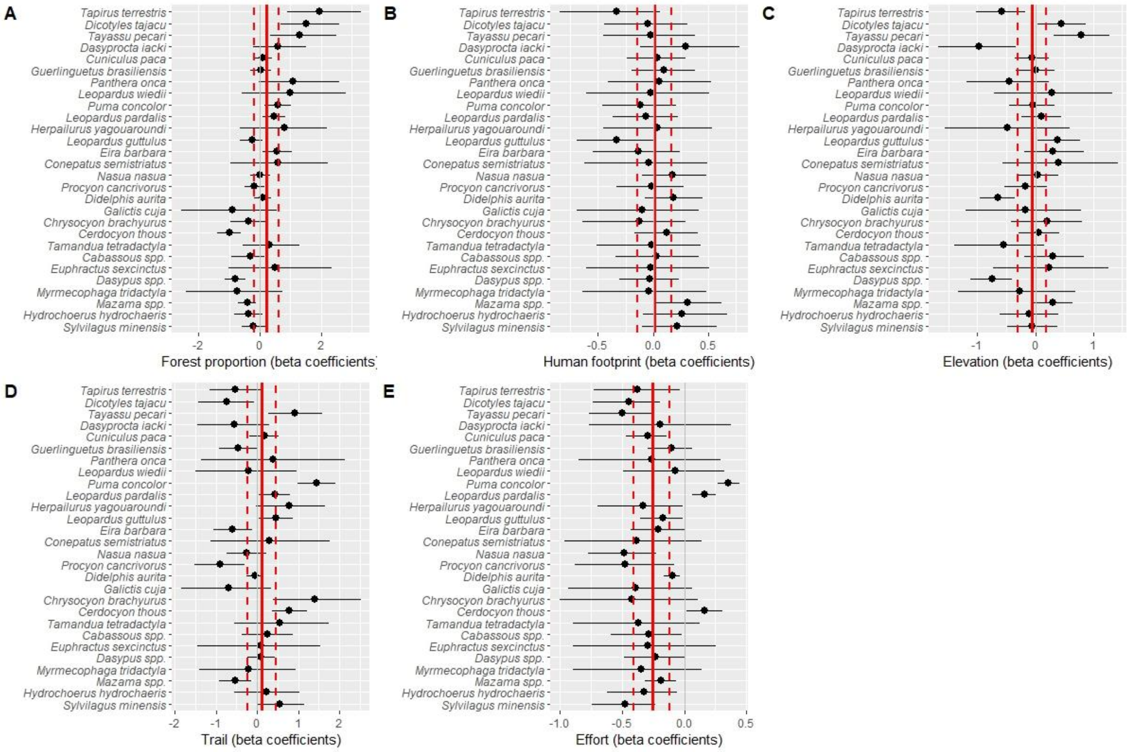
Galictis cuja	Lesser grison	Omn	9	0.03
Guerlinguetus brasiliensis	Squirrel	Fru	119	0.18
Hydrochoerus hydrochaeris	Capybara	Her	32	0.06
Leopardus guttulus	Oncilla	Car	147	0.29
Leopardus pardalis	Ocelot	Car	176	0.30
Leopardus wiedii	Margay	Car	5	0.02
Mazama spp.	Brocked deer	Her	156	0.20
Myrmecophaga tridactyla		Ins	5	0.02
Nasua nasua	Coati	Omn	107	0.19
Panthera onca	Jaguar		11	0.01
Puma concolor	Cougar	Car	179	0.25
Procyon cancrivorus	Crab-eating raccoon	Omn	103	0.13
Sylvilagus sp.	Brazilian cottontail	Her	93	0.09
Tapirus terrestris	Tapir	Fru	79	0.08
Tayassu pecari	White-lipped peccary	Fru	67	0.07
Tamandua tetradactyla	Collared Anteater	Ins	9	0.03

Appendix 2. Correlation matrix among covariates used in multi-scale multi-species occupancy models. Values in bold indicate statistically significant relationship ($P < 0.05$).

	Elevation	Human footprint	Forest (0.25 km)	Forest (0.5 km)	Forest (1 km)	Forest (2km)	Forest (4 km)	Forest (8 km)	Forest (15 km)	Forest (30 km)	Forest (60 km)
Elevation	1.00										
Human footprint	**-0.40**	1.00									
Forest (0.25 km)	0.04	-0.09	1.00								
Forest (0.5 km)	0.06	-0.07	**0.71**	1.00							
Forest (1 km)	**0.12**	-0.02	**0.68**	**0.74**	1.00						
Forest (2 km)	**0.16**	**-0.20**	**0.55**	**0.69**	**0.76**	1.00					
Forest (4 km)	**0.16**	**-0.28**	**0.48**	**0.59**	**0.66**	**0.82**	1.00				
Forest (8 km)	**0.17**	**-0.24**	**0.39**	**0.55**	**0.54**	**0.71**	**0.73**	1.00			
Forest (15 km)	0.11	**-0.28**	**0.39**	**0.46**	**0.50**	**0.56**	**0.61**	**0.78**	1.00		
Forest (30 km)	0.10	**-0.30**	**0.31**	**0.40**	**0.38**	**0.48**	**0.53**	**0.85**	**0.85**	1.00	

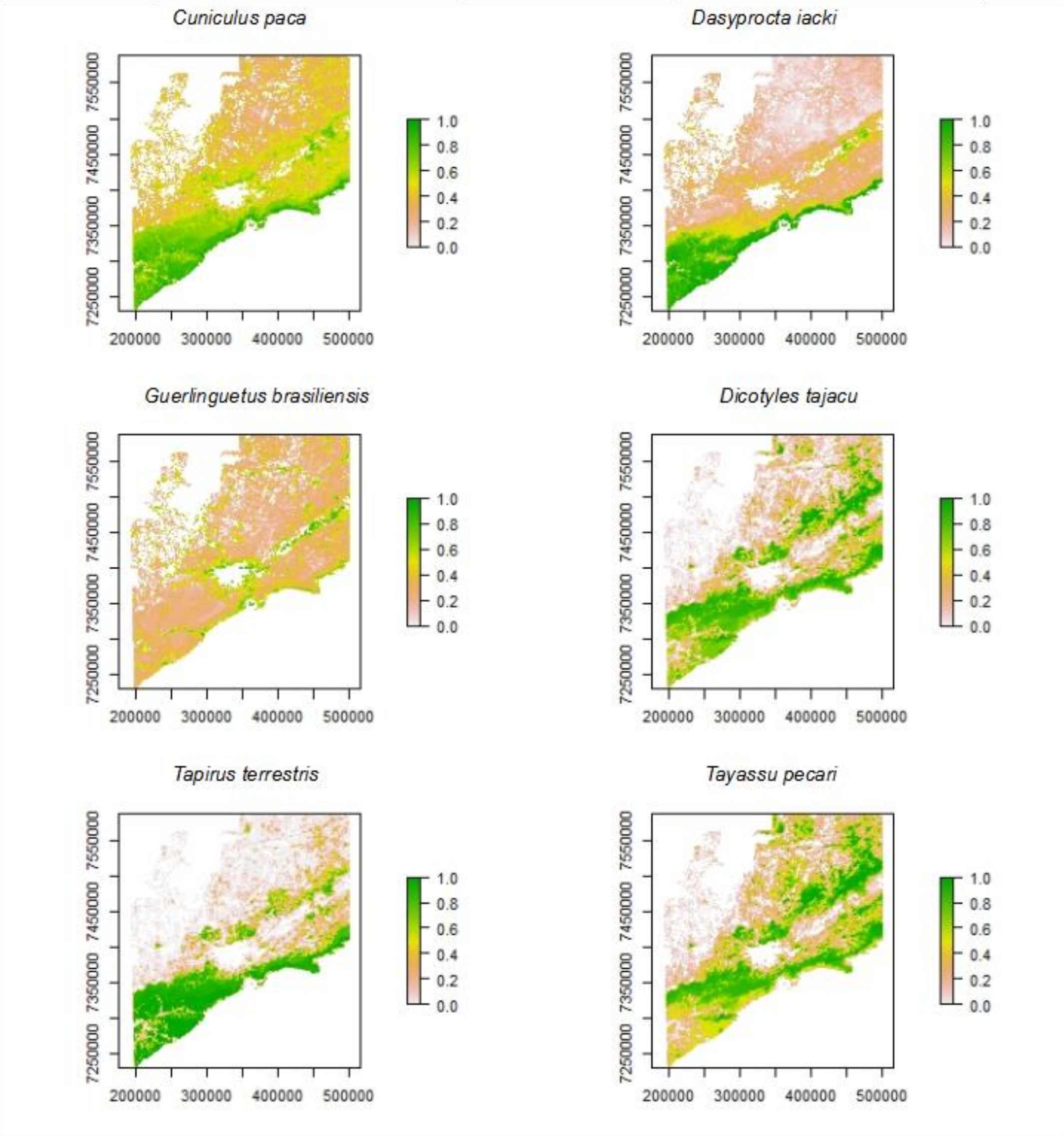
Forest (60 km)	0.08	-0.09	**0.29**	**0.38**	**0.37**	**0.44**	**0.49**	**0.75**	**0.80**	**0.72**	1.00

Appendix 3. Beta coefficients for covariates influencing the probabilities of use and detection of mammals across a human dominated Atlantic Forest landscape for Model 1 at the best extent, 2x2 km.

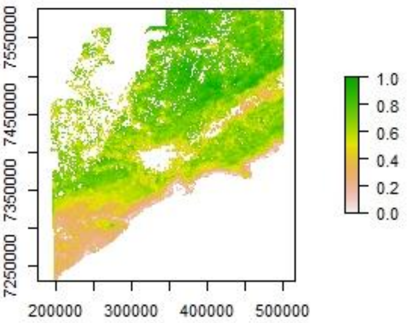


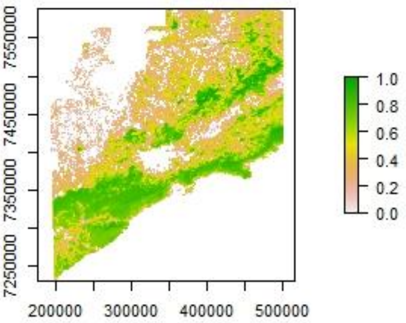
Appendix 4. Prediction maps for 28 mammal species using parameter estimates obtained from Model 1 at 2x2 km extent for forest amount at a human-modified Atlantic Forest landscape, southeastern Brazil.

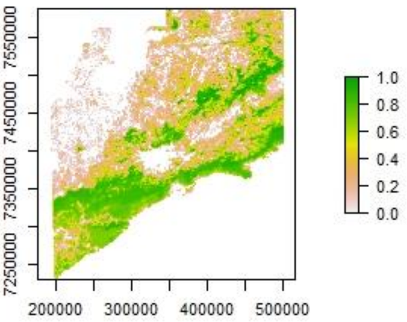
Frugivores

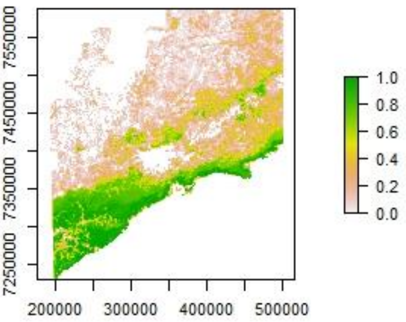


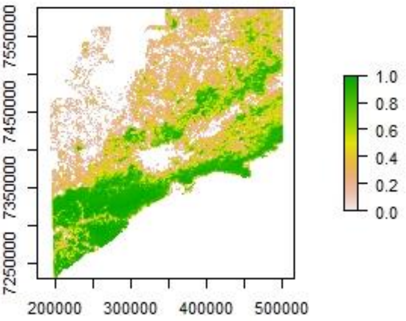
Carnivores

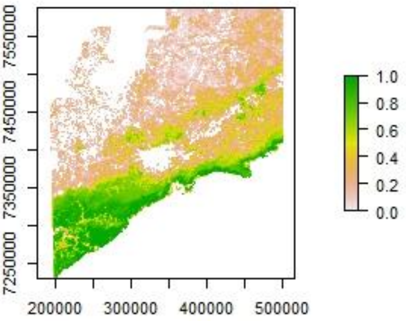

Leopardus guttulus


Leopardus pardalis

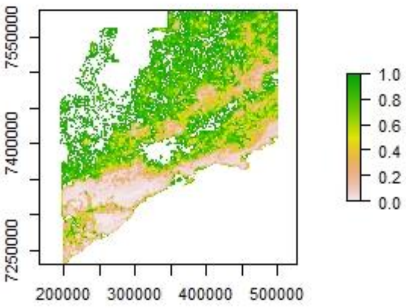

Leopardus wiedii

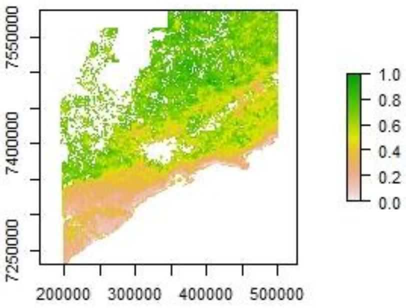

Panthera onca

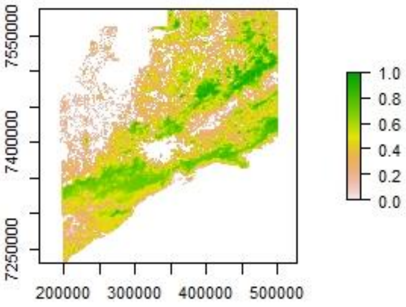

Puma concolor

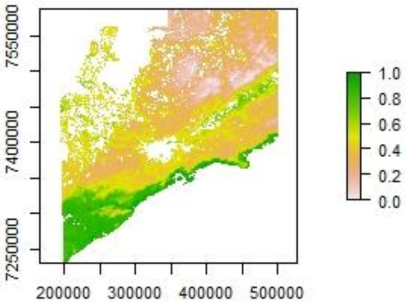

Herpailurus yagouaroundi

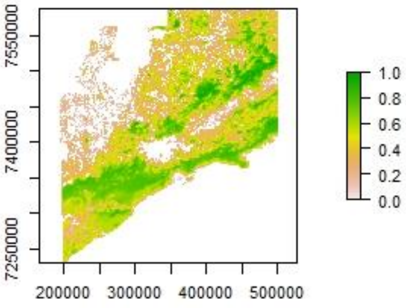
Omnivores

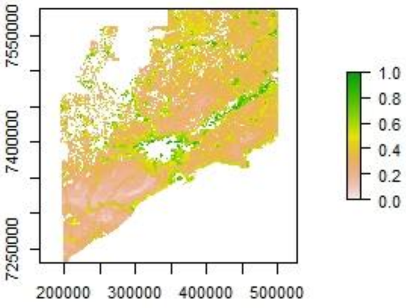

Cerdocyon thous

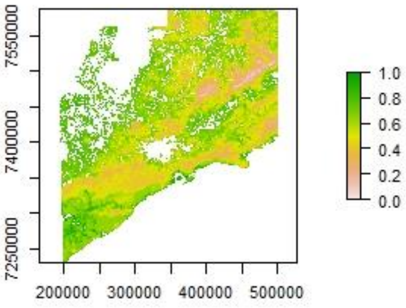

Chrysocyon brachyurus

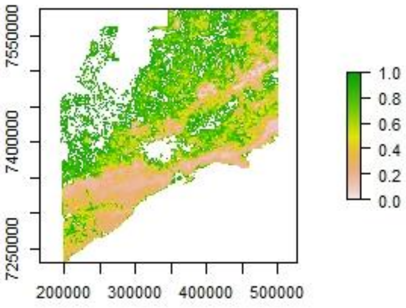

Conepatus semistriatus


Didelphis aurita


Eira barbara

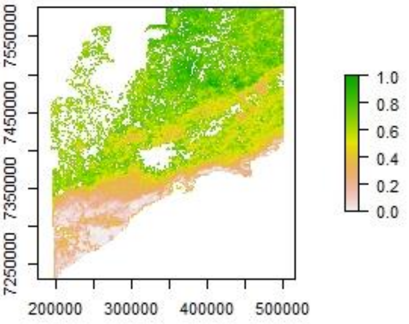

Nasua nasua


Procyon cancrivorus

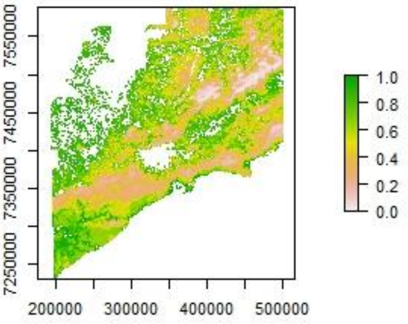

Galictis cuja

Insectivores

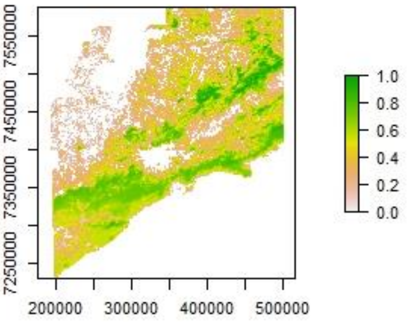
Cabassous sp.



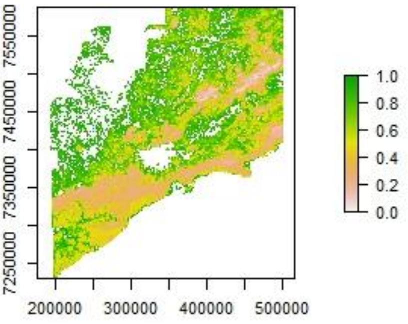
Dasypus sp.



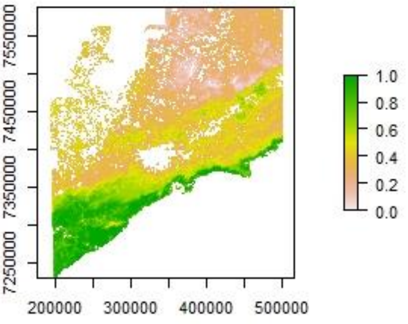
Euphractus sexcinctus



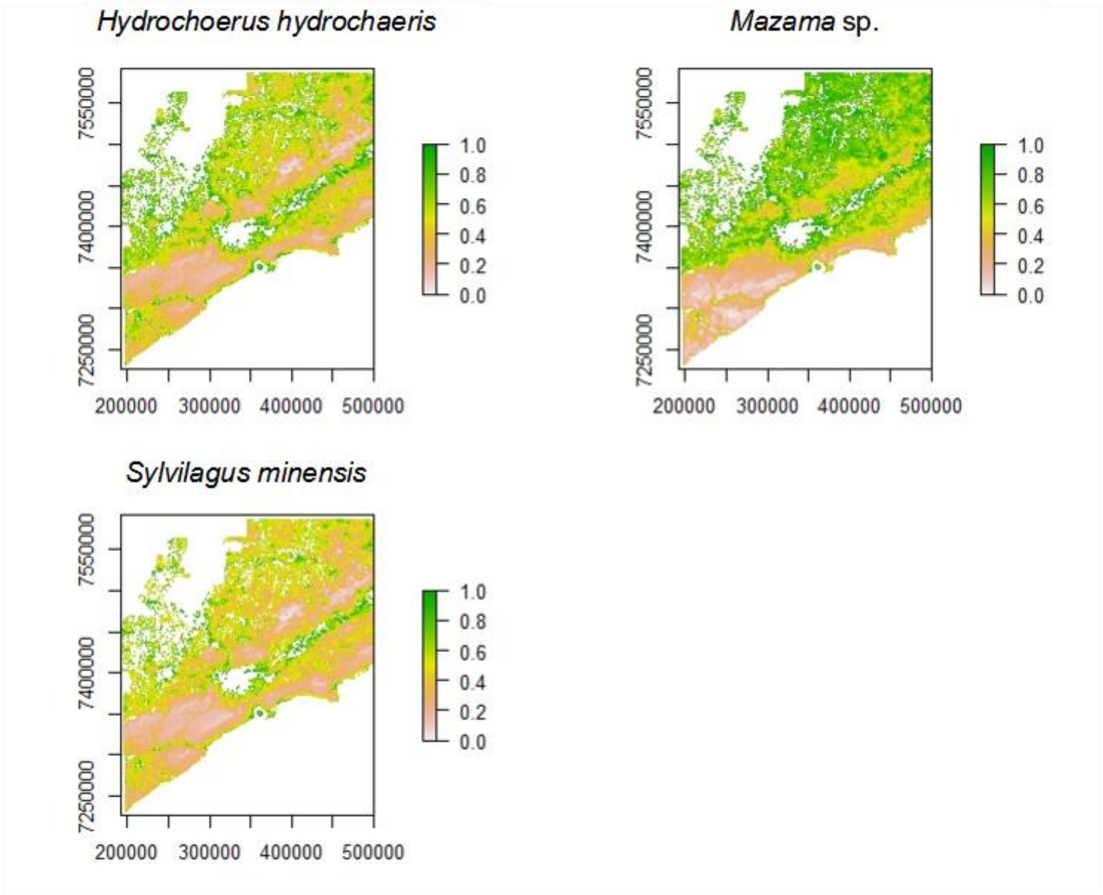
Myrmecophaga tridactyla



Tamandua tetradactyla



Herbivores


Hydrochoerus hydrochaeris
Mazama sp.
Sylvilagus minensis
7550000
7400000
7250000
200000
300000
400000
500000
1.0
0.8
0.6
0.4
0.2
0.0

CHAPTER 4 - EVALUATING MULTISPECIES CONNECTIVITY IN A HUMAN-DOMINATED LANDSCAPE IN THE ATLANTIC FOREST, SOUTHEASTERN BRAZIL

ABSTRACT

With more than 75% of ecosystems worldwide having suffered human modification, besides setting aside protected areas for biodiversity conservation, it is also crucial to focus on connectivity to maintain the existent metapopulations in human-dominated landscapes. This chapter involves a multi-species and multi-scale evaluation of habitat connectivity for forest-dependent medium- to large-bodied mammals occupying a gradient of habitat fragmentation within the Atlantic Forest. The most vulnerable mammal species to further habitat loss identified in chapter 3 were selected for the connectivity analysis using a graph-theoretic approach to measure network connectivity among core habitat patches for each target species. I validated model predictions from a multi-scale multi-species occupancy model (chapter 3) to identify areas of high habitat suitability, which were retained to identify core habitat patches for the connectivity analyses. I evaluated the contribution of each node to overall connectivity for each species by systematically removing each node in turn and quantifying its' individual impact in terms of the full network. Considering the value of protected areas in ensuring multispecies connectivity in this region, one third of the most important nodes for connectivity fell outside any protected area designation. Carnivores and frugivores shared 68.59-86.21% of the most important nodes, which indicates that relying on one species does not represent well what each species needs individually, given their divergent distribution across landscape and anthropogenic gradients. This study provided the identification of key areas to maintain the connectivity under existing habitat conditions for a suite of forest-dependent mammals in the human-dominated, Brazilian Atlantic Forest.

INTRODUCTION

Ongoing intensification of human activities remains an existential threat to species persistence (Doak et al. 1992; Goodwin and Fahrig 2002), with less than 25% of ecosystems world-wide being considered “free” from anthropogenic modification (Parrish et al. 2003; Grantham et al. 2020). Setting aside protected areas remains a primary tool for stemming the tide of biodiversity losses (Geldmann et al. 2013; Le Saout et al. 2013; Gray et al. 2016), and the Convention on Biological Diversity set a target for 17% of the earth’s surface to be covered by “effectively and equitably managed, ecologically representative and well connected” protected areas by 2020 (CBD 2010). As of 2018, terrestrial coverage of protected areas reached 14.9% (Belle et al. 2018), yet only 9.3-11.7% of the existing protected areas was considered connected based on dispersal distances for most terrestrial vertebrates (Saura et al. 2017; Ward et al. 2020). Enhancing the movement potential of species among protected areas remains critically important to ensure effectiveness of the world’s protected area network (Secretariat of the Convention on Biological Diversity 2005).

Measures of connectivity attempt to quantify the degree to which landscapes facilitate or impede the flow of individuals among patches of suitable habitat (Taylor et al. 1993), an important evaluation given that connectivity plays an important role in maintaining viable populations for many wide-ranging species Funcitonal connectivity, which represents the behavioral responses of individuals, species or ecological processes to landscape structure (Crooks and Sanjavan 2006), relates to how organisms move through a landscape in relation to both the structural connectivity of the landscape (spatial arrangement of different types of habitats) and the organisms’ biological characteristics, e.g., movement constraints (Paquet et al., 2006). Functional connectivity influences individual survival and reproduction, population dynamics and persistence, gene flow and genetic diversification of populations, and predator-prey dynamics (Wiens 2006). In this sense, the isolation of populations may lead to a loss of genetic diversity, and inbreeding in the short term, which in the long term could jeopardize species adaptation and evolution to changing environmental conditions (Crooks and Sanjavan 2006).

Network analysis is a key approach to evaluating functional connectivity, more specifically potential connectivity, based on the organism's dispersal ability (Fagan and Calabrese 2006). Graph-theoretic approaches have been largely used to measure network connectivity, helping guide decisions about the relative importance of individual patches to overall landscape connectivity (Urban and Keitt 2001; Urban et al. 2009). By removing each habitat patch in turn, graph-theoretic approaches have the advantage of identifying which of the existing habitat patches contribute the most to upholding species dispersal and other ecological flows in a landscape context (Saura and Pascual-Hortal 2007). Other approaches, such as least-cost path analyses, focus on identifying direct linkages among specific habitat patches (e.g., protected areas), but it remains unclear how effective protecting a single least-cost path between a pair of patches would be in providing functional connectivity across the landscape (Cushman and Landguth 2012).

Many studies have focused on evaluating connectivity only among protected areas, assuming that the species of interest would be present within such areas (Pinto and Keitt 2009; Minor and Lookingbill 2010; Wegmann et al. 2014; Castilho et al. 2015). Yet, by assuming protected areas to be suitable and occupied habitat while the rest of the landscape is "matrix" risks overlooking patches that are not just "corridor habitat", i.e., that facilitate movement, but serve as core habitat, i.e., contributing to population residency. As a result, consideration of connectivity among protected areas only may fail to recognize the critical contributions of patches of unprotected habitat (Ashrafzadeh et al. 2020). Moreover, protected areas may lack the species of interest or even represent sink conditions, and ensuring connectivity among sink populations alone could compromise metapopulation persistence (Taylor et al. 1993). Viewing the landscape as a gradient of varying habitat suitability should provide a richer consideration of landscape connectivity than the traditional patch-corridor view based solely on protected areas as patches.

Another core consideration for connectivity studies is the choice of study species. Although the majority of connectivity studies have focused on large-bodied, wide-ranging, or so-called “umbrella” species (Noss 1990; Beier 1993; Rabinowitz and Zeller 2010; Castilho et al. 2015; Keeley et al. 2017; Pitman et al. 2017), recognition that what may facilitate movement for some species may filter the movements of others (Lomolino et al. 2017) calls for multispecies assessments (Cushman and Landguth 2012; Lechner et al. 2017; Liu et al. 2018; Ashrafzadeh et al. 2020; Brennan et al. 2020; Fedorca et al. 2020). Moreover, the varying ecological responses of each species to landscape variables (e.g., human disturbances, fragmentation, elevation), and at different scales leads to different core habitat areas or patches for different species (Blazquez-Cabrera et al. 2014; Ashrafzadeh et al. 2020; Brennan et al. 2020; Pliscoff et al. 2020). Therefore, limiting a connectivity analysis to a single species or definition for what constitutes habitat, e.g., protected areas only, will invariably fail to represent the conservation needs of the larger community (Cushman and Landguth 2012; Brennan et al. 2020). Moreover, biological characteristics of a species (i.e., dispersal ability) highly influences apparent levels of connectivity, with the degree of connectivity decreasing when shorter potential dispersal distances are considered (Cushman and Landguth 2012). Where protecting regional biodiversity is the goal, connectivity studies should involve multiple species having different life history requirements, movement propensities, and sensitivity to human activities (Brodie et al. 2015; Ersoy et al. 2019).

This study involves a multi-species and multi-scale evaluation of habitat connectivity for forest-dependent medium- to large-bodied mammals occupying a gradient of habitat fragmentation within the Atlantic Forest, São Paulo and Minas Gerais states, Brazil. My specific objectives were to 1) compare connectivity measures among species with different body sizes and life history traits (e.g., frugivores versus carnivores), 2) evaluate the connectivity value of different levels of land protection in this region—from strictly protected "park" areas to multiple use landscapes, and 3) identify critical gaps in the protected area network with respect to areas of high connectivity importance. Given these objectives I defined habitat patches following a gradient model, using species-specific predictions of site occupancy across the region (Bonjorne de Almeida Chapter 3) rather than simply focusing on connections among existing protected areas.

METHODS

MODELING HABITAT FOR FOREST-DEPENDENT SPECIES

As only 12% of the original Atlantic Forest remains, in fragmented, mostly small, and isolated patches, I chose to focus my assessment for community connectivity on forest-dependent mammals. I identified forest-dependent species as those having a positive association between forest amount and the probability of site use in a previous analysis (Bonjorne de Almeida Chapter 3)—yielding eight species that included four carnivores (*Eira barbara*, *Leopardus pardalis*, *Panthera onca*, and *Puma concolor*) and four frugivores (*Dasyprocta iacki*, *Dicotyles tajacu*, *Tapirus terrestris*, and *Tayassu pecari*). Of the selected species, four were listed in the Brazilian red list of threatened species (*T. terrestris*, *T. pecari*, *P. onca*, and *P. concolor*; (MMA, 2014), and two were considered threatened at the state level (*L. pardalis* and *D. tajacu*; (COPAM, 2010; São Paulo, 2018).

Using the same data and approach described in Chapter 3, I refit to these eight species alone a multi-species, multi-session hierarchical occupancy model, using a 2x2 km sampling unit to quantify proportion forest cover, and including linear covariate effects as:

$$logit(\psi_{ij}) = u_{im} + \beta1_i\, forest_j + \beta2_i\, elevation_j + \beta3_i\, human\, footprint_j,$$

where u_{im} represented random intercepts for each species *i* and session m, and followed a normal distribution with the means and variances governed by the community hyperparameters (i.e., $u_{im} \sim Normal(\mu_u, \sigma_u^2), \sigma_u \sim Uniform(0,10)$). Forest cover was mapped using Landsat 7 images at 30 m resolution (MMA/PROBIO, 2007). I included two additional site-specific metrics thought to influence species distribution across the region – human disturbance and elevation. For the former, I used the human footprint index produced by (Venter et al., 2016), whose values range 0-100 and were derived from a combination of human population density, human land use and infrastructure, and human access (mapped at a 1-km resolution). Lastly, the elevation of each camera site was recorded using Shuttle Radar Topography Mission (SRTM) data at 89 m resolution (Weber et al., 2004).

To identify core habitat patches, I applied this model to landscape covariates to predict the probability of site use, ψ, for each species within each 2-km cell across the study area. Prior to defining high quality habitat patches, I validated model predictions using a sample of 306 independent, out-of-sample records of species occurrence drawn from the literature (Lima et al., 2017; Nagy-Reis et al., 2020; Souza et al., 2019). I retained only species records collected since the year 2000, that were directly collected by researchers (e.g., camera traps, footprints, line transects), and that had high specificity in terms of the location of the observation (reported as having high precision). Following Boyce et al. (2002), for each species I rescaled predicted ψ values to sum to 1 across the study region (Gould et al. 2019) and then grouped the resulting values into 10 “equal area” bins such that each bin represented 10% of the landscape rather than 10% of the range of predicted values. Within each bin, *i*, I quantified:

$$P(use)_i = \sum_{j=1}^{N} \hat{\psi}_j$$

where $\hat{\psi}_j$ is the estimated probability of habitat use for grid cell *j* (Boyce et al. 2002; Howlin et al. 2003; Gould et al. 2019). The proportion of out-of-sample occurrences within each bin *i* was then calculated as:

$$O(use)_i = \sum_{j=1}^{N} \frac{r_{ij}}{r}$$

where r_{ij} is an observed point of occurrence within bin *i* and grid cell *j* obtained from the literature or unpublished data and *r* is the total number of observed occurrences considering all bins. I then assessed the correlation between predicted and observed habitat use for each species by conducting a Spearman’s rank correlation test, where $\rho \geq 0.60$ indicates a positive correlation (Boyce et al. 2002). Because of the lack of independent points to validate occurrence of *D. iacki* (N=12) and *P. onca* (N=3), these species were not included in subsequent analyses.

Following validation, I identified high versus low habitat suitability based on the observed levels of use from the out-of-sample data. Having previously grouped predicted probabilities of use into 10 equal-area bins, one would expect 10% of the observed points to fall into each bin by random chance alone. Therefore, O(use) < 0.1 indicates disproportionately lower use than expected (poor suitability) while O(use) > 0.1 indicates use disproportionately greater than expected (high suitability). For each species, areas of high habitat suitability were retained to identify core habitat patches for the connectivity analyses. If a 2 x 2 km cell of high suitability shared a physical connection with neighboring cells of high suitability (using the 8-neighbor rule), the group of linked cells was considered as a core habitat patch. However, the minimum mapping unit for habitat patches was a 2x2 km cell of high suitability habitat (4 km^2), given that even small forested areas can be important to connectivity if they are used as stepping stones by animals (Saura et al. 2014; Herrera et al. 2017).

ASSESSING CONNECTIVITY VIA NETWORK ANALYSIS

A graph theory approach was used to measure network connectivity among core habitat patches for each of the six target species. A graph represents a landscape as a set of *nodes*, i.e., core habitat patches, and *edges*, i.e, functional connections among nodes (Urban and Keitt, 2001; Urban et al., 2009). A graph is connected when there exists a path (edge) between each pair of nodes, meaning that every node is reachable from some other node. On the other hand, an unconnected graph may include several connected components or subgraphs, which are clusters of interconnected nodes (reachable for each species based on their dispersal distance) that are completely disconnected from other clusters. A graph component is a connected subgraph (Bunn et al. 2000; Urban and Keitt 2001; Urban et al. 2009).

Using Conefor 2.6 (Saura and Torné 2009), for each species I first calculated the probability of connectivity (PC) index, considered effective in identifying the habitat areas that most contribute to overall landscape connectivity (Saura and Pascual-Hortal 2007; Bodin and Saura 2010; Rubio and Saura 2012). This index is based on a probabilistic connection model, where the dispersal probability between two habitat patches is obtained as a decreased function of edge-to-edge interpatch distance following a negative exponential function. The PC index is based on the habitat availability concept, which considers a patch itself as a space where connectivity occurs, integrating habitat patch area (intrapatch connectivity) and connections between different patches (interpatch connectivity) in a single measure (Saura and Pascual-

Hortal, 2007). Therefore, habitat availability for a species may be low if habitat patches are poorly connected, but also if the habitat is connected but scarce (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007).

For this analysis, the median dispersal distances for each mammal species was calculated following (Bowman et al., 2002) as:

$$Median\ dispersal\ distance = 7\sqrt{home\ range},$$

where the home range was the average of home range estimates reported in the literature for each species (Eisenberg 1989; Fragoso 1998; Emmons and Feer 1999; Henry 1999; Presley 2000; Jacomo 2004; Keuroghlian et al. 2004; Silveira 2004; Oliveira and Cassaro 2005; A.L.J. Desbiez et al. 2009; Cañas 2010; Mazzolli 2010; Medici 2010; de Oliveira et al. 2010; Reis et al. 2010; Desbiez et al. 2012; Keuroghlian et al. 2012; Medici et al. 2012; de Almeida Jácomo et al. 2013; Azevedo et al. 2013a; Oliveira et al. 2013; Rodrigues et al. 2013; Azevedo et al. 2020). The input files (node and connection files) were generated using the Conefor Inputs 1.0.218 extension for ArcGIS (Jenness 2016), by considering the core habitat areas and attributing the median dispersal distances to each species. Next, I evaluated the contribution of each node to overall connectivity for each species by systematically removing each node in turn and quantifying its' individual impact in terms of the difference in PC values ((i.e., dPC) relative to the full network (Saura and Pascual-Hortal, 2007). Following (Wang et al., 2014), I identified the top 1%, 5%, 10%, and 20% of important nodes for each species, meaning the nodes with the highest dPC values (highest 1, 5, 10, and 20% of dPC values).

Following the calculation of species-specific measures of connectivity, I evaluated to what degree important patches (nodes) or areas (components) were shared among species, and particularly whether an umbrella species (*P. concolor*) captured all the salient aspects of connectivity for the community or whether key differences in connectivity were observed between species groups according to body size or dietary guild. Comparisons were made by calculating the overlap between the core habitat patches most important to connectivity for (1) pumas versus the other five species, pumas and frugivores (*D. tajacu*, *T. pecari*, *T. terrestris*), or pumas and mesocarnivores (*E. barbara*, and *L. pardalis*), and (2) between carnivores (*E. barbara*, *L. pardalis*, and *P. concolor*) and frugivores.

Lastly, I evaluated the degree to which strictly protected areas (7.47% of the landscape) versus sustainable use protected areas (26.40%) contributed to connectivity in the study area. Following gap analysis methodology, I calculated the percentage of the top 1, 5, 10, and 20% of important habitat nodes that fell within the boundaries of protected areas (Scott et al. 1993; Jennings 2000). Important patches falling outside of protected area boundaries were identified as critical "gaps" in the protected area network. To identify the most important core habitat areas for connectivity across the six species, the results from single species analyses were combined to represent core connectivity areas for all species. ArcGIS 10.7.1 and the free software R 3.6.0 were used for all geoprocessing analyses (R Core Team 2019).

RESULTS

In contrast to the modeling results reported by Bonjorne de Almeida (Chapter 3), which included 28 species rather than being restricted solely to forest-dependent species, the multispecies occupancy model refit herein yielded larger effect sizes and showed seven of the eight species to have positive and informative coefficients with respect to the forest amount variable (Table 1; Appendix 1). The model achieved convergence for all parameters: Gelman-Rubin statistic ≈ 1 (Kéry, 2010). Model validation with out-of-sample data revealed that ~20% of the landscape (represented by bins 9 and 10) represented suitable (core) habitat for *D. tajacu*, *T. pecari*, *E. barbara*, and *L. pardalis*, ~30% of the landscape (bins 8-10) was suitable for

P. concolor, and ~40% was suitable for *T. terrestris* (Figure 1, Appendices 2 , 3, 4). For *P. concolor and T. terrestris*, I considered the peak in occurrence records around bins 7 or 8 followed by a decline with increasing bin rank to reflect a lack of recorded observational data within the larger patches represented by strictly protected areas where the species are known to occur (see Appendix 4) rather than by an actual decline in suitability within the higher bin ranks. This interpretation was confirmed by state park staff, who commonly find footprints of both species but do not record them. Except for *P. concolor*, which had limited validation data especially at high bin values, all species yielded $\rho \geq 0.6$, indicating valid model predictions.

Habitat appeared most aggregated for *D. tajacu*, with 145 nodes, and most fragmented for *E. barbara*, and *T. pecari*, with 206, and 205 nodes, respectively (Figure 2). Yet, *T. pecari*, with its large dispersal distance (~55 km) proved to be the least isolated species, exhibiting the most connections among nodes (3890 edges) and a unique component (i.e., totally connected graph). In contrast, *D. tajacu*, the species with the smallest dispersal distance (~10 km), had the highest number of isolated habitat areas, exhibiting 21 components and showed the fewest connections among nodes (145 edges).

Core habitat patches were ranked in importance based on the dPC index and mapped to show for each species the most important 1%, 5%, 10%, and 20% of nodes along with everything else (>20%; Figure 3). A small portion of the nodes exhibited much larger dPC values, with the top 1%, 5%, and 10% of nodes, representing 56%, 89%, and 95% of the total dPC values, respectively. The nodes showing the highest 5% dPC values (top 5%) represented large habitat patches (Figure 3). In terms of the value of *P. concolor* as a potential umbrella species, 62.26-64.18% of the important nodes were shared between *P. concolor* and all the other species (60.29-74.56% shared between puma and mesocarnivores). Likewise, when comparing species of differing natural history requirements, carnivores and frugivores shared 68.59-86.21% of the most important nodes (Table 3).

Considering the value of protected areas in ensuring multispecies connectivity in this region, one third (up to 33.86%) of the most important nodes for connectivity fell outside any protected area designation (Figure 4). Figures 5 shows the multispecies connectivity model considering the top 1% most important nodes and the protected areas in the studied area. Only 10 out of the 60 state or federal protected areas in the landscape studied had more than 80% of its area indicated as priority areas for connectivity. Three of these were sustainable use protected areas: Cananeia-Iguape-Peruíbe Environmental protected area, Serra do Mar Environmental protected area, and Despraiado Reserve for sustainable development, and seven were strictly protected areas: Serra do Mar, Jurupará, Campos do Jordão, Carlos Botelho state parks, Jureia-Itatins, Banhados de Iguape, and Chauás Ecological stations. However, 37 protected areas failed to encompass critical areas for connectivity within their boundaries when considering the highest priority nodes (top 1% of dPC values). That dropped to 23 when considering the top 20% of most important nodes (Appendix 5).

DISCUSSION

Ideally, protected areas designed to maintain biodiversity cover a representative sample of regional biodiversity and are functionally connected, facilitating movements of individuals within the protected areas network (Bauduin et al. 2020) and forming the basis for metapopulation dynamics (Hanski 1998). An even better scenario might establish protection around the core habitats most important to regional connectivity, yet few assessments of the gaps in the protected area network consider connectivity directly. My multi-species, network-based assessment of connectivity in southeastern Brazil revealed that despite the studied landscape having a relatively large proportion of area under protection (up to 33% of the study area and covering ~66% of the core habitat areas for the six forest-dependent mammals in this study), fully one third of the key habitats supporting community connectivity in the region lacked any sort of protection. On the flip side, that means the majority of priority areas for community connectivity in this study fell under some form of protection, either in strictly protected areas (up to 32.16%) or multiple use protected areas (up to 40.90%). The type (or level) of protection matters as many species show increased likelihood of occurrence given higher levels of protection (Nagy-Reis et al. 2017; Ferreira et al. 2020), which often leads to greater species richness in strictly protected areas compared to areas of lesser protection (Ferreira et al. 2020). Most of the strictly protected areas in the studied landscape are state parks (IUCN category II; Dudley, 2013), the majority represented entirely by public lands (Brazil 2000). Sustainable use protected areas in the region mostly represent Environmental protected areas (*Áreas de Proteção Ambiental*, APA) – IUCN category V (Dudley 2013), typically large areas allowing various forms of natural resource use or extraction, where biodiversity protection remains a secondary objective (Rylands and Brandon 2005). In fact, APAs are closer to a mechanism of land-use management than actual land protection (Rylands and Brandon 2005). Nevertheless, sustainable use protected areas sustain forest cover better than unprotected landscapes (Geldmann et al. 2015), and could play a fundamental role in biodiversity conservation when covering areas important for connectivity as observed in this study. Nevertheless, in this Atlantic Forest biome, nearly half of all protected areas lacked any apparent value for connectivity, at least with respect to the medium- to large-bodied and forest-dependent mammals considered in this study—demonstrating the risks involved in considering only protected areas when assessing landscape connectivity.

Likewise, designating areas for conservation based on umbrella species, which may be undertaken largely for expediency reasons, leaves uncertain the degree to which other species may be afforded “trickle-down” protection (Favreau et al. 2006). In fact, many studies suggest the failure of the umbrella species approach for community conservation (Andelman and Fagan 2000; Minor and Lookingbill 2010; Brodie et al. 2015; Meurant et al. 2018; Brennan et al. 2020). Similarly, the focus on one group of species (usually carnivores, which represent many wide-ranging species) has often been done when evaluating connectivity in fragmented landscapes (Crooks et al. 2011; Kanagaraj et al. 2013; Castilho et al. 2015; Ashrafzadeh et al. 2020; Diniz et al. 2020). However, to target only one group would likely miss the prioritization of important areas for other groups of species (e.g., frugivores), as has been found by other studies (Brodie et al. 2015; Mimet et al. 2016). Although I observed that the majority of important areas for connectivity were shared between pumas and the other species (~62-64%), or between carnivores and frugivores (~69-86%), important areas were missed when targeting one species or one specific group as an umbrella since landscape and anthropogenic factors have differing effects on each species probability of occurrence.

In this study, we considered all forest-dependent mammals reliably detectable by trail cameras as representatives of a broader forest mammalian community. Our six focal species demonstrated a wide range of dispersal capabilities (median dispersal distances from 10 to 70 km), encompassing the dispersal distances for many other medium and large-sized mammals (Minor and Lookingbill 2010). And, importantly, we identified core habitat patches specific to each species rather than by the boundaries of protected areas. Overall, core habitat appeared to be well connected for the species studied, with the exception of *D. tajacu*, the species exhibiting the lowest dispersal capability. The dPC index integrates intra- and inter-patch connectivity in one measure and highlighted the importance of larger habitat patches for connectivity. A patch itself is a space where connectivity occurs (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007), and the dPC index ascribes large contributions to connectivity from larger habitat patches. Given the configuration of large patches in my study landscape, the landscape seemed much more connected, with few isolated core habitat areas (represented by the number of components in each graph), for species having a median dispersal distance >20 km. However, it is important to note that representing movement ability as a mean dispersal distance alone may fail to effectively capture habitat isolation should the landscape offer differential resistance to species' movements (Cushman et al. 2006). Therefore, a step forward to address connectivity in this landscape would be to identify pathways among core habitat areas by building resistance to movement layers, ideally analyzing data on movement of forest-dependent mammal species on human-dominated landscapes, and genetic data, two of the best approaches to build resistance to movement layers (Cushman et al. 2006). Additionally, not all forested areas were considered in the network analysis, rather core habitat was defined specific to each species based on their responses to forest cover, human developments, and elevation. Given the combination of residual forest patches and other land cover types, combined with differential use of the landscape by humans, it is likely that that the so-called "matrix" will lead to varying degrees of permeability for dispersal among habitat patches (Castilho et al. 2015; Zeller et al. 2016).

For a long time, the creation of protected areas had been done opportunistically in Brazil, but since 2000 Brazilian environmental policy included connectivity as one of the important components when establishing and managing reserves (Brazil 2000). Recently a new and relatively small strictly protected area, Mantiqueira Paulista natural monument, with 10,363 ha (São Paulo, 2021) was created that my analysis indicated as encompassing a considerable amount of area critical to connectivity for the mammalian community – highlighting the potential for new protected areas to provide critical habitat value, especially by inclusion of less represented characteristics within the Atlantic Forest hotspot such as old-growth forest remnants (Faria et al. 2009; Galetti et al. 2009; Tabarelli et al. 2010). Nevertheless, inevitably other approaches need to be considered in addition to an increase in the protected area system coverage, such as defining zones to conserve the most important patches for connectivity within multiple use protected areas, or even planning management practices compatible with forest conservation on private lands. It is important that the identification of core habitat areas that also contribute strongly to landscape connectivity both within and outside of protected areas is made available for managers and policy makers, especially when considering sustainable use protected areas, which are subjected to different activities (e.g., mining, agriculture, logging; (Brazil, 2000). On the other hand, with ongoing habitat loss and fragmentation outside protected areas, landscape planning becomes crucial for maintaining connectivity for different species (Sala et al. 2000). Rural properties in the Atlantic Forest are required to maintain at least 20% of their land as legal reserve, which may include riparian forests (Brazil 2012). The small patches maintained on private parcels can play an important role as stepping stones connecting larger habitat patches (Diniz et al. 2020). Yet many land holdings do not follow what is stated by law (Soares-Filho 2013), and as such there is room to better target conservation of existing forest remnants especially on properties that overlap core habitat areas for connectivity. In this sense, establishing legal reserves on public and private lands could play an important role in maintaining connectivity for forest-dependent mammals across the human-dominated Atlantic Forest biome. Recent forest regeneration in parts of the study area has been shown to benefit landscape connectivity (Lira et al. 2012). Additionally, the implementation of payment for ecosystem services that has started in some regions of São Paulo and Minas Gerais states has the potential to contribute to forest maintenance, with properties participating in the program showing a positive effect on forest cover (Ruggiero et al. 2019). Thus, my maps of areas critical to connectivity for the forest-dependent mammalian community may be useful for strategic planning as well as more localized tactical conservation operations in the region.

In particular, targeting the conservation of riparian forests has a potential of increasing connectivity for many species in this region (Gillies and Clair 2008; Lees and Peres 2008;

Zimbres et al. 2017), and in particular *D. tajacu*. Although the conservation of riparian forest is mandatory by the forest code (Brazil 2012), it is estimated that an area of 1.5 M ha should be reforested to meet the law in the Atlantic Forest biome considering riparian forests, with a total of 6 M ha in need of restoration overall, with São Paulo and Minas Gerais states having some of the largest areas in need of restoration (Soares-Filho 2013). Considering only the area of this study, that leaves 238,302 ha (~3.6%) in the area in need of restoration or compensation scheme to achieve private conservation targets (Soares-filho et al. 2014; Sparovek 2018). The restoration of these areas is expected to have a large effect on current connectivity, increasing it by over 400% for apex predators (Castilho et al. 2015). Recently, Brazil has set a target of restoring at least 12 M ha of native vegetation considering all biomes by 2030 so that more properties meet the requirements of legal reserves set by the forest code (Brazil 2012; Brazil 2017).

This study provided the identification of key areas to maintain the connectivity under existing habitat conditions for a suite of forest-dependent mammals in the human-dominated, Brazilian Atlantic Forest. Most of these areas are already in strictly or multiple use protected areas, so setting the most important areas in higher protection zones in protected areas' management plans could be beneficial for maintaining connectivity, which stimulates gene flow through the movement of mammals among habitat patches, contributing to metapopulation survival (Sharma et al. 2013). Additionally, using a functional connectivity approach, the potential connectivity of core habitat patches was identified based on mammals' dispersal capabilities (Fagan and Calabrese 2006). Considering multiple species for identifying the key areas to connectivity showed that relying on only one species (i.e., as an umbrella species) or a group of species (i.e., carnivores), does not represent well what is needed by each species individually, since each species shows divergent distributions in response to landscape and anthropogenic factors. Therefore, when there are many threatened species (in this case, the focus was on forest-dependent species), the best approach is to consider all species to build connectivity models. Finally, at least for one species the study indicates the isolation of some populations, so evaluating whether this isolation reflects in the decrease of genetic variability could be an important next step to evaluate whether efforts of forest restoration should be implemented (Lira et al. 2012) in a way that could in time complement the existing core habitat areas for the forest-dependent mammal species, which are the species most likely to have their persistence in jeopardy in the landscape in case of deforestation of new areas (Brook et al. 2003). If we consider other vertebrate groups (e.g., birds, amphibians), whose core habitat areas probabibly differ than those for mammals, it is likely that priority areas for connectivity would be more comprehensive of what would be priority areas for connectivity of vertebrate populations (Liu et al. 2018). Therefore, the allocation of restoration efforts to serve both as new habitat areas and increase functional connectivity would be highly beneficial for the regional vertebrate community.

Table 1. Standardized beta coefficients from the multi-species, multi-session occupancy model fit to eight forest-dependent species within the Atlantic Forest study area, Brazil. Values followed by an asterisk indicate statistical significance (95% credible intervals not overlapping zero).

		Beta coefficients (SE)			
Species	Group	Intercept	Forest proportion	Human footprint	Elevation
Dasyprocta iacki	Frugivore	0.44 (4.55)	0.91 (0.56)	0.31 (0.38)	-1.28 (0.44)*
Dicotyles tajacu	Frugivore	0.36 (4.54)	1.96 (0.61)*	-0.11 (0.23)	0.47 (0.23)*
Tapirus terrestris	Frugivore	0.37 (4.54)	2.81 (0.95)*	-0.53 (0.33)*	-0.73 (0.26)*
Tayassu pecari	Frugivore	0.37 (4.54)	1.92 (0.72)*	-0.08 (0.27)	0.92 (0.28)*
Eira barbara	Carnivore	0.38 (4.65)	0.67 (0.27)*	-0.23 (0.23)	0.31 (0.33)
Leopardus pardalis	Carnivore	0.37 (4.42)	0.50 (0.20)*	-0.12 (0.16)	0.09 (0.19)
Panthera onca	Carnivore	0.34 (4.68)	2.25 (1.23)*	-0.03 (0.33)	-0.66 (0.45)
Puma concolor	Carnivore	0.48 (4.57)	0.63 (0.23)*	-0.19 (0.19)	-0.08 (0.22)
8 forest-dependent species	Community	0.37 (4.36)	1.45 (0.59)*	-0.12 (0.20)	-0.10 (0.38)

Table 2. Mean home range, and median dispersal distances estimated for six mammal species based on Bowman et al. (2002).

Species	Average home range (km^2)	Median dispersal distance (km)	References for home range
Dicotyles tajacu	2	10	(A. L. Desbiez et al., 2009; Desbiez et al., 2012; Henry, 1999; Keuroghlian et al., 2004)
Tapirus terrestris	8	20	(Cañas, 2010; Medici, 2010; Medici et al., 2012)
Eira Barbara	16.5	30	(Eisenberg, 1989; Emmons and Feer, 1999; Presley, 2000; Reis et al., 2010; Rodrigues et al., 2013)
Leopardus pardalis	20	30	(de Oliveira et al., 2010; Oliveira et al., 2013; Oliveira and Cassaro, 2005)
Tayassu pecari	64	55	(de Almeida Jácomo et al., 2013; A. L. J. Desbiez et al., 2009; Fragoso, 1998; Jacomo, 2004; Keuroghlian et al., 2012, 2004)
Puma concolor	94	70	(Azevedo et al., 2020, 2013b; Mazzolli, 2010; Silveira, 2004)

Table 3. Percentage of the nodes prioritized for each group of species when connectivity model was optimized for a potential umbrella species (Puma concolor) or other group (carnivores).

Most important nodes and focal groups or species for network analysis	Percentage of core habitat areas (nodes) prioritized for non-focal groups or species		
	All species but puma	Frugivores	Mesocarnivores
Top 1%			
Puma	64.18	60.88	74.56
Carnivores	-	68.59	-
Top 5%			
Puma	62.26	63.18	60.29
Carnivores	-	84.47	-
Top 10%			
Puma	62.89	63.68	61.27
Carnivores	-	85.55	-
Top 20%			
Puma	63.17	64.06	61.21
Carnivores	-	86.21	-

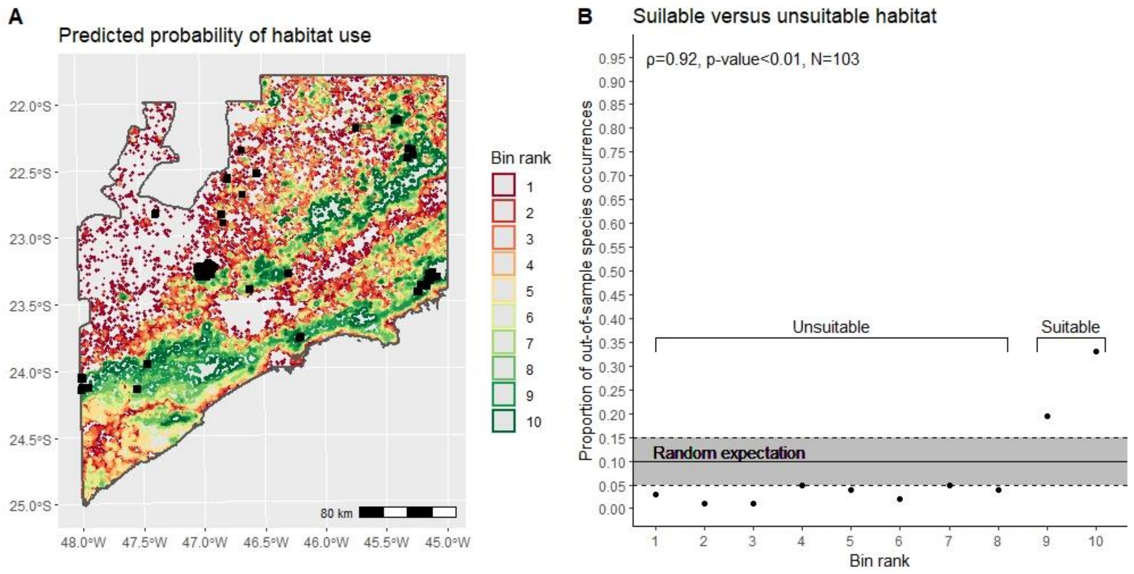


Figure 1. Map (A) showing the predicted probability of habitat use for Eira Barbara, displayed as 10 equal-area bins, along with out-of-sample observations (black dots) used for model validation. Model validation (B) showing the proportion of out-of-sample locations corresponding to each of the equal-area bins, with a proportion of 0.10 being expected to occur at random. For this species, the top two bins corresponded to suitable habitat for the connectivity analysis.

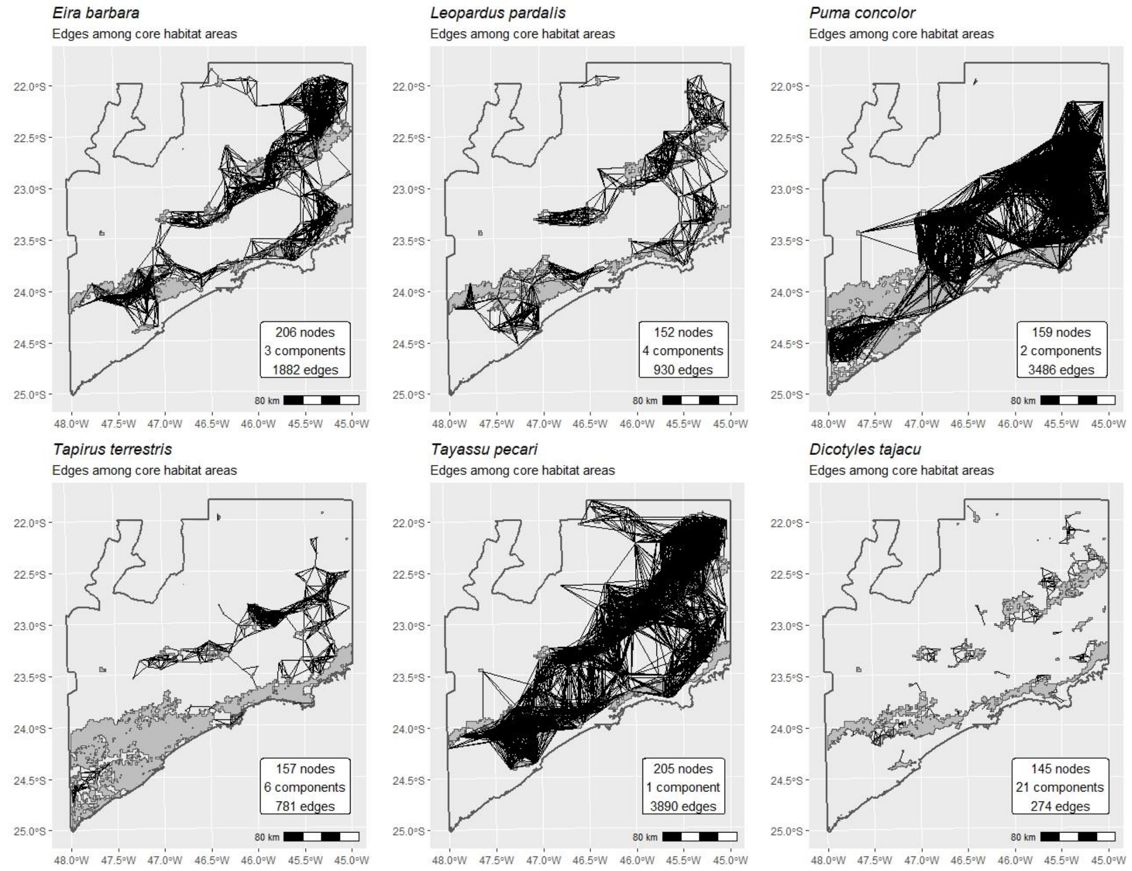


Figure 2. Nodes (core habitat patches; gray polygons) and edges (connections between nodes; black lines) for six forest-dependent species in the Atlantic Forest study area, Brazil. For each species, the number of nodes, components (connected subgraphs), and edges are also indicated.

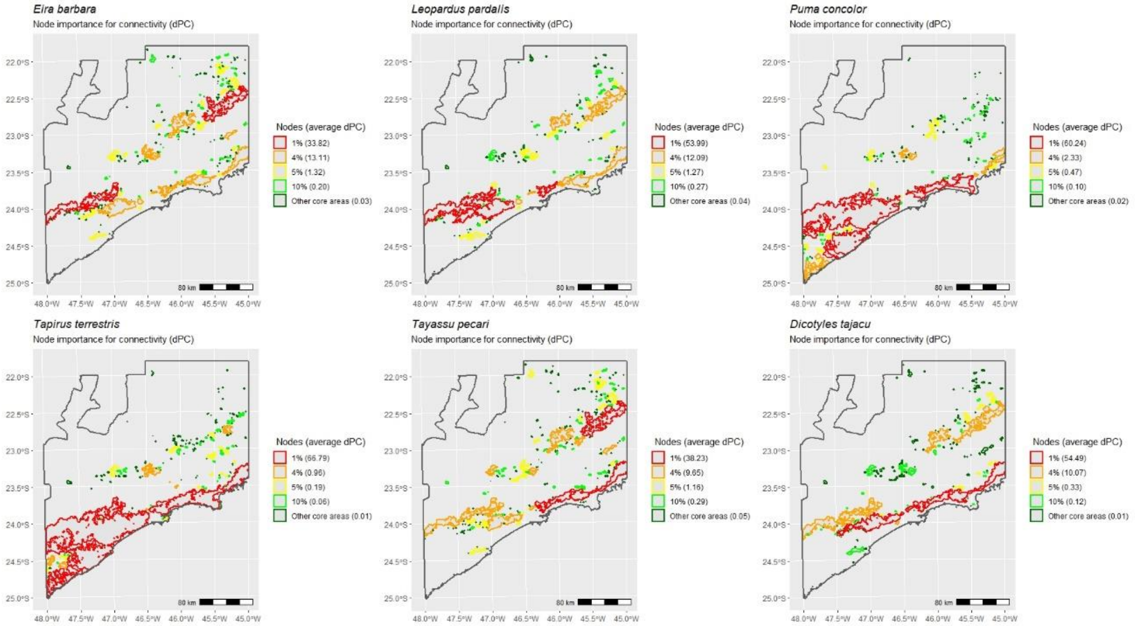


Figure 3. Core habitat classified by node importance to connectivity based on the dPC index and ranked from the highest (top 1% of the nodes) to lowest values (other core areas). Average dPC values are given in parentheses for each species and node category.

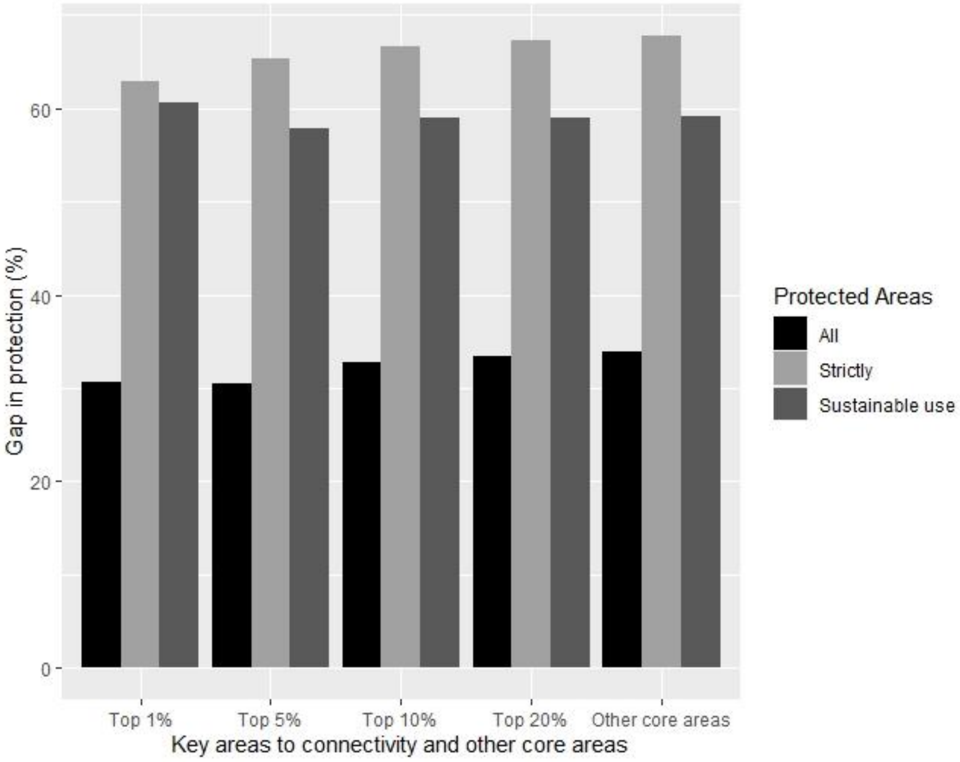


Figure 4. Gap in protection considering all core habitat areas (core areas) across the six forest-dependent mammals, and key nodes for community connectivity identified as the top 1, 5, 10 or 20% of dPC values.

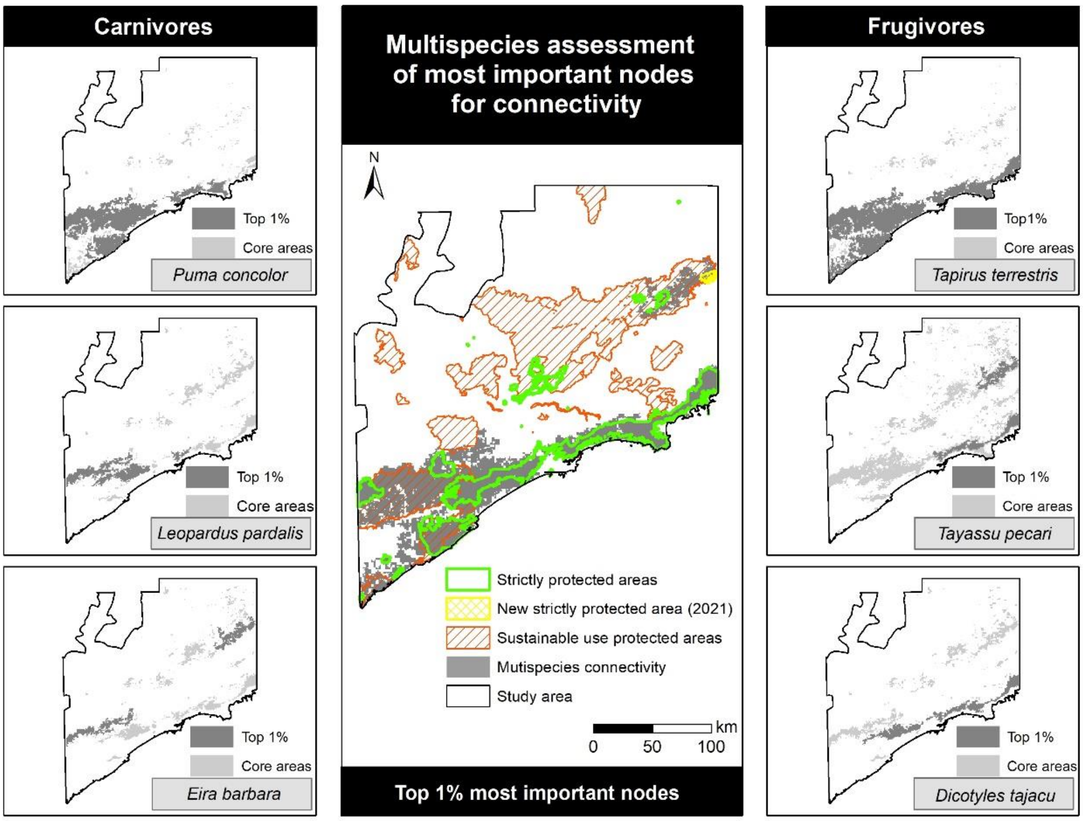
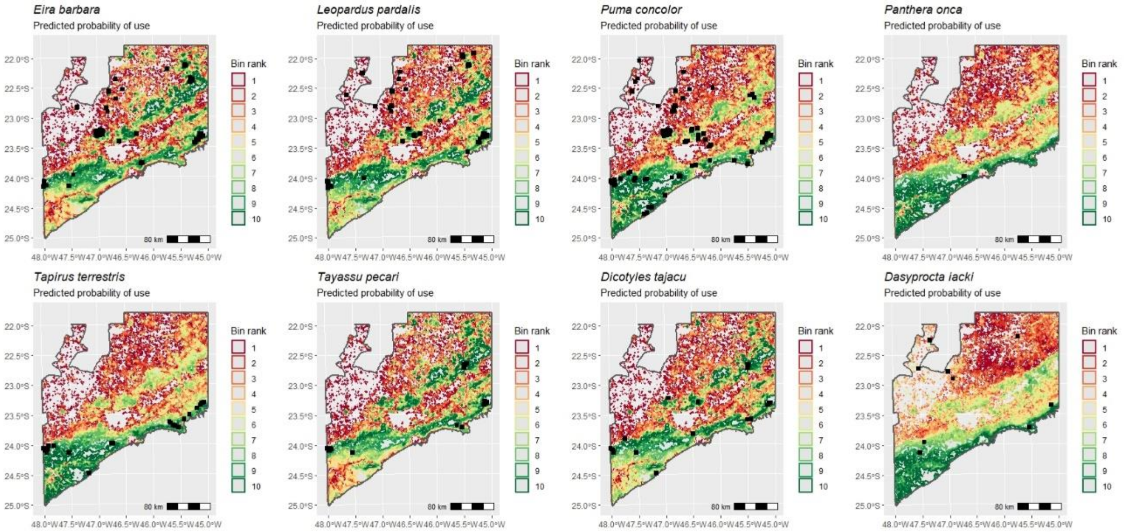


Figure 5. Most important nodes for single species summed together to generate a multispecies connectivity model. Areas in light grey indicate the core habitat areas and in dark grey, the most important nodes (habitat patches) for connectivity for each species (insert maps) and for all of them altogether (central map).

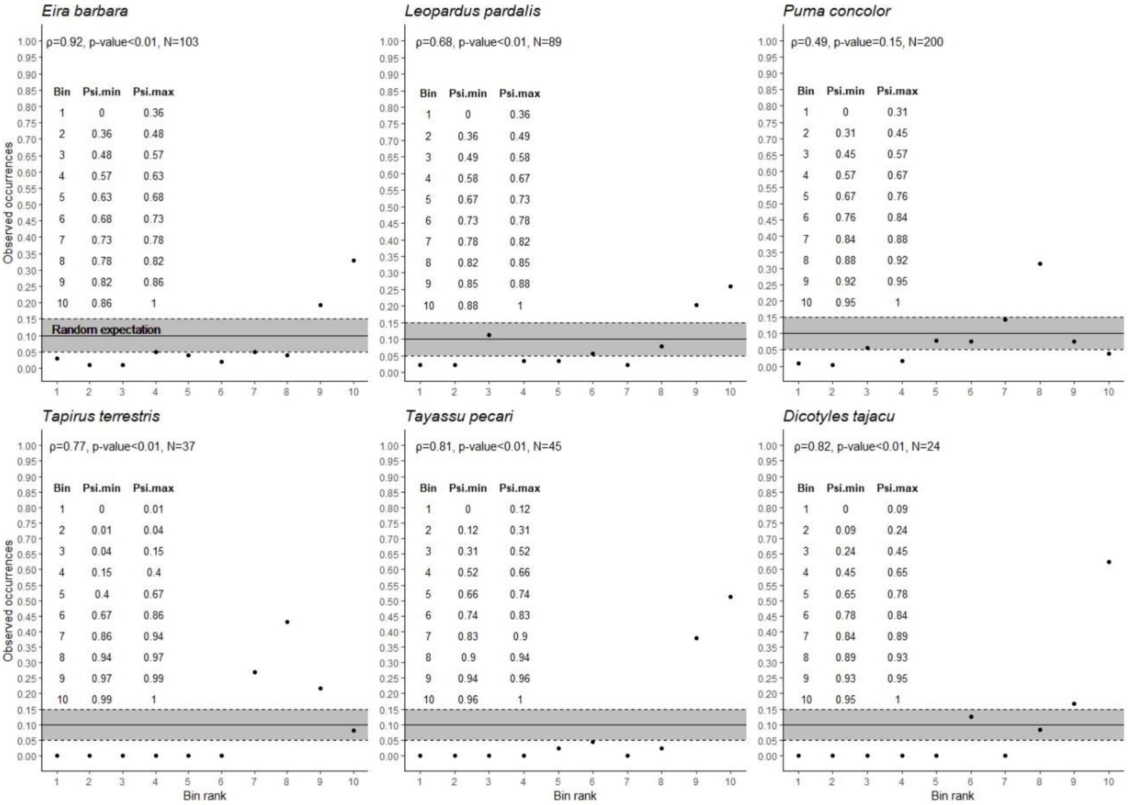
Appendix 1. Beta coefficients (SE) for the forest amount covariate at 2x2 km grid cell extents following Model 1 (linear effects for all covariates) when including 28 or eight mammal species in the multispecies occupancy models. Bold values indicate significant results (credible intervals not overlapping zero).

Species	Beta coefficients (SE) for the forest amount covariate	
	Chapter 2 (28 mammal species)	Chapter 3 (eight forest-dependent species)
Dasyprocta iacki	0.58 (0.44)	0.91 (0.56)
Dicotyles tajacu	**1.52 (0.49)**	**1.96 (0.61)**
Tapirus terrestris	**1.95 (0.61)**	**2.81 (0.95)**
Tayassu pecari	**1.29 (0.56)**	**1.92 (0.72)**
Leopardus pardalis	**0.46 (0.19)**	**0.50 (0.20)**
Panthera onca	1.07 (0.69)	**2.25 (1.23)**
Puma concolor	**0.58 (0.23)**	**0.63 (0.23)**
Eira Barbara	**0.57 (0.25)**	**0.67 (0.27)**

Appendix 2. Prediction maps based on a multispecies occupancy model for eight forest-dependent mammal species. Black squares represent species' points of occurrences from the literature or unpublished data (records after year 2000). Each bin rank encompasses 10% of the extent of the study area, where bin 1 have the lowest probability of use by each species, whereas bin 10, the greatest.



Appendix 3. Model validation of six mammal species probability of use across a human-modified Atlantic Forest landscape. The observed occurrences (N) were not used for modeling and came from the literature or unpublished data. Each bin rank encompasses 10% of the extent of the study area. The expectation is that 10% of the observed occurrences should correspond to each bin were they governed by random chance alone. Lower values or higher values would indicate non-suitability or suitability for each species probability of use, respectively. Significant Spearman-rank correlation (ρ) indicate little evidence for poor model performance.



Eira barbara

Bin	Psi.min	Psi.max
1	0	0.36
2	0.36	0.48
3	0.48	0.57
4	0.57	0.63
5	0.63	0.68
6	0.68	0.73
7	0.73	0.78
8	0.78	0.82
9	0.82	0.86
10	0.86	1

Leopardus pardalis

Bin	Psi.min	Psi.max
1	0	0.36
2	0.36	0.49
3	0.49	0.58
4	0.58	0.67
5	0.67	0.73
6	0.73	0.78
7	0.78	0.82
8	0.82	0.85
9	0.85	0.88
10	0.88	1

Puma concolor

Bin	Psi.min	Psi.max
1	0	0.31
2	0.31	0.45
3	0.45	0.57
4	0.57	0.67
5	0.67	0.76
6	0.76	0.84
7	0.84	0.88
8	0.88	0.92
9	0.92	0.95
10	0.95	1

Tapirus terrestris

Bin	Psi.min	Psi.max
1	0	0.01
2	0.01	0.04
3	0.04	0.15
4	0.15	0.4
5	0.4	0.67
6	0.67	0.86
7	0.86	0.94
8	0.94	0.97
9	0.97	0.99
10	0.99	1

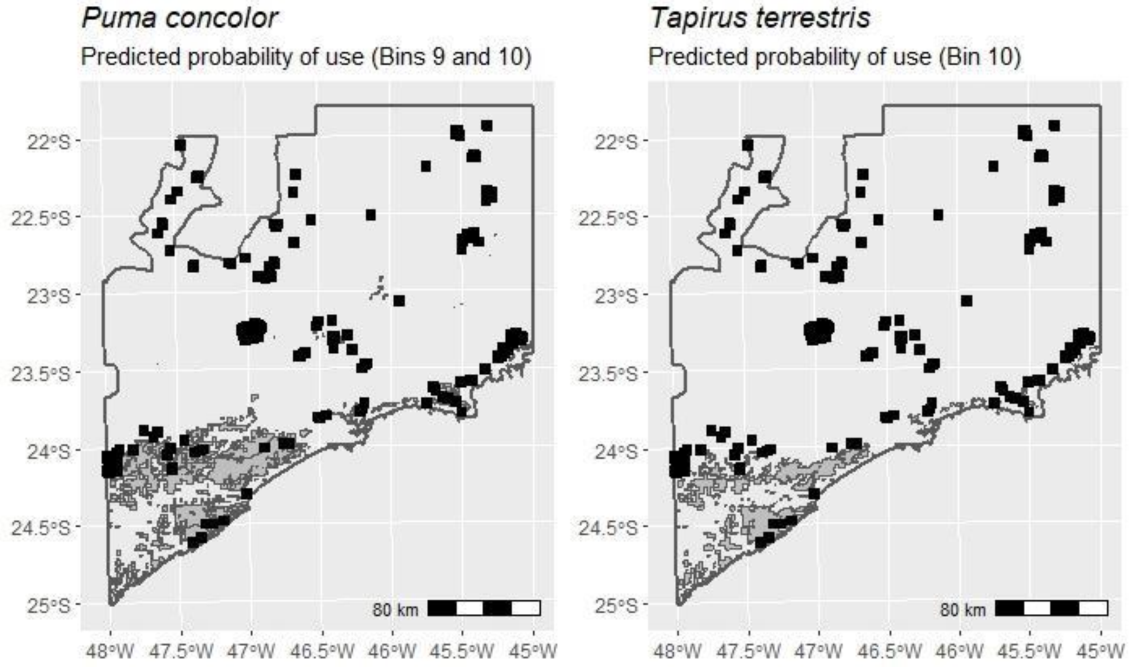
Tayassu pecari

Bin	Psi.min	Psi.max
1	0	0.12
2	0.12	0.31
3	0.31	0.52
4	0.52	0.66
5	0.66	0.74
6	0.74	0.83
7	0.83	0.9
8	0.9	0.94
9	0.94	0.96
10	0.96	1

Dicotyles tajacu

Bin	Psi.min	Psi.max
1	0	0.09
2	0.09	0.24
3	0.24	0.45
4	0.45	0.65
5	0.65	0.78
6	0.78	0.84
7	0.84	0.89
8	0.89	0.93
9	0.93	0.95
10	0.95	1

Appendix 4. Prediction maps indicating bins 9 and 10 for Puma concolor and bin 10 for Tapirus terrestris. Each bin rank encompasses 10% of the extent of the study area, with bin 10 having the largest probability of use as indicated by the multispecies multisession occupancy model. Black squares represent points of occurrences for all eight forest-dependent species from the literature or unpublished data (records after year 2000).



Puma concolor

Predicted probability of use (Bins 9 and 10)

Tapirus terrestris

Predicted probability of use (Bin 10)

Appendix 5. Prioritization of areas for connectivity for six forest-dependent mammals within strictly and sustainable use protected areas. The important areas for connectivity within the protected areas are reported considering the top 1%, 5%, 10%, and 20% nodes with highest dPC index.

Protected Area	Administration	Type	IUCN category	Year of creation	Area (km^2)	Priority areas for connectivity within protected areas (%)			
						Top 1% nodes	Top 5% nodes	Top 10% nodes	Top 20% nodes
Serra do Mar State Park	State	Strict Protection	II - National Park	1977	3320.00	81.43	82.68	82.68	82.68
Bacia do Paraíba do Sul Environmenal Protected Area	Federal	Sustainable Use	V - Protected Landscape/ Seascape	1982	2926.00	3.09	10.21	11.06	11.79
Piracicaba Juqueri-Mirim Área II Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1987	2727.08	0.00	3.39	3.41	3.96
Serra do Mar Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1984	2682.26	87.48	87.48	87.48	87.48
Sistema Cantareira	State	Sustainable Use	V - Protected	1998	2528.01	0.00	4.86	6.89	7.62

Environmenal Protected Area			Landscape/ Seascape						
Serra da Mantiqueira Environmenal Protected Area	Federal	Sustainable Use	V - Protected Landscape/ Seascape	1985	1815.96	45.40	47.99	48.64	49.78
Fernão Dias Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1997	1791.59	1.05	19.07	19.07	20.08
Cananeia-Iguape-Peruíbe Environmenal Protected Area	Federal	Sustainable Use	V - Protected Landscape/ Seascape	1984	1400.65	86.44	86.50	86.50	86.50
Itupararanga Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1998	941.30	2.74	2.76	2.76	3.96
Jureia-Itatins Ecological Station	State	Strict Protection	Ia - Strict Nature Reserve	1986	840.75	95.19	95.28	95.28	95.28
Jundiaí Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1984	495.33	0.00	7.51	7.83	8.77

Tietê Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1983	461.74	0.00	0.00	0.00	0.00
Bacia Hidrográfica do Rio Machado Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1999	436.23	0.00	0.00	0.00	0.00
Sapucaí Mirim Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1998	386.45	4.41	6.53	6.53	10.60
Cabreúva Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1984	371.98	0.00	13.21	13.21	14.37
Campos do Jordão Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1984	287.02	57.74	57.74	57.74	57.74
Carlos Botelho State Park	State	Strict Protection	II - National Park	1982	273.68	88.90	88.90	88.90	88.90
Jurupará State Park	State	Strict Protection	II - National Park	1978	262.50	81.61	81.61	81.61	81.61
Piracicaba Juqueri Mirim	State	Sustainable Use	V - Protected	1987	247.15	0.00	0.00	0.00	0.00

Área I Environmenal Protected Area			Landscape/ Seascape						
Banhados de Iguape Ecological Station	State	Strict Protection	Ia - Strict Nature Reserve	2006	165.89	99.65	99.65	99.65	99.65
Itaberaba State Park	State	Strict Protection	II - National Park	2010	151.13	0.00	56.19	57.13	57.13
Cajamar Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1984	133.09	0.00	0.00	0.00	7.07
São Francisco Xavier Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	2002	113.33	0.00	53.93	53.93	53.93
Itapetinga State Park	State	Strict Protection	II - National Park	2010	101.92	0.00	31.55	53.66	53.66
Várzea do Rio Tietê Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1987	97.78	0.00	0.00	0.00	0.00
Restinga de Bertioga State Park	State	Strict Protection	II - National Park	2010	91.15	77.75	77.75	77.75	77.75

Mantiqueira Paulista Natural Monument	State	Strict Protection	III - Natural Monument or Feature	2021	91.03	65.11	65.11	65.11	65.11
Campos do Jordão State Park	State	Strict Protection	II - National Park	1941	81.30	86.34	86.34	86.34	86.34
Cantareira State Park	State	Strict Protection	II - National Park	1968	76.19	0.00	0.00	51.77	56.87
Ipanema National Forest	Federal	Sustainable Use	VI - Protected area with suistainable use of natural resources	1992	53.90	0.00	0.00	0.00	25.08
Despraiado Reserve for Sustainable Development	State	Sustainable Use	VI - Protected area with suistainable use of natural resources	2013	39.53	95.86	95.86	95.86	95.86
Pedra Grande Natural Monument	State	Strict Protection	III - Natural Monument or Feature	2010	32.97	0.00	60.48	64.29	64.29

Pedra do Baú Natural Monument	State	Strict Protection	III - Natural Monument or Feature	2010	31.54	0.00	0.00	0.00	11.62
Campina do Encantado State Park	State	Strict Protection	II - National Park	1994	31.27	0.00	92.87	92.87	92.87
Chauás Ecological Station	State	Strict Protection	Ia - Strict Nature Reserve	1978	26.45	97.02	97.02	97.02	97.02
Edmundo Navarro de Andrade State Forest	State	Sustainable Use	VI - Protected area with suistainable use of natural resources	2002	22.24	0.00	0.00	0.00	0.00
Juquery State Park	State	Strict Protection	II - National Park	1993	19.78	0.00	0.00	0.00	0.00
Parque e Fazenda do Carmo Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1989	19.74	0.00	0.00	0.00	0.00
Lagamar de Cananeia State Park	State	Strict Protection	II - National Park	2008	12.19	40.13	40.13	40.13	40.13

Barra do Uma Reserve for Sustainable Development	State	Strict Protection	VI - Protected area with suistainable use of natural resources	2013	10.74	28.39	28.39	28.39	28.39
Represa Bairro da Usina Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1986	9.93	0.00	0.00	0.00	0.00
Pedra Branca Area with relevant ecological importance	State	Sustainable Use	IV - Habitat/Species Management Area	1987	6.30	0.00	31.64	31.64	31.64
Marinha do Litoral Centro Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	2008	6.26	0.00	0.00	0.00	0.00
Xixová-Japuí State Park	State	Strict Protection	II - National Park	1993	6.16	0.00	0.00	0.00	0.00
Mananciais de Campos do Jordão State Park	State	Strict Protection	II - National Park	1993	5.17	71.63	71.63	71.63	71.63

Jaraguá State Park	State	Strict Protection	II - National Park	1961	4.89	0.00	0.00	0.00	0.00
Marinha do Litoral Norte Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	2008	3.78	1.96	1.96	1.96	1.96
Lorena National Forest	Federal	Sustainable Use	VI - Protected area with suistainable use of natural resources	2001	2.81	0.00	0.00	0.00	0.00
Mata de Santa Genebra Area with relevant ecological importance	Federal	Sustainable Use	IV - Habitat/Species Management Area	1985	2.42	0.00	0.00	0.00	0.00
Nova Baden State Park	State	Strict Protection	II - National Park	1974	2.13	0.00	0.00	0.00	0.00
Alberto Löefgren State Park	State	Strict Protection	II - National Park	1963	1.85	0.00	0.00	0.00	0.00
São Sebastião Area with relevant ecological importance	State	Sustainable Use	IV - Habitat/Species Management Area	2008	0.95	1.29	1.29	1.29	1.29

Corumbataí Botucatu-Tejupá Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1983	0.94	0.00	0.00	0.00	0.00
Itapeti Ecological Station	State	Strict Protection	Ia - Strict Nature Reserve	1952	0.90	0.00	0.00	0.00	0.00
Ara State Park	State	Strict Protection	II - National Park	1969	0.67	0.00	0.00	0.00	0.00
Haras de São Bernardo Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1987	0.43	0.00	0.00	0.00	0.00
Mata do Iguatemi Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	1993	0.34	0.00	0.00	0.00	0.00
Fontes do Ipiranga State Park	State	Strict Protection	II - National Park	1969	0.33	0.00	0.00	0.00	0.00
Valinhos Ecological Station	State	Strict Protection	Ia - Strict Nature Reserve	1966	0.18	0.00	0.00	0.00	0.00
Marinha do Litoral Sul Environmenal Protected Area	State	Sustainable Use	V - Protected Landscape/ Seascape	2008	0.04	0.00	0.00	0.00	0.00

CONCLUSIONS

The primary goal of this dissertation was to evaluate how responses by medium and large-sized mammals to landscape (primarily forest amount) and anthropogenic factors (especially the presence of dogs or humans in forest remnants) influence their persistence in a human-modified Atlantic Forest landscape. This study has brought new insights on how vulnerable the persistence of forest-dependent species, represented especially by frugivore (e.g., tapir, white-lipped peccary, collared peccary) and some carnivore species (jaguar, puma, ocelot), is to forest loss that has occurred in the past, in an landscape where the majority of forest loss has occurred more than 40 years ago. In fact, these species might be even more threatened than previously thought, given that they tend to be replaced by more generalist species in landscapes with less than 78% of forest amount in 2x2 km landscapes, a threshold much higher than previously reported (Andrén 1994; Banks-Leite et al. 2014; Lima and Mariano-Neto 2014; Boesing et al. 2017; Leite et al. 2018).

One distinguishing aspect of this study was inclusion of the whole gradient of forest amount in the sampling design. Previous studies have failed to do so, and often included landscapes with up to 50% of forest cover but not beyond this proportion, possibly influenced by theoretical or logistical reasons (Swift and Hannon 2010). Another distinguishing aspect was my desire to demonstrate how different thresholds might be based on different scales used when calculating forest amount in landscapes. Failure to address the influence of scale when looking for thresholds might compromise the reliability of the results, given the wide range of thresholds found when using very small landscapes (0.25x0.25 km) to very large ones (60x60 km), with critical points varying from 45-87% depending upon the scale used. Some species (especially forest-dependent frugivores) showed that their probability of use is influenced not only by the grid cell where they were detected but also on the neighboring context of that area. This indicates that their higher probability of use is influenced by the availability of larger forest amount at a landscape-context, suggesting the need for contiguous forests for their long-term persistence.

Anthropogenic factors, such as the use of forest remnants by domestic dogs or humans, also have an important influence on some medium-sized mammals, and a few species (ocelot, oncilla, and armadillo) have shown significant spatial avoidance of areas where dogs and/or humans were present. Behavioral responses such as changes in activity patterns in areas with higher or lower probability of use by dogs were only observed for paca. However, the fact that this study found that the probability of use of dogs in any of the sampled Atlantic Forest remnants is always higher than 41% could have prevented the finding of behavioral responses by native species, as dogs are widespread in the study area and thus wildlife are unable to escape them. Therefore, studies comparing landscapes like mine to areas that could still be considered in a primitive state, with the absence of dogs or people, could help in evaluating more clearly how mammal species change their spatial use or whether they adapt temporally to the presence of potential new predators in the system. Such studies would not be possible within the Atlantic Forest, where more than 70% of the Brazilian population lives and most of the major cities and most developed infrastructure systems are, but this still could be done in other regions, such as the Amazon.

Another important finding was that dogs in the Atlantic Forest have a free-ranging behavior, and their probability of use is usually independent of humans. This finding means that it is certainly very challenging to address the problem of free-ranging dogs in forest remnants (and especially in protected areas that were created for biodiversity conservation), given that those dogs could either be owned by people living near the forest fragments or could already be feral and independent of humans. The important take-home message is that the problem of having so many dogs in Atlantic Forest remnants must start being discussed by scientists, stakeholders and managers if we are to increase the chance of persistence of native mammal species. Not only do dogs act as predators and competitors with native mammals, they are also vectors of diseases and there are many examples throughout the world how medium and large-sized mammal populations could be jeopardized because of diseases spread by domestic dogs (Butler et al. 2004; Roeke-Palmer et al. 1995; Cleveland et al., 2000; Fiorello et al., 2004; Funk et al., 2001), which is another question important for investigation by future studies.

My analyses indicated that most of the core habitat areas for forest-dependent mammals are well connected, given that the current forest cover is maintained and considering the dispersal capabilities of most of the species evaluated, except for collared peccaries, the species with the lowest dispersal capability (~ 10 km). This study has shown which are the key areas to maintain existing connectivity (i.e., 1% core areas that contribute the most to connectivity), and could help guide protected areas managers when elaborating or updating management plans and classifying those areas important to connectivity as having a larger restriction of use (i.e., areas to be preserved as forests). A step forward to address connectivity in this landscape would be to consider functional connectivity (and not only actual connectivity as has been done in this study) by incorporating data on movement of forest-dependent mammal species on human-dominated landscapes, and genetic data in order to identify important pathways in between core habitat areas. Also, it would be interesting to investigate whether areas pointed as having isolated populations (especially of collared peccary) by the developed connectivity model already show differences in genetic variability among isolated populations.

In conclusion, maintaining more than 78% forest cover (within units of 2 x 2 km) across the Atlantic Forest landscape is crucial to enhance the probability of persistence of complete medium and large-sized mammal communities, but this often means protecting large contiguous forest remnants. This is a very challenging target in a highly fragmented biome, where most forest remnants are smaller than 100 ha with average distance of 1.4 km among them (Ribeiro et al. 2009), so that forest restoration would be required to meet such a large forest proportion in Atlantic Forest landscapes. In this sense, the deficit of forest amount in private lands required by the Brazilian forest code and the proclamation of the decade of 2021-2030 as the United Nations decade on ecosystem restoration, could be propulsors of initiatives to not only identify core habitat areas (and the ones that contribute the most to connectivity, which could be targeted as potential new protected areas) as has been done in this study for medium and large-sized mammals, for other taxa as well (e.g., birds, amphibians) but also to identify areas where restoration would be most beneficial to biodiversity conservation in the Atlantic Forest. The results found in this dissertation concerning the impact of dogs and humans in forest remnants on spatial habitat use or temporal activity of medium and large size mammals, the high proportion of forest needed to ensure the persistence of the whole medium and large size mammal community, besides the need of conservation of areas prioritized for connectivity of forest-dependent mammal populations are contributions that could help guide the conservation planning for medium and large mammals in a human-dominated landscape in the Atlantic Forest.

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CURRICULUM VITAE

Biography

Lilian Bonjorne de Almeida is a Biologist (São Carlos Federal University, 2003) with a Master's Degree in Ecology, Conservation and Wildlife Management (Minas Gerais Federal University, 2007), who has studied mammal seed dispersal and frugivory in fragmented landscapes. In 2005 she started to work at the Brazilian Institute of Environment and Natural Resources (institute linked to the Brazilian ministry of environment) as an environmental analyst at Cavernas do Peruaçu National Park, working mainly on the protected area management, including planning the public use of the park, but also collaborating on ongoing mammal research. In 2009 she started to work at the Research Center for Carnivore Mammal Conservation (CENAP), linked to the Chico Mendes Institute for Conservation and Biodiversity (ICMBio), an institution that integrates the ministry of environment, where she started to focus her research on population and spatial ecology of small and large felids in Atlantic Forest landscapes situated in Southern and Southeastern Brazil. In 2015 she initiated her PhD at the State University of New York/ College of Environmental Science and Forestry (SUNY/ESF), and the aims of her project are to evaluate how landscape and anthropogenic factors influence the persistence of medium and large-sized mammals in an Atlantic Forest human-dominated landscape in Southeastern Brazil.

Personal Information

Name/ Surname	**Lilian Bonjorne de Almeida**
Address	Rua Humberto I, 908, apt. 101, Vila Mariana, São Paulo, SP, Brazil, 04018-900
E-mail	bonjorne@gmail.com, lilian.almeida@icmbio.gov.br
Nationality	Brazilian

Competencies

Research on spatial ecology of medium and large mammals, occupancy, co-occurrence, connectivity, seed dispersal, frugivory, geoprocessing, evaluation of conservation status of mammals, participating in action plans for threatened mammals

Educational Experience

Period	**2015 – 2021**
Program	PhD in Conservation Biology
Scholarship	Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)/ Science without borders/ LASPAU
University	State University of New York/ College of Environmental Sciences and Forestry (SUNY/ ESF)

Period	**2005 – 2007**
Title of Qualification Awarded	Master’s degree in Ecology, Conservation and Wildlife Management.
Main subjects/ occupational skills covered	- Research on "Phenology and Seed Dispersal of Arecaceae Species in Serra do Cipó, MG, southeastern Brazil". - Study on phenology of *Allagoptera campestris, Butia archeri* and *Syagrus glauscecens* (Arecaceae). - Experience in seed dispersion of *Allagoptera campestris*, *Syagrus flexuosa* and *Syagrus glauscecens* (evaluation of fate and distance of diaspores from parent plants). - Identification of animals which use the fruits of these species as food resources.
Scholarship	Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) - 2005
University	Universidade Federal de Minas Gerais (UFMG) – *Federal University of Minas Gerais*

Period	**1999 – 2003**
Title of Qualification Awarded	Biological Sciences (Bachelor’s Degree with Teaching Certificate)
Main subjects	Research on "Phenology and dispersion of seeds of *Attalea geraensis* (Arecaceae) in Cerrado areas in the southeast of Brazil".
University	Universidade Federal de São Carlos (UFSCar) – *Federal University of São Carlos*

Professional Experience

Period	**2008 – current**
Function	Environmental Analyst
Main Activities	Research on ecology and conservation of terrestrial medium and large-sized mammals (occupancy, density estimation, monitoring, and spatial ecology), instruction to farmers on how to prevent conflicts related to predation of domestic animals and livestock by carnivores, revision of the regional list (Brazil) of endangered species (groups: Artiodactyla, Carnivora, Didelphimorphia, Perissodactyla, Rodentia), elaboration of distribution maps of Brazilian terrestrial mammals, action plans

Name and address of employer	INSTITUTO CHICO MENDES DE CONSERVAÇÃO DA BIODIVERSIDADE (ICMBio) – *Chico Mendes Institute for Conservation and Biodiversity* *Estrada Municipal da Usina, 8600, Atibaia, SP, Brazil*
Department	Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros (CENAP) – *Research Center for Carnivore Mammal Conservation*
Type or Sector of Business	Brazilian Federal Government

Period	**2005 – 2008**
Function	Environmental Analyst
Main Activities	Protected areas management, public use planning
Name and address of employer	Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) – Brazilian Institute of Environment and Natural Resources
Departments	Parque Nacional Cavernas do Peruaçu – *Cavernas do Peruaçu National Park*, Área de Proteção Ambiental Cavernas do Peruaçu – *Cavernas do Peruaçu Environmental Protected Area*

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ALMEIDA, L. B.; QUEIROLO, D.; OLIVEIRA, T.G.; Beisiegel, B. M. Avaliação do risco de extinção do gato-do-mato *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) no Brasil. Biodiversidade Brasileira, v. 5, p. 84-90, 2013.

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ALMEIDA, L. B.; QUEIROLO, D.; BEISIEGEL, B. M.; OLIVEIRA, T. G. Avaliação do risco de extinção do gato-mourisco *Puma yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803) no Brasil. Biodiversidade Brasileira, v. 5, p. 99-106, 2013.

AZEVEDO, F. C.; LEMOS, F. G.; ALMEIDA, L. B.; CAMPOS, C. B.; BEISIEGEL, B. M.; PAULA, R. C.; CRAWSHAW JUNIOR, P. G.; FERRAZ, K. M. P. M. B.; OLIVEIRA, T. G. Avaliação do risco de extinção da onça-parda *Puma concolor* (Linnaeus, 1771) no Brasil. Biodiversidade Brasileira, v. 5, p. 107-121, 2013.

KEUROGHLIAN, A.; DESBIEZ, A. L. J.; BEISIEGEL, B. M.; MEDICI, E. P.; GATTI, A.; PONTES, A. R. M.; CAMPOS, C. B.; TOFOLI, C. F.; MORAES JUNIOR, E. A.; AZEVEDO, F. C.; PINHO, G. M.; CORDEIRO, J. L. P.; SANTOS JUNIOR, T. S.; MORAIS, A. A.; MANGINI, P. R.; FLESHER, K.; RODRIGUES, L. F.; ALMEIDA, L. B. Avaliação do risco de extinção do queixada *Tayassu pecari* Link, 1795, no Brasil. Biodiversidade Brasileira, v. 3, p. 84-102, 2012.

MEDICI, E. P.; FLESHER, K.; B., B. M. ; KEUROGHLIAN, A.; DESBIEZ, A. L. J.; GATTI, A.; PONTES, A. R. M.; CAMPOS, C. B.; TOFOLI, C. F.; MORAES JUNIOR, E. A.; AZEVEDO, F. C.; CORDEIRO, J. L. P.; SANTOS JUNIOR, T. S.; MORAIS, A. A.; MANGINI, P. R.; RODRIGUES, L. F.; ALMEIDA, L. B. Avaliação do risco de extinção da anta brasileira *Tapirus terrestris* Linnaeus, 1758, no Brasil. Biodiversidade Brasileira, v. 3, p. 103-116, 2012.

DESBIEZ, A. L. J.; KEUROGHLIAN, A.; BEISIEGEL, B. M.; MEDICI, E. P.; GATTI, A.; PONTES, A. R. M.; CAMPOS, C. B.; TOFOLI, C. F.; MORAES JUNIOR, E. A.; AZEVEDO, F. C.; PINHO, G. M.; CORDEIRO, J. L. P.; SANTOS JUNIOR, T. S.; MORAIS, A. A.; MANGINI, P. R.; FLESHER, K.; RODRIGUES, L. F.; ALMEIDA, L. B. Avaliação do risco de extinção do cateto *Dicotyles tajacu* Linnaeus, 1758, no Brasil. Biodiversidade Brasileira, v. 3, p. 74-83, 2012.

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DUARTE, J. M. B.; VOGLIOTTI, A.; ZANETTI, E. S.; OLIVEIRA, M. L.; TIEPOLO, L. M.; ALMEIDA, L. B. Avaliação do risco de extinção do veado-galheiro *Odocoileus virginianus* Zimmermann, 1780, no Brasil. Biodiversidade Brasileira, v. 3, p. 15-19, 2012.

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DUARTE, J. M. B.; ABRIL, V. V.; VOGLIOTTI, A.; ZANETTI, E. S.; OLIVEIRA, M. L.; TIEPOLO, L. M.; RODRIGUES, L. F.; ALMEIDA, L. B. Avaliação do risco de extinção do veado-cambuta *Mazama nana* Hensel, 1872, no Brasil. Biodiversidade Brasileira, v. 3, p. 59-67, 2012.

DUARTE, J. M. B.; VOGLIOTTI, A.; ZANETTI, E. S.; OLIVEIRA, M. L.; TIEPOLO, L. M.; RODRIGUES, L. F.; ALMEIDA, L. B. Avaliação do risco de extinção do veado-roxo *Mazama nemorivaga* Cuvier, 1817, no Brasil. Biodiversidade Brasileira, v. 3, p. 68-73, 2012.

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ALMEIDA, L. B.; FRAIR, J. Cachorros-domésticos e pessoas em remanescentes de Mata Atlântica: implicações espaciais e temporais para mamíferos silvestres. In: XI Seminário de Pesquisa e Iniciação Científica do Instituto Chico Mendes de Conservação da Biodiversidade, virtual, 2020.

ALMEIDA, L. B.; VILLARES, R.C.; SIMÃO, C.G.; BEISIEGEL, B.M.; GUIMARÃES, T.C.S. Padrão de ocupação de javalis (*Sus scrofa*) na Floresta Nacional de Ipanema como ferramenta para guiar esforços de manejo. In: XI Seminário de Pesquisa e Iniciação Científica do Instituto Chico Mendes de Conservação da Biodiversidade, virtual, 2020.

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ALMEIDA, L. B. Levantamento de Mamíferos de Médio e Grande Porte em Fragmentos de Mata Atlântica dos Municípios de São Tomás de Aquino, MG e Itirapuã, SP. In: 6º Congresso Brasileiro de Mastozoologia, 2012, Corumbá, MS, Brasil. Anais do 6º Congresso Brasileiro de Mastozoologia, 2012.

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ALMEIDA, L. B.; GARCIA, Q. S. Diversidade e Distribuição Espacial de Palmeiras na Serra do Cipó, MG. In: 58º Congresso Nacional de Botânica, 2007, São Paulo. Anais do Congresso Nacional de Botânica, 2007. v. 58.

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ALMEIDA, L. B.; NORDI, N.; GALETTI, M. Dispersão de Sementes de *Attalea geraensis* Barb. Rodr. (Arecaceae) em Área de Cerrado. In: VII Congresso de Ecologia do Brasil, 2005, Caxambu. Anais do Congresso de Ecologia do Brasil, 2005. v. VII.

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DAVID, V. A.; EMÍLIO, T.; KLEINE, P.; ALMEIDA, L. B. Protein Synthesis Game. In: XXXIII Reunião Anual da Sociedade Brasileira de Bioquímica e Biologia Molecular (SBBq), 2004, Caxambu. Anais da Reunião Anual da Sociedade Brasileira de Bioquímica e Biologia Molecular (SBBq), 2004. v. 33.

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ALMEIDA, L. B. Métodos para estudos de mamíferos. In: Dez anos de atividades da Trilha da Natureza, 2002, São Carlos. Resumos dos "Dez Anos de atividades da Trilha da Natureza", 2002.

FUSHITA, A. T.; ALMEIDA, L. B.; OLIVEIRA, F. F.; FIGUEIREDO, I. C. S.; LIMA, M. I. S. Trilha da Natureza: 9 anos a serviço da educação e da pesquisa. In: I Semana de Biologia da UFSCar, 2001, São Carlos. Anais da Semana de Biologia da UFSCar, 2001. v. 1.

Scholarships and Awards

Period **2015 – 2019**

Award LASPAU-administered scholarship to pursue a doctorate degree in the United States.

Details Selected candidate of the Science Without Borders program (Brazilian government program for financial support of graduate studies).

Period **2005**

Function	Master’s in Ecology, Conservation and Wildlife Management.
Scholarship	CNPq
Institution	Universidade Federal de Minas Gerais (UFMG) – *Federal University of Minas Gerais*

Period	**2003**
Function	Trainee
Main Activities	Development of educational materials on genetics for use in public schools of São Carlos region, State of São Paulo.
Institution	Universidade de São Paulo (USP) – 2003
Scholarship	
Name and address of employer	Universidade de São Paulo (USP) – *São Paulo University*, Centro de Divulgação Científica e Cultural, Center of Scientific and Cultural Disclosure (CDCC), São Carlos, SP, Brazil

Period	**1999 – 2003**
Function	Trainee
Main Activities	- Work on Environmental Education with students of schools of São Carlos municipality and region. - Monitoring guided tours in the Cerrado vegetation located on the campus of the Federal University of São Carlos. 2001 – Universidade Federal de São Carlos 1999, 2000, 2002, 2003 – voluntary work
Additional Coursework	**2021:** Global and regional IUCN Red List Assessments (Workload: 80h) **2020:** II Workshop of Community Ecology (Workload: 40h) **2020:** Biodiversity monitoring: management, analysis, and data synthesis (Workload: 49h) **2017:** Intermediate-level workshop on Bayesian integrated population modeling (Workload: 40h **2017:** Modeling patterns and dynamics of species occurrence workshop (Workload: 64h)

Additional Coursework

2016: Camera trapping study design and data analysis for occupancy and density (Workload: 72h)

2015: Statistical Modeling in Population Ecology (Workload: 90h)

2014: Road Ecology (Workload: 120h)

2014: Use of R Language for the Analysis of Ecological Data (Workload: 60h)

2013: Digital Image Processing (Workload: 40h)

2013: Spatial Analysis of Geographic Data (Workload: 40h)

2012: Occupancy Modeling (Workload: 43h)

2012: Landscape Ecology: concepts and research methods (Workload: 60h)

2012: Introduction to Road Ecology (Workload: 16h)

2011: Planning and Analysis of Ecological Research (Workload: 90h)

2011: Trophic Ecology of Carnivore Vertebrates (Workload: 60h)

2011: Geographical Data Management (Workload: 40h)

2011: Geographical Data Management (Workload: 40h)

2010: Introduction to Remote Sensing (Workload: 90h)

2010: Fundaments in Geoprocessing (Workload: 40h)

2010: Species Distribution Modeling (Workload: 30h)

2008: Conservation Biology Latin American Course (Workload: 220 h)

2006: Introduction to Education in the Process of Environmental Management (Workload: 136 h)

2004-2005: Botanical Illustration Course (Workload: 100 h)

2003: Frugivory and Seed Dispersal Latin American Course (Workload: 120 h)

2003: Remote Sensing and GIS applied to Biological Conservation (Workload: 62 h)

2002: Tropical Ecology Brazil-England Course (Workload: 120 h)

Personal skills and competencies

Mother tongue **Portuguese**

Other languages

Auto Evaluation	**Understanding**		**Speaking**		**Writing**
European level (*)	Listening	Reading	Take part in a conversation	Fluency	
French	B1	B1	B1	B1	B1
English	C1	C1	C1	C1	C1
Italian	B2	B2	B1	A2	A2

(*) Common European Framework of Reference (CECR)

Computer skills and competencies

- Knowledge of Microsoft Office (Word, Excel, Powerpoint)
- Knowledge of geoprocessing software: ArcGis, GPS Trackmaker, Spring, R
- Knowledge of statistical software: R, MARK, PRESENCE, SAS, Systat
- Knowledge of Corel Draw
- Knowledge of software for reference management (Reference Manager, Mendeley).