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FERNANDA DA SILVA SANTOS

**Padrões de diversidade, ocupação e coexistência de mamíferos
terrestres na região Neotropical**

Belém
2019

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Doutora em Ecologia.

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Orientador: Dr Carlos A. Peres
Co-orientador: Dr Leandro Juen

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*À Floresta Nacional de Caxiuanã,
um segundo lar, por todas as
experiências vividas.*

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What you do makes a difference, and
you have to decide what kind of
difference you want to make.

Jane Goodall

Padrões de diversidade, ocupação e coexistência de mamíferos terrestres na região Neotropical

RESUMO

A estrutura de uma comunidade resulta de um fenômeno complexo e dinâmico que envolve características ambientais, fatores espaciais, disponibilidade de recursos alimentares, bem como as interações entre as espécies, seja por competição ou predação. Para investigar parte dos processos que configuram as comunidades animais, esta tese utilizou o grupo dos mamíferos terrestres como modelo. O objetivo principal foi explorar os fatores que influenciam os padrões de diversidade, ocupação e coexistência de mamíferos terrestres na região Neotropical. Para isso, foram utilizados dados provenientes de oito áreas de florestas protegidas, nas quais foi realizado o monitoramento sistematizado de vertebrados terrestres através de armadilhas fotográficas. Os locais de estudo abrangem seis países da região Neotropical (Costa Rica [1], Panamá [1], Equador [1], Peru [2], Suriname [1] e Brasil [2]), os quais possuem diferentes contextos de preservação. Primeiramente, foi estimada a diversidade β entre as oito comunidades de mamíferos terrestres a fim de identificar: quais as áreas e quais as espécies têm maior contribuição para a diversidade β (LCBD e SCBD, respectivamente); se os padrões são explicados pela substituição ou diferença na riqueza de espécies; e quais os fatores influenciam a diversidade β encontrada (LCBD e SCBD). Posteriormente, investigou-se quais os mecanismos que permitem a coexistência de espécies que apresentam grande similaridade, tanto morfológica quanto no uso de recursos alimentares. Assim, utilizou-se os dados de cinco espécies simpátricas de felinos [onça pintada (*Panthera onca*), onça parda (*Puma concolor*), jaguatirica (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*) e gato maracajá (*Leopardus wiedii*)], que potencialmente ocorrem nas oito áreas de estudo, para descrever padrões de organização espaço-temporal entre as espécies. Por fim, os dados de uma das áreas foi utilizado para testar a hipótese de que existe uma movimentação sazonal dos mamíferos terrestres, principalmente de espécies frugívoras e granívoras, em resposta às mudanças na disponibilidade de água e de recursos alimentares entre as estações seca e chuvosa em uma floresta de terra firme. Os resultados demonstram que as áreas consideradas fragmentadas apresentam maior contribuição para a diversidade β e que a variação é determinada pela diferença na riqueza de espécies e não pela substituição. Além disso, as espécies que mais contribuíram para a diversidade β entre os sítios foram aquelas com maior variação nas estimativas de abundância. Entre os felinos, o estudo revelou aparente partição espaço-temporal entre a maioria dos pares de espécies analisados, sendo a abundância de presas mais importante na ocorrência e distribuição espacial dos felinos do que as interações entre as espécies. Quanto à sazonalidade, apenas três espécies apresentaram diferença na ocupação entre as estações seca e chuvosa, enquanto as demais espécies analisadas não parecem alterar sua área de uso em função da variação na disponibilidade de água e alimentos. Ao final deste estudo, os resultados fornecem uma ampla caracterização dos mamíferos terrestres que ocorrem na região Neotropical, abordando o estado de conservação, fatores que influenciam a ocorrência, assim como os padrões espaciais e temporais de algumas espécies de felinos ao longo de oito florestas protegidas da região Neotropical.

Palavras-chave: monitoramento, armadilhas fotográficas, diversidade β , felinos neotropicais, partição espacial, partição temporal, dinâmica sazonal, floresta tropical, áreas protegidas

Diversity, occupancy and coexistence of Neotropical terrestrial mammals

ABSTRACT

Community structure and diversity result from a complex and dynamic phenomenon, determined by a large number of processes in space and time, which are driven by environmental conditions, spatial factors, resource availability, and species interactions, including competition and predation. This study used the terrestrial mammal group as a model to investigate part of the processes shaping communities, and to understand patterns of diversity, occupancy, and coexistence in the Neotropical forests. Data from a long-term camera trapping monitoring of terrestrial vertebrates across eight protected area sites were combined. The study sites comprise eight areas distributed through six countries (Costa Rica [1], Panama [1], Ecuador [1], Peru [2], Suriname [1] e Brazil [2]), and include both intact forest and fragmented forest landscapes. Firstly, β diversity was estimated among the eight mammal communities to identify: which sites and species contributed to differences in the variation of community composition (LCBD and SCBD, respectively); which process (species replacement or richness difference) explain the observed β -diversity patterns; and which factors affect local contribution (LCBD) and species contribution (SCBD) to β diversity. Posteriorly, data from five sympatric cat species [jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*) and margay (*Leopardus wiedii*)], that potentially occur across the eight sites, were used to examine mechanisms that allow coexistence among ecologically similar species. Finally, data from one of the sites was used to test the hypothesis that terrestrial mammals, mainly frugivores and granivores, move seasonally as a response to resource availability fluctuation (e.g., water and fruits) between rainy and dry seasons in a terra-firme forest. The results indicated that fragmented forests contribute more to β diversity than intact forest sites, and that variation in species composition is determined by richness difference rather than replacement. The eleven species ranked as the most important in structuring the communities were also the ones with the highest abundance variation among sites. Regarding felids' coexistence, the study reveals an apparent spatial and temporal partitioning for most species pairs, with prey abundance being more important than species interactions to the local occurrence and spatial distribution of Neotropical forest cats. Concerning seasonal dynamics, only three species presented differences on occupancy between dry and rainy seasons, while the other analyzed species did not seem to move as a response to variation in water and food availability. In summary, the results provide a broad characterization of terrestrial mammals occurring in the Neotropical region, assessing their conservation status, factors that influence their occurrence, as well as the spatial and temporal patterns of several felid species along eight Neotropical protected forests.

Keywords: camera trap monitoring, β diversity, Neotropical cats, spatial partitioning, temporal partitioning, seasonal dynamic, tropical forest, protected areas

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1. INTRODUÇÃO GERAL

Compreender os padrões de distribuição, riqueza e abundância das espécies, bem como os fatores que os afetam, tem sido um dos principais objetivos das pesquisas em ecologia (CHASE, 2003; RICKLEFS, 1987). Sabe-se que a estrutura de uma comunidade resulta de um fenômeno complexo e dinâmico, determinado por um grande número de processos (BADGLEY, 2010; RICKLEFS, 1987; 2006). Além dos processos históricos, responsáveis por grande parte dos padrões biogeográficos que observamos atualmente, a distribuição de espécies depende de características ambientais, de fatores espaciais, da disponibilidade de recursos alimentares, bem como das interações entre as espécies, seja por competição ou por predação (DOBROVOLSKI et al., 2012; JETZ & FINE, 2012; MACARTHUR & LEVINS, 1967; SVENNING, FLØJGAARD & BASELGA, 2011).

Embora muito se conheça sobre estes padrões em grandes escalas, compreender os aspectos que influenciam a distribuição e ocorrência das espécies local e/ou regionalmente permanece um desafio (GASTON, 2000). O estudo dessa diversidade é cada vez mais relevante diante de um cenário de crescente avanço das atividades humanas, responsáveis por mudanças na paisagem e fragmentação dos habitats, com consequência para a fauna (CHIARELLO, 1999; ESPINOSA, CELIS & BRANCH, 2018; MICHALSKI & PERES, 2007; PALMEIRIM et al., 2018).

Mesmo com os desafios, estudos documentando a diversidade, em suas diversas formas e relações, vem num crescimento exponencial diante de grandes bancos de dados e inúmeras ferramentas analíticas disponíveis (DEFRIES et al., 2010; GASTON, 2000). Um exemplo prático foi como a expansão no uso de armadilhas fotográficas (também conhecidas como *camera traps*) para o registro de vertebrados terrestres, principalmente aves e mamíferos, incrementou os estudos e criou novas abordagens e metodologias para acessar a diversidade dessa fauna (BURTON et al., 2015; MACKENZIE et al., 2002; O'BRIEN et al., 2010; RIDOUT & LINKIE, 2009; ROVERO & ZIMMERMANN, 2016; ROWCLIFFE et al., 2016).

As armadilhas fotográficas têm se mostrado uma ferramenta eficiente, econômica e um método facilmente replicável para o estudo e monitoramento das mais variadas espécies (AHUMADA et al., 2011; ROVERO & ZIMMERMANN, 2016). Através dos registros fotográficos obtêm-se desde parâmetros populacionais, como estimativas de riqueza, abundância, densidade e ocupação, até padrões de atividade, uso do habitat, interação entre espécies e comportamento desses animais (CARBONE et al., 2001; CUSACK et al., 2017; KARANTH et al., 2011; MONTERROSO, ALVES & FERRERAS, 2014).

Diversos projetos de pesquisa têm amostrado as comunidades de vertebrados sistematicamente, gerando um grande volume de dados de alta qualidade, principalmente em florestas tropicais [por exemplo, o projeto *Tropical Ecology Assessment and Monitoring (TEAM) Network* (JANSEN et al., 2014; TEAM NETWORK, 2011)]. Estes dados tem permitido analisar as comunidades de

vertebrados terrestres em escala global e avaliar os impactos atuais nestas populações (AHUMADA et al., 2011; BEAUDROT et al., 2016).

Neste contexto, esta tese reuniu dados de um monitoramento padronizado de vertebrados terrestres realizado em oito áreas florestais protegidas. O objetivo principal foi investigar os padrões de diversidade, ocupação e coexistência de mamíferos terrestres na região Neotropical. Mamíferos são um grupo chave para a conservação, pois incluem predadores de topo de cadeia e uma variedade de espécies de herbívoros, os quais são responsáveis pela predação e dispersão de sementes no ambiente (TERBORGH, 1992; TERBORGH et al., 1999). Além disso, os mamíferos terrestres têm uma alta capacidade de dispersão e podem ocupar os mais diversos tipos fisionômicos na paisagem (EISENBERG, 1990; EMMONS & FEER, 1997), o que os torna um grupo interessante para compreender padrões de diversidade e resposta à distúrbios.

As áreas estudadas abrangem seis países das Américas Central e Sul (Costa Rica [1], Panamá [1], Equador [1], Peru [2], Suriname [1] e Brasil [2]), os quais possuem diferentes históricos e contextos de preservação (BEAUDROT et al., 2016). Estudos realizados anteriormente mostram que a estrutura das comunidades de mamíferos varia entre as áreas, podendo apresentar diferenças na riqueza, abundância e ocupação das espécies (AHUMADA et al., 2011; BEAUDROT et al., 2016). Com base no conhecimento prévio sobre a mastofauna destas áreas, foram propostas três abordagens para esta tese, as quais foram desenvolvidas separadamente em formato de artigos. A saber:

(1) Estimando a *Diversidade* β em comunidades de mamíferos terrestres Neotropicais – a diversidade β pode ser definida como a variação na composição de espécies entre os locais de uma região de interesse (WHITTAKER, 1972). Diferente da diversidade α , a diversidade β e os fatores que a influenciam ainda foram pouco estudados, mas o seu uso é considerado fundamental para a compreensão do funcionamento dos ecossistemas e para fornecer subsídios aos planos de manejo, restauração de habitats e para a conservação da biodiversidade (LEGENDRE, BORCARD & PERESNETO, 2005). Inúmeros métodos e índices já foram propostos para estimar a diversidade β (BASELGA, 2010; KOLEFF, LENNON & GASTON, 2003; LEGENDRE, BORCARD & PERESNETO, 2005; LENNON et al., 2001) e abordagens mais recentes sugerem que a dissimilaridade entre as comunidades é um resultado de dois diferentes processos, a substituição de espécies (também chamada *turnover*) e a diferença na riqueza ou *Nestedness* (BASELGA, 2010; LEGENDRE & DE CÁCERES, 2013; LENNON et al., 2001).

Na primeira sessão desta tese foi utilizada a abordagem proposta por Legendre & De Cáceres (2013), na qual a diversidade β é estimada com base na variação total das comunidades e particionada em “Contribuição Local para a Diversidade β ” (*Local Contributions to Beta Diversity* [LCBD]) e “Contribuição das Espécies para a Diversidade β ” (*Species Contributions to Beta Diversity* [SCBD]). LCBD é um indicador comparativo da singularidade ecológica dos locais, enquanto que SCBD

corresponde ao grau de variação de cada espécie em toda a área de estudo. As principais questões investigadas foram: a) quais as áreas protegidas e quais as espécies tem maior contribuição para a diversidade β ; b) se os padrões de diversidade β são explicados pela substituição ou diferença na riqueza/abundância de espécies; e c) quais os fatores influenciam na variação encontrada entre os sítios e entre as espécies. Os dois índices foram relacionados às métricas de comunidade, variáveis ambientais e atributos biológicos.

(2) *Mecanismos de coexistência entre felinos neotropicais* – a interação entre as espécies é um dos fatores mais importantes na manutenção e estrutura da diversidade biológica. Na investigação destas interações, os carnívoros, principalmente os felinos, figuram como um grupo modelo, pois apresentam hábitos de vida bastante semelhantes e uma grande similaridade morfológica, influenciando umas às outras, tanto por competirem diretamente pelos mesmos recursos, quanto pelo risco de morte intraguilda (DONADIO & BUSKIRK, 2006; PALOMARES & CARO, 1999). Acredita-se que exista um limite de similaridade no uso dos recursos e, a partir deste limite, a competição entre duas espécies semelhantes acabaria por excluir uma delas (MACARTHUR & LEVINS, 1967). Assim, a coexistência seria possível quando estas espécies utilizam o tempo, o espaço e/ou os recursos alimentares de maneira diferente uma das outras (SCHOENER, 1974).

Para avaliar os mecanismos de coexistência entre os felinos, a segunda sessão da tese combinou os dados das oito áreas de estudo nas quais podem ser encontradas até seis espécies de felinos simpátricos: onça pintada (*Panthera onca*), onça parda (*Puma concolor*), jaguatirica (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*), gato maracajá (*Leopardus wiedii*) e gato do mato pequeno (*Leopardus tigrinus*). O objetivo principal foi investigar os padrões de diferenciação de nicho entre cinco das seis espécies (excluindo *L. tigrinus*) ocorrentes na região. Utilizou-se as seguintes abordagens: (a) modelagem de ocupação para identificar quais as características influenciavam o uso do habitat das três espécies de maior porte (onça pintada, onça parda e jaguatirica); (b) modelagem incorporando as estimativas de ocupação das outras espécies competidoras a fim de explorar a coocorrência espacial entre as três espécies; (c) modelagem das atividades temporais das cinco espécies (onça pintada, onça parda, jaguatirica, jaguarundi e gato-maracajá) para avaliar e quantificar a sobreposição nos padrões de atividade entre os pares de espécies com maior potencial competitivo; e (4) modelagem das atividades temporais de uma mesma espécie entre os diferentes sítios a fim de comparar se o padrão de atividade e nível de atividade diferem de acordo com os níveis potenciais de competição.

(3) *Dinâmica sazonal de uma comunidade de mamíferos terrestres na Amazônia Oriental* - As florestas tropicais possuem uma sazonalidade pronunciada, alternando entre períodos secos e chuvosos em diversos níveis (PRIMACK & CORLETT, 2005). Essa variação tem diversas implicações em relação a disponibilidade de recursos necessários para os mamíferos terrestres (como

por exemplo, água e frutos), podendo influenciar nos padrões de atividade e movimentação das espécies (HAUGAASEN & PERES, 2005; MENDES PONTES & CHIVERS, 2007). Em geral, estudos envolvendo mamíferos são de curto prazo, com metodologias e esforços amostrais variados, o que torna difícil a comparação e o entendimento dos processos que conduzem a dinâmica espaço-temporal das espécies (BURTON et al., 2015). A estação chuvosa em florestas tropicais, por exemplo, foi poucas vezes contemplada em estudos com mamíferos terrestres (TEAM NETWORK, 2011), devido às dificuldades de acesso em algumas áreas e potenciais danos que a alta umidade pode causar às armadilhas fotográficas (MARTIN, NDIBALEMA & ROVERO, 2017). A fim de avaliar o efeito da variação sazonal na comunidade de mamíferos terrestres, a terceira sessão da tese reuniu os dados de uma das áreas de estudo, a Floresta Nacional de Caxiuanã (Pará, Brasil), para testar a hipótese de que existe uma movimentação sazonal dos mamíferos terrestres, principalmente de espécies frugívoras e granívoras, em resposta às mudanças na disponibilidade de água e de recursos alimentares. Utilizou-se a abordagem de análise de ocupação, contabilizando a probabilidade de detecção, para examinar a influência de seis variáveis (estação, precipitação, temperatura, elevação, distância ao rio principal e distância vertical à drenagem) na distribuição espacial das espécies.

Ao final deste estudo, os resultados fornecem uma ampla caracterização dos mamíferos terrestres que ocorrem na região Neotropical, abordando o estado de conservação das espécies ao longo de oito florestas protegidas. Além disso, a tese discute os fatores que influenciam a ocorrência e distribuição espacial dos mamíferos, assim como os padrões espaciais e temporais de algumas espécies de felinos sendo modulados pela disponibilidade de recursos e características do habitat.

2. Sessão I

Assessing β -diversity components to conserve mammal communities in Neotropical forests

A primeira sessão desta tese foi elaborada e formatada conforme as normas da publicação científica *Diversity and Distributions*, disponível em:

<https://onlinelibrary.wiley.com/page/journal/14724642/homepage/forauthors.html>

1 Assessing β -diversity components to conserve mammal
2 communities in Neotropical forests
3

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32 **Abstract**

33 **Aim:** β -diversity indices have become an important tool to understand the functioning of ecosystems,
34 and improve knowledge of the effects of landscape modifications, identifying mechanisms for
35 biological conservation and ecosystem management. In this study, we analyzed patterns of β -diversity
36 of ground-dwelling mammal communities from the perspective of site ecological uniqueness to
37 understand (1) which sites and species contributed most to differences in the variation of community
38 composition, (2) which process (species replacement or richness/abundance difference) best explain
39 observed patterns of β -diversity, and (3) what are the factors affecting either site or species
40 contributions to β -diversity. .

41 **Location:** Forests in Mesoamerica and South America

42 **Methods:** We used the total variance of the communities to estimate the total beta diversity (BD_{Total}),
43 and partitioned it into ‘Local Contributions to Beta Diversity’ [i.e., comparative indicators of the
44 ecological uniqueness of the sites (LCBD)] and ‘Species Contributions to Beta Diversity’ [i.e., degree
45 of variation of individual species across the study area (SCBD)]. We also used partial redundancy
46 analysis and beta regression to examine which factors (i.e., environmental, spatial, community
47 metrics) affect these indices.

48 **Results:** Our results primarily show differences between fragmented and intact forest sites, and
49 higher uniqueness in species composition ($> LCBD$) at fragmented forest sites. Variation in species
50 composition was largely determined by the overall difference in species richness/abundance (59%)
51 rather than the replacement component of β -diversity (41%). SCBD indices ranked 11 species that
52 were most important in structuring mammal communities, and varied the most in abundances among
53 sites. We found that LCBD was largely explained by the variation in species richness and landscape
54 characteristics (protected area size, NDVI and tree basal area). SCBD was strongly associated with
55 species abundance and naïve occupancy, but less so with biological traits.

56 **Conclusion:** Uniqueness in community composition provides useful ecological information to the
57 current status of mammal communities at our Neotropical study sites, which can support terrestrial
58 mammal conservation plans.

59

60 **KEYWORDS:** ecological uniqueness, terrestrial mammals, LCBD, SCBD, environmental factors,
61 spatial scale

62 1 INTRODUCTION

63

64 Community structure and diversity result from complex and dynamic phenomena, which are
65 determined by a large number of processes in space and time (Ricklefs, 2006). Understanding patterns
66 of species distributions at different scales (i.e., local, landscape, and regional) and the factors that
67 govern these patterns have been goals in ecology research (Chase, 2003; Gaston, 2000; Jetz & Fine,
68 2012; Ricklefs, 1987). To account for multiple spatial scales, species diversity can be decomposed
69 into α -diversity, corresponding to the number of species at individual sites, γ -diversity, related to the
70 diversity of the entire geographic region of interest, and β -diversity or the variation in species
71 composition among sites within a region (Whittaker, 1972).

72 The origin of β -diversity can be explained by different hypotheses involving species dispersal
73 limitation in space, environmental conditions, and biological interactions (Hubbell, 2001;
74 Hutchinson, 1957; Legendre, Borcard, & Peres-Neto, 2005). Testing these hypotheses is important
75 for understanding the functioning of ecosystems, the biophysical geography that underpins
76 conservation of biodiversity, and for ecosystem management (Legendre et al., 2005).

77 Studies on the spatial distribution of species have been widely implemented, mainly to
78 understand broad patterns of diversity (Penone et al., 2016; Qian, 2009; Safi et al., 2011). One of the
79 most discussed geographic patterns of species distributions involves a latitudinal gradient, which
80 establishes that diversity increases towards low latitudes (Gaston, 2000; Hillebrand, 2004; Koleff,
81 Lennon, & Gaston, 2003; Qian, 2009). However, different factors such as climate, topography, spatial
82 scale, historical and geographic characteristics can also influence these patterns (Calderón-Patrón,
83 Moreno, Pineda-López, Sánchez-Rojas, & Zuria, 2013; Qian, 2009; Qian & Ricklefs, 2008). For
84 example, elevation and temperature are key predictors explaining variation in β -diversity in bird and
85 mammal assemblages (Maestri & Patterson, 2016; Melo, Rangel, & Diniz-Filho, 2009; Qian, 2009).
86 In general, β -diversity tends to be higher for vertebrate taxa such as reptiles and amphibians, which
87 exhibit lower dispersal ability, than for birds and mammals (Dobrovolski, Melo, Cassemiro, & Diniz-
88 Filho, 2012; Qian, 2009).

89 In addition to broad-scale diversity patterns, β -diversity indices have become an important tool
90 to understand the effects of landscape modification on species assemblages, and to identify effective
91 conservation strategies. These studies have spanned different taxa, including plants (Bergamin et al.,
92 2017; Grass, Brandl, Botzat, Neuschulz, & Farwig, 2015; Heydari, Omidipour, Abedi, & Baskin,
93 2017) insects (Kim, Bartel, Wills, Landis, & Gratton, 2018; Van Allen, Rasmussen, Dibble, Clay, &
94 Rudolf, 2017), birds (Grass et al., 2015; Meynard et al., 2011), and mammals (Palmeirim, Benchimol,
95 Morante-Filho, Vieira, & Peres, 2018; Pardini, De Souza, Braga-Neto, & Metzger, 2005). In a global
96 scenario where increasing disturbance, habitat loss, and fragmentation affect species abundances and

97 distributions, variation in community composition may increase due to differences in local extinction,
98 competition, and colonization rates among sites (Legendre, 2014; Legendre & De Cáceres, 2013;
99 Pardini et al., 2005).

100 Different indices and methods have been proposed to estimate β -diversity over the years, using
101 presence-absence or abundance data, multiplicative indices, and additive partitioning of community
102 diversity (Baselga, 2010; Koleff et al., 2003; Legendre et al., 2005; Lennon, Koleff, Greenwood, &
103 Gaston, 2001). Some approaches propose methods that partition the dissimilarity indices, suggesting
104 that β -diversity is a result of two concomitant processes, namely species replacement (or turnover)
105 and richness/abundance differences or nestedness (Baselga, 2010; Legendre & De Cáceres, 2013;
106 Lennon et al., 2001). These methods ensure a better understanding of the origin and maintenance of
107 β -diversity (Legendre, 2014; Legendre & De Cáceres, 2013).

108 In a recent advance, Legendre & de Cáceres (2013) developed a method allowing total β -
109 diversity (BD_{Total}) to be deconstructed into its local contributions of either the sites (hereafter, LCBD
110 indices) or the species to β -diversity (hereafter, SCBD indices), using a species-by-site abundance
111 matrix. LCBD values indicate the degree of ecological uniqueness of each sampling site, whereas
112 SCBD represents the degree of the relative importance of individual species to β -diversity across
113 sites. From a conservation planning perspective, large LCBD values indicate sites that have either
114 unusual species combinations of high conservation value or degraded and species-poor sites that may
115 be prioritized for ecological restoration (Legendre, 2014).

116 In this study, we used data on the abundance and distribution of terrestrial mammals across eight
117 comprehensively sampled Neotropical forests to investigate β -diversity patterns at a regional scale,
118 and understand how spatial and environmental factors influence these patterns. To our knowledge,
119 there are no studies linking abundance and β -diversity of terrestrial mammals to environmental
120 gradients in order to understand the processes behind the maintenance of diversity.

121 Mammals are a key group for conservation, as they fulfil multiple trophic roles including apex
122 predation, herbivory, seed predation and seed dispersal (Terborgh, 1992; Terborgh et al., 1999). In
123 addition, Neotropical terrestrial mammals often have considerable dispersal capacity and can occupy
124 the most diverse types of landscape physiognomy from southern Mexico to northern Argentina
125 (Eisenberg, 1990), which makes them an interesting group to understand patterns of diversity and
126 responses to disturbances.

127 We examined the contribution of individual sites (LCBD) and individual species (SCBD) to the
128 total β -diversity among all eight Neotropical terrestrial mammal communities, focusing on three main
129 questions:

130 1) Based on the variation in the ecological uniqueness, which study site and species contributed
131 most to overall β -diversity? Our study sites comprise small to large spatial extents (hereafter,

132 fragmented and continuous landscapes, Beaudrot et al 2016), so we expect that LCBD values should
133 increase in fragmented sites due to local extinction of some specialists species and increases in
134 generalist species (Chiarello, 1999; Michalski & Peres, 2007). Also, we predict that species showing
135 higher variation among sites (above average SCBD values) would contribute most to β -diversity. This
136 is based on the fact that some forest mammals are highly vulnerable to landscape modifications, while
137 others can persist or increase in abundance even in a modified landscape;

138 2) Are the β -diversity patterns primarily explained by species replacement (*Repl*) or difference
139 in species richness (*RichDiff*)? Mammal β -diversity is affected by differences in habitat quality and
140 heterogeneity (Kerr & Packer, 1997; Melo et al., 2009). Thus, we formulate two contrasting
141 hypotheses: a) Species replacement component (*Repl*) explains variation in overall β -diversity since
142 species tend to replace one another along ecological gradients, implying the simultaneous species
143 gains or losses due to environmental filtering, competition or historical events (Legendre, 2014); or
144 b) Richness difference component (*RichDiff*) explains variation in overall β -diversity because some
145 communities may include a large number of species than others, reflecting the diversity of niches
146 available at different locations throughout the study area (Legendre, 2014).

147 3) Is the variation in β -diversity primarily influenced by environmental conditions or spatial
148 factors? And which factors affect LCBD indices. We hypothesize that environmental characteristics
149 have stronger effects on the variation in β -diversity than spatial factors, as other studies have shown
150 that local habitat structure, climate, and forest size are highly associated with mammal diversity
151 (Chiarello, 1999; Michalski & Peres, 2007). Furthermore, we used community metrics (richness and
152 abundance) and environmental variables to investigate variation in LCBD, as well as species metrics
153 (relative abundance and naïve occupancy) and species characteristics (i.e., biological traits) to
154 investigate variation in SCBD.

155

156 2 METHODS

157 2.1 Study sites

158

159 We used data from eight Neotropical forest sites that are part of the Tropical Ecology
160 Assessment and Monitoring (TEAM) Network, a global standardized biodiversity monitoring
161 program. Neotropical TEAM sites are distributed across six countries in Central and South America:
162 Volcán Barva Transect, Costa Rica (VB), Barro Colorado Nature Monument, Panamá (BCI), Central
163 Suriname Nature Reserve, Suriname (CSN), Yasuni Research Station, Ecuador (YAS), Caxiuanã
164 National Forest, Brazil (CAX), Manaus, Brazil (MAN), Cocha Cashu - Manu National Park, Peru
165 (COU) and Yanachaga National Park, Peru (YAN) (Table 1).

166 Following the categorization criteria for landscapes adopted by Beaudrot et al (2016), study
 167 sites were divided into intact protected forest landscapes, in which protected areas were either
 168 indistinguishable from the continuous forest in surrounding areas (i.e., CAX, COU, CSN, and YAS),
 169 and fragmented forest landscapes, in which protected areas were embedded within a patchwork
 170 mosaic of forest and non-forest areas (i.e., BCI, MAN, VB, and YAN).

171

172 **Table 1. Location and area of the eight Neotropical forest sites analysed in this paper.**

Code	Study site, Country	Longitude, Latitude	Area (ha)	Landscape type ^a
BCI	Barro Colorado Nature Monument, Panama	-79.851, 9.092	32631.22	FR
CAX	Caxiuanã National Forest, Brazil	-51.534, -1.775	471192.63	CF
COU	Cocha Cashu - Manu National Park, Peru	-71.409, -11.843	1704505.53	CF
CSN	Central Suriname Nature Reserve, Suriname	-56.207, 4.741	1630233.61	CF
MAN	Manaus, Brazil	-59.935, -2.415	1198944.01	FR
VB	Volcan Barva Transect, Costa Rica	-84.021, 10.422	49502.04	FR
YAN	Yanachaga National Park, Peru	-75.303, -10.316	293234.07	FR
YAS	Yasuni Research Station, Ecuador	-76.458, -0.609	1040686.74	CF

173 ^aClassification based on [33]: FR – fragmented forest and CF – continuous forest.

174

175 2.2 Mammal surveys

176

177 Terrestrial mammals were sampled during a camera trapping monitoring conducted between
 178 2010 and 2014. The sampling design consisted of a regular matrix of 60 camera trap points (or two
 179 matrices of 30 camera trap points each) spaced apart by ≈ 1.4 km from each other and covering an
 180 area of about 120 km². The sampling period at each study site was within the dry season and cameras
 181 remained in the field for 30 days, once a year (Jansen, Ahumada, Fegraus, & O'brien, 2014; TEAM
 182 Network, 2011). Our dataset comprised four sampling periods at each study site (excepted for
 183 Manaus, where data were available only for 2010 and 2011). Camera traps (Models RM45 and
 184 HC500, Reconyx Inc.) were configured to take three pictures per trigger with no delay or intervals
 185 between photos, working 24 hours/day. No baits were used to attract animals, and cameras were
 186 deployed off trails.

187 Images of the same species were considered independent detections when at least one hour had
 188 passed between consecutive photographs (Rovero & Spitalè, 2016). For data analysis, we excluded
 189 images of species that were primarily arboreal (e.g. primates) and water dependent, in order to avoid

190 sampling bias or particularities of any given study area. We also pooled congeneric species into an
191 "ecospecies" taxon, thereby avoiding overestimating mammal assemblage differences between study
192 sites that contained ecologically analogous species (for example, *Nasua narica* and *Nasua nasua*
193 represent a unique ecospecies '*Nasua*') (Jones et al., 2009). To streamline, we hereafter use "species"
194 to refer to both species and ecospecies.

195

196 2.3 Patch and landscape variables

197

198 Variables were selected based on forest structure and bioclimatic patterns that have shown to
199 influence the distribution and diversity of mammals (Maestri & Patterson, 2016; Qian, 2009). For
200 each camera trap point, we recorded (1) elevation range and (2) NDVI (Normalized Difference of
201 Vegetation Index), while for each study site we recorded (3) tree density (tree/ha), (4) tree basal area,
202 (5) mean annual temperature, (6) mean annual precipitation, (7) precipitation seasonality (coefficient
203 of variation), and (8) protected area size.

204 Elevation data were calculated using a digital elevation model (DEM) based on the NASA
205 Shuttle Radar Topographic Mission (SRTM), with a spatial resolution of one arc-second ($\approx 30\text{m}$).
206 Elevation range was obtained by the difference between the highest and lowest elevations of camera
207 trap points within each study site. Normalized Difference of Vegetation Index (NDVI) was generated
208 from eMODIS NDVI scenes (Vegetation monitoring). We obtained the mean NDVI within a 500-m
209 radial buffer around each camera trap point. DEM and eMODIS data were downloaded from the U.S.
210 Geological Survey (Earth Explorer, 2017) and pooled estimates were obtained using QGIS software
211 (QGIS Development, 2015).

212 Tree density and tree basal area were calculated from six 1 ha-plots that had been monitored
213 within each of the eight sites (Data available from the TEAM Network database; See information on
214 (TEAM Network, 2010)). Tree density measurement consists of the number of trees with DBH $>$
215 10cm within each one-hectare plot. We calculated the total basal area for each 1-ha plot and used the
216 average ($n=6$) total basal area as a site covariate. Bioclimatic data came from WorldClim - Global
217 Climate Database. Climate variables (temperature, precipitation, and seasonality) were extracted
218 through a script using the R software (Team R Core, 2018).

219

220 2.4 Data Analysis

221

222 To assess which study site and species contributed most to total β -diversity, we calculated the
223 local contribution to β -diversity (LCBD) and species contributions to β -diversity (SCBD), following
224 the procedures proposed by Legendre & De Cáceres (2013). Firstly, we Hellinger-transformed the

225 abundance-based species-by-site community matrix and subsequently calculated the total β -diversity
226 (BD_{Total}) for all eight sites and all camera trap points combined. Finally, BD_{Total} was decomposed into
227 the LCBD value for each camera trap point and SCBD value for each species. LCBD values are
228 comparative indicators of the ecological uniqueness of the sites in terms of community composition,
229 computed as the relative contribution of a site to BD_{Total} so that the LCBD indices sum to 1. SCBD
230 coefficients represent the degree of variation of individual species across all sites, i.e., indicates how
231 much a species contributes to overall β -diversity (Legendre & De Cáceres, 2013). SCBD indices that
232 were higher than the mean of SCBD values identified the taxa that were the most important
233 contributors to BD_{Total} . LCBD and SCBD indices were computed using the “beta.div” function
234 available from the *adespatial* package in R (Dray et al., 2018).

235 We assessed differences in LCBD indices, and also community abundance (expressed as the
236 number of images per camera trap/day), among all eight study sites using ANOVA tests (or Kruskal-
237 Wallis tests, when data did not conform to assumptions of normality and homogeneity of variance),
238 and associated multiple comparisons to test for pairwise differences among sites.

239 To answer our second question and assess which of the two processes, replacement or
240 richness/abundance differences, best explain differences among mammal communities, we used the
241 “beta.div.comp” function of the *adespatial* R package to partition total β -diversity (Borcard, Gillet,
242 & Legendre, 2018). This method is used for both presence-absence and abundance data, computing
243 the dissimilarity, replacement and richness or abundance difference. Local replacement (*Repl*) and
244 richness/abundance difference (*RichDiff/AbDiff*) measure how unique each camera trap point is
245 compared to other camera traps, in terms of either replacements or richness/abundance differences
246 (Legendre & De Cáceres, 2013). As we have species-by-site abundance data, the dissimilarity
247 coefficients used was the Ružička index, which is the quantitative equivalent to Jaccard (Legendre,
248 2014). As such, we used Podani’s Jaccard-based indices to extract the dissimilarity (*D*), replacement
249 (*Repl*) and richness difference (*RichDiff*) matrices. The function output produces a list containing
250 these three matrices, as well as global results: BD_{Total} , total replacement diversity ($Repl_{Total}$) and total
251 richness diversity ($RichDiff_{Total}$) (Borcard et al., 2018). While the $Repl_{Total}$ and $RichDiff_{Total}$ indices are
252 useful to determine which of the two processes were most dominant across the sampling sites, the
253 *Repl* and *RichDiff* components are required for detailed gradient analysis and were mapped for better
254 interpretation (Legendre, 2014).

255 Lastly, we investigated if variation in community composition was influenced by either
256 environmental or spatial processes, or both, and which factors are the strongest determinants of the
257 LCBD index. We tested the relationships between β -diversity, environment and spatial predictors
258 using partial redundancy analysis (pRDA) (Borcard, Legendre, & Drapeau, 1992). This analysis was
259 performed using: the Hellinger-transformed species-by-site abundance matrix, an environmental

260 variables matrix, and a spatial filter matrix. Our environmental matrix included all variables
261 considered here: elevation range, NDVI, tree density, tree basal area, annual mean temperature,
262 annual mean precipitation, precipitation seasonality, and protected area size. Variables were
263 standardized and to avoid overestimating the amount of variance explained by the environmental
264 covariates, we used the *forward selection* method with 9999 permutations and stopping criteria of
265 0.05 significance level (Blanchet, Legendre, & Borcard, 2008). To then obtain the spatial filter matrix
266 we used geographical coordinates (latitude and longitude) of each camera trap point. Firstly, we
267 calculated principal coordinates of neighborhood matrix (PCNM) which generates eigenvalues and
268 eigenvectors through a truncated distance matrix. PCNM considers that the first vectors show a wide
269 scale variation and later vectors show smaller scale variation (Borcard & Legendre, 2002).
270 Subsequently, we performed a *forward selection* of these PCNM eigenvectors, through 9999
271 permutations, considering a 0.05 significance level, thereby obtaining a spatial filter matrix. The
272 pRDA results included a portion of the (a) variation explained by environmental variables; b)
273 variation explained by spatial factors; c) variation attributed to both environmental and spatial factors;
274 and d) residual variation. Statistical analyses were carried out using *vegan* (Oksanen et al., 2019) and
275 *Packfor* (Miller & Farr, 1971) libraries. For all tests, $p < 0.05$ indicated statistical significance.

276 After obtaining the results for variation partitioning, we further assessed the influence of
277 landscape variables on LCBD. Because our response data (LCBD) varied between 0 and 1, we used
278 beta regression as our modeling tool (Cribari-Neto & Zeileis, 2010). Beta regression is based on the
279 assumption that the dependent variable is beta-distributed and that its meaning is related to a set of
280 regressors through a linear predictor with unknown coefficients and a link function (Cribari-Neto &
281 Zeileis, 2010). We used beta regression with a logit link function for two separate models. First, we
282 related LCBD to community metrics, namely species richness and community abundance. Second,
283 we ran a beta regression of LCBD using environmental variables as predictors. Prior to analyses, we
284 used variance inflation factor (VIF) to detect multicollinearity between predictors in a model. Only
285 variables with $VIF < 3$ were incorporated into the model (i.e., NDVI, tree basal area, precipitation
286 seasonality, and protected area size). We ran beta regression analysis using the “betareg” function
287 from the *betareg* package (Zeileis et al 2018) and VIF were calculated using the *car* package (Fox &
288 Weisberg, 2018).

289 Similarly, we used beta regression to relate SCBD to both species metrics and biological traits.
290 Species metrics included the total abundance of each species, i.e., number of images of each species
291 per camera trap/day, and naïve occupancy, i.e., mean number of camera trap points occupied by any
292 given species. Biological traits included trophic guild (each species was categorized based on its
293 dietary guilds: carnivore, herbivore-frugivore, herbivore-granivore, herbivore-browser, insectivore or
294 omnivore), log-transformed body mass (kg) and order (taxonomic category grouping species by

295 resemblances and differences) (Table S2; Emmons & Feer, 1997; Jones et al., 2009; Paglia et al.,
 296 2012).

297

298 3 RESULTS

299

300 A total of 30,870 terrestrial mammal images were recorded across all eight study sites,
 301 representing a γ -diversity of 48 species (= 33 ecospecies) belonging to 30 genera. The number of
 302 species per site (α -diversity) ranged from 16 to 27 species (23.12 ± 3.75 species; mean \pm SD) (Figure
 303 1; See Table S1 for a complete species checklist per site). Most species were shared among two or
 304 more study sites, and just two species were exclusive to a single site: *Canis latrans* (Coyote) at BCI
 305 and *Tremarctos ornatus* (Spectacled bear) at YAN, but they were rarely recorded (2 and 1 images,
 306 respectively) (Figure 1). Total species abundance was significantly different among sites ($F = 65.64$,
 307 $df = 7$, $p < 0.001$; Figure 2A). The most abundant species was *Dasyprocta* spp. (Agouti), a medium-
 308 sized rodent recorded at all sites. Other species were often abundant whenever present, such as
 309 *Cuniculus paca* (Spotted paca), *Mazama* spp. (Red brocket deer), *Pecari tajacu* (Collared peccary)
 310 and *Dasyus* spp (armadillos).

311

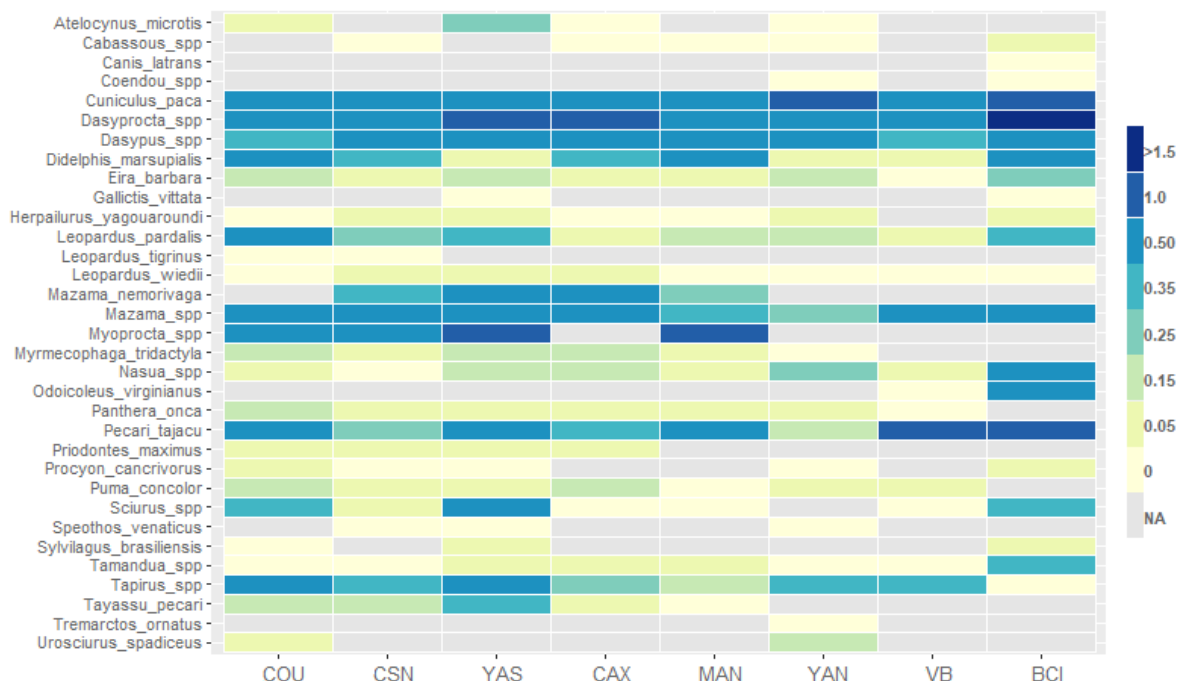


FIGURE 1 – Species-by-site abundance (images/100 camera trap-day) matrix for 33 mammal species surveyed across eight Neotropical forest sites. Abundance data are expressed on a \log_{10} scale. Rectangles representing at least one individual recorded per site are colored; Grey rectangles (NA) indicate that species was not recorded. Species were ordered alphabetically and study sites ordered from the largest to the smallest study area.

312 3.1 β -diversity: LCBD and SCBD indices

313

314 The total β -diversity (BD_{Total}) was 0.442 for all mammal communities. The local contributions
315 (LCBD) of individual camera trap points ranged from 0.0007 to 0.0061. LCBD indices indicate the
316 uniqueness of the mammal community at each study site. Sites with the highest LCBD values were
317 VB, MAN, BCI, and YAN, indicating higher uniqueness in species composition. Comparisons
318 between sites evidenced significant compositional differences (Kruskal-Wallis test, 170.75, $df = 7$,
319 p -value < 0.001 ; Figure 2B), highlighting differences in pairwise comparisons between the above
320 four sites and all other sites (COU, CSN, CAX, and YAS). Pairwise comparisons between BCI-MAN
321 and BCI-YAN did not present significant difference. Results indicate that mammal communities from
322 fragmented landscapes contributed more to the overall BD_{Total} than communities in areas of
323 continuous forests.

324

325

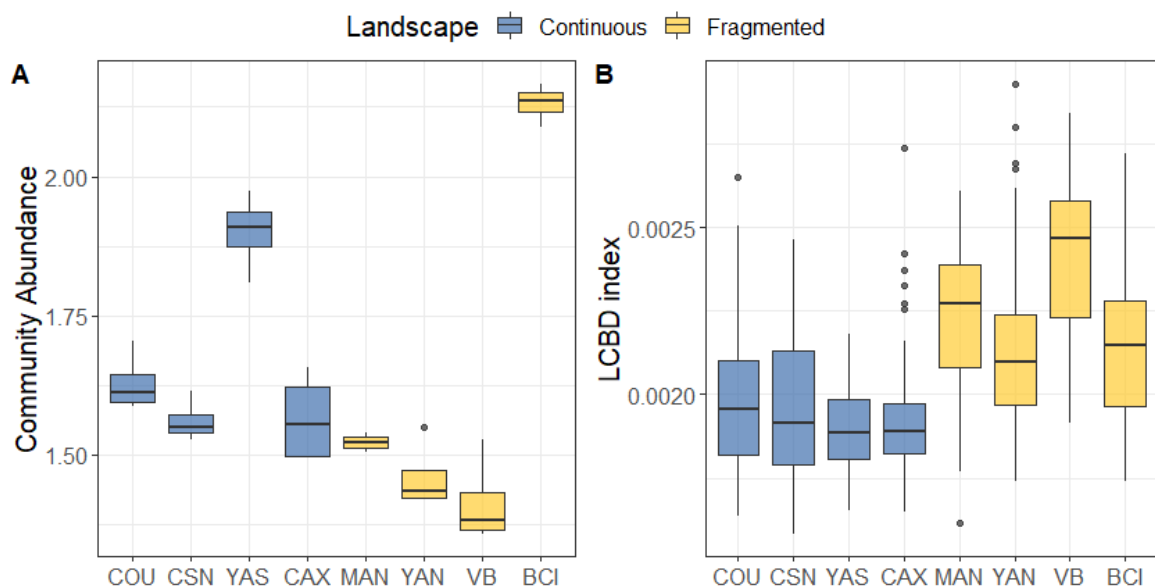


FIGURE 2 – Difference in total community abundance (A) and local contribution to beta diversity (B) among the eight Neotropical forest sites. Study areas are ordered from the largest to the smallest.

326

327 Partitioning the total BD_{Total} revealed a greater percentage of total richness difference
328 ($RichDiff_{Total} = 0.241$; 59%), indicating that richness differences were more important to explain
329 variation in species composition among sites than the replacement component ($Repl_{Total} = 0.166$;
330 41%). Looking at the eight study sites, the mammal community was dominated by richness
331 differences at BCI, VB and YAS sites (>60% of their camera trap points), while COU, CSN, CAX,
332 and YAN sites were dominated by species replacements (>60% of their camera trap points). Only
333 MAN showed an equal contribution of *Repl* and *RichDiff* components to β -diversity (Figure 3).

334 Regarding SCBD, 11 species contributed to beta diversity well above the mean of 33 species:
335 *Myoprocta* spp. (acouchy), *Cuniculus paca* (spotted paca), *Dasyprocta* spp. (agouti), *Pecari tajacu*
336 (collared peccary), *Mazama* spp. (Red brocket deer), *Tapirus* spp. (tapir), *Dasyopus* spp. (armadillo),
337 *Didelphis marsupialis* (common opossum), *Mazama nemorivaga* (Amazonian brown-brocket deer),
338 *Nasua* spp. (coati) and *Leopardus pardalis* (ocelot) (Table S2). The Hellinger-transformed
339 abundances of important taxa varied the most among sites.

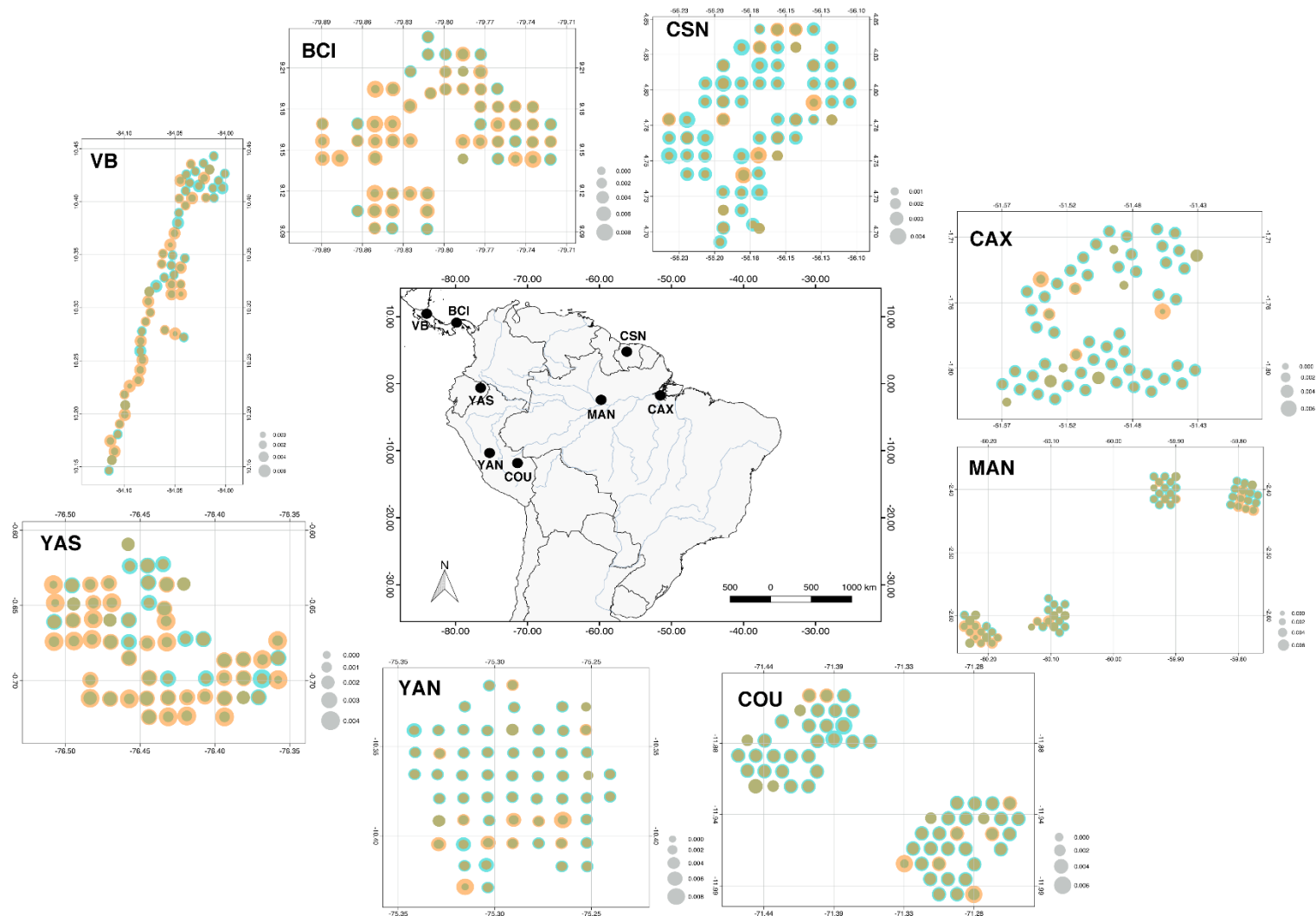


FIGURE 3 – Location of the eight Neotropical forest sites (map in the center) and schematic maps of the camera trap arrays at each site showing partitioning of BD_{Total} : Replacement (*Repl*) represented by blue circles and Richness difference (*RichDiff*) represented by yellow circles. Circle sizes are proportional to LCBD values.

340 3.2 Explaining variations on LCBD and SCBD indices

341

342 Overall, the relative contribution of either environment or space in explaining variation in
343 diversity were small compared with the contribution of both spatial structure and its interaction with
344 the environmental variables (Figure 4).

345

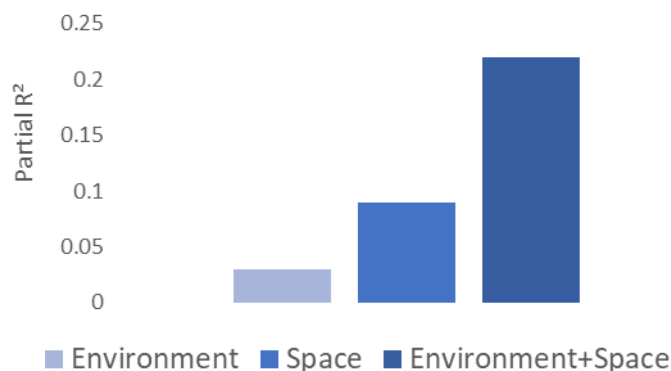


FIGURE 4 - Partial R^2 values for which species composition is the response variable and environmental factors and spatial coordinates are the predictors.

346

347

348 Our model for community metrics explained 0.81% of the variation in LCBD, indicating that
349 LCBD was negatively related to species richness and exhibited no significant association with total
350 abundance (Table 1). Also, tree basal area, protected area size, and NDVI were negatively associated
351 with LCBD, indicating that the uniqueness of the mammal community was higher in fragmented
352 landscapes containing low tree basal areas and little green vegetation. The model including landscape
353 variables accounted for 75% of the variation in LCBD (Table 1).

354 Beta regression including species metrics showed that variation in SCBD was significantly
355 related to naive occupancy (i.e., number of sites occupied) and overall species abundance, and model
356 set explained 65% of the variation in SCBD. Beta regression also showed that SCBD-biological trait
357 relationships were weak (11%), and only trophic guild (Carnivores and Herbivore-Frugivores)
358 explained a significant amount of variation in SCBD (Table 2).

Table 1 – Results of beta regression analysis when the response variable, LCBD, was explained by community metrics (Model 1) and landscape covariates (Model 2). Asterisks show the level of significance for each variable (*0.05; **0.01;***0.001).

	Estimate	SE	z value	Model Pseudo R ²
<hr/>				
(1) Community metrics				
(Intercept)	-1.953	0.022	-88.023***	
Richness	-0.140	0.023	-6.114***	
Total abundance	-0.009	0.023	-0.399	0.811
<hr/>				
(2) Landscape covariates				
(Intercept)	-6.176	0.022	-275.920	
Tree basal area	-0.092	0.032	-2.830**	
Protected area size	-0.139	0.028	-4.939***	
NDVI	-0.062	0.027	-2.297*	
Precipitation seasonality	0.034	0.030	1.125	0.758
<hr/>				

Table 2 – Results of beta regression analysis when the response variable, SCBD, was explained by species metrics (1) and biological traits (2). Asterisks show the level of significance for each variable (***0.001; *0.05).

	Estimate	SE	z value	Model Pseudo-R ²
(1) Species metrics				
Intercept	-5.338	0.272	19.627***	
Naive occupancy	6.744	0.811	8.312***	
Abundance	-0.281	0.116	-2.418*	0.652
(2) Biological traits				
Trophic guild				
Carnivores	-4.192	0.394	-10.639***	
Herbivore-browsers	0.281	0.497	0.565	
Herbivore-frugivores	0.959	0.471	2.038*	
Herbivore-granivores	0.031	0.811	0.038	
Insectivores	0.213	0.533	0.400	
Omnivores	0.484	0.698	0.694	
Body mass	-0.094	0.172	-0.548	
Order	0.090	0.071	1.265	0.113

360

361

362 4 DISCUSSION

363

364 To our knowledge, this is the first study to estimate β -diversity of Neotropical terrestrial
 365 mammals as the total variance (BD_{Total}) of the communities found at different study sites and
 366 computed the contributions of each sampling unit to the overall β -diversity. Our findings showed that
 367 both the local (LCBD) and species contributions to β -diversity (SCBD) are important in
 368 understanding the current conservation status of mammals across our eight Neotropical sites.

369 Our results showed a low value of BD_{Total} (0.442 of a maximum of 1), which suggests that study
370 sites were similar in their species composition and hosted relatively few exclusive species. This is a
371 predictable pattern for Neotropical terrestrial mammals, even though our sites were relatively species
372 rich. In general, ground-dwelling medium to large-sized mammals have a wide geographic
373 distribution (e.g., *P. onca* or *C. paca*) and/or are replaced by parapatric congeners throughout the
374 region (e.g., three agouti species recorded in this study: *Dasyprocta leporina*, *D. punctata*, *D.*
375 *fuliginosa*) (Eisenberg, 1990). In summary, low β -diversity among study sites was related to the
376 higher dispersal ability, larger spatial requirements and smaller population sizes of most medium to
377 large-sized mammals in our study assemblages (Chiarello, 1999; Qian, 2009).

378 As predicted, sites associated with high LCBD values — i.e., with a higher degree of species
379 uniqueness — were those considered as fragmented areas. Also, richness difference, not species
380 replacement, was the main contributor to variation in LCBD of mammal communities across sites.
381 Such pattern appears to result from a small set of common or dominant species occupying fragmented
382 forests, while continuous forests harbor a more complex mammal community. Local extinctions,
383 habitat conditions and other ecological processes are the main factors associated with richness
384 difference (Borcard et al., 2018; Legendre, 2014). Indeed, we observed that common and/or more
385 generalist species, such as *Dasyprocta* spp., *Cuniculus paca* and *Pecari tajacu*, were the most
386 abundant species in smaller areas (Figure 1), where large-bodied mammals had often been extirpated
387 (e.g., *Tayassu pecari*, *Priodontes maximus*, *Myrmecophaga tridactyla*, *Mazama nemorivaga*, and
388 *Panthera onca*). A similar pattern was observed in Amazonian land-bridge islands, which are
389 comparable to our BCI site (Palmeirim et al., 2018).

390 Our results did not support the prediction that compositional uniqueness was more strongly
391 related to environmental variables. Indeed, environmental factors alone had a weak contribution in
392 explaining variation in species composition. Ecological uniqueness is related to both environmental
393 factors and geographic distance. This finding is different from other studies conducted in Amazonian
394 forest, where β -diversity of plants, oribatid mites, mesoinvertebrates, lizards, anurans (Landeiro,
395 Franz, Heino, Siqueira, & Bini, 2018) and small and mid-sized to large mammals (Palmeirim et al.,
396 2018) was more strongly correlated with environmental conditions than spatial distance. We believe
397 that such differences can be explained by the spatial grain size of our study. β -diversity can be scale-
398 dependent (Calderón-Patrón et al., 2013; Ochoa-Ochoa et al., 2014; Qian, 2009), and our results may
399 reflect that variation in species composition decreases with increasing spatial scale of sites and their
400 camera trap sampling arrays (Qian, 2009; Qian & Ricklefs, 2008). An alternative, but not exclusive
401 explanation, is that environmental conditions change as the distance increases, and study sites
402 contained different forest types, habitat structure, resource availability, and spatial configuration
403 shaping mammal communities.

404 Our beta regression analysis also showed some important factors explaining LCBD patterns.
405 This analysis accounted for community metrics, revealing that LCBD was significantly related to
406 species richness. β and α -diversity were not positively associated, as we observed at the VB site,
407 which had the highest LCBD index and the lower species richness. Same patterns were observed for
408 mammals (Melo et al., 2009; Ochoa-Ochoa et al., 2014) and also for other taxonomic groups (Heino
409 & Grönroos, 2017; Landeiro et al., 2018; Legendre & De Cáceres, 2013).

410 Regarding landscape characteristics, LCBD was significantly correlated with NDVI, tree basal
411 area, and protected area size. These first two variables may represent a gradient of habitat quality to
412 mammals, while protected area size is well recognized as a factor limiting mammal species with large
413 spatial requirements (Chiarello, 1999; Michalski & Peres, 2007; Pardini et al., 2005). Also,
414 fragmentation and habitat modification can result in environmental heterogeneity, which leads to new
415 niches available and environmental conditions that can either favour or inhibit the occurrence and
416 distribution of some mammal species, as observed for small mammals in Atlantic forest fragments
417 (Pardini et al., 2005).

418 SCBD indices identified species with a large variation in abundance across sites, and ranked
419 the eleven most important taxa contributing to variation in BD_{Total} . For example, *Myoprocta* spp. and
420 *Mazama nemorivaga* were quite abundant whenever present but occurred at only four sites, while
421 *Dasyprocta* spp., *Cuniculus paca*, *Mazama* spp., and *Dasyopus* spp. were recorded at all sites and
422 exhibited high abundances. *Leopardus pardalis*, *Tapirus* spp., *Pecari tajacu*, *Didelphis marsupialis*,
423 and *Nasua* spp. were also recorded at all sites but showed a wide variation in abundances across sites,
424 from rare to relatively common depending on the study site. In addition, our findings suggest that
425 SCBD is governed by abundance and naïve occupancy of species, while biological traits were less
426 important (based on Pseudo R^2 of our models). That is, species with high occupancy across sites and
427 high total abundance in the dataset contributed most to β -diversity. This pattern was also observed
428 for stream insect communities (Heino & Grönroos, 2017).

429 Most of the important taxa characterizing the variation among sites were herbivores (7 of 11
430 species), and at that mainly herbivore-frugivores, while carnivores contributed less to β -diversity
431 (Table S2). For those herbivore species that ranged widely in abundance across sites, we hypothesize
432 that occurrence (or absence) of apex predators may influence the abundance of herbivores. A previous
433 study comparing three of our eight sites, COU, MAN, and VB, showed a decrease in species richness
434 and occupancy of carnivores along a gradient from continuous to fragmented forest landscape
435 (Ahumada et al., 2011), which could explain these observed variations. The top-down control of large
436 carnivores influences the abundance of herbivore populations (Ripple & Beschta, 2012; Terborgh et
437 al., 1999). Also, our study sites comprise protected areas where hunting pressure had been controlled
438 or exerted in low intensity (Beaudrot et al., 2016), probably favoring herbivore species. *L. pardalis*,

439 the only carnivore contributing most to BD_{Total} , was relatively abundant across all sites and exhibited
440 even higher abundances at BCI. The high abundance of *L. pardalis* at Barro Colorado Island can be
441 attributed to different historical factors related to the formation of the island, a mesopredator release
442 phenomenon (due to the absence of a resident jaguar and puma population), high prey availability
443 and effective measures against poaching (Glanz, 1990; Moreno & Kays, 2006; Rodgers et al., 2014).

444 Studies describing SCBD for other groups also found similar positive relationships with species
445 abundance. In fact, Legendre & De Cáceres (2013) explicitly discuss that SCBD is strongly
446 influenced by abundance. However, none of the studies using their approach seems to account for
447 any bias regarding sampling methods or life history of recorded species [but see (Krasnov et al.,
448 2018)]. For mammals, for example, sampling methods including either camera trapping or line-
449 transect censuses would be fairly selective (Santos & Mendes-Oliveira, 2012), so surveying species
450 with different habits, as strictly terrestrial or arboreal species, would require using more than one
451 method. In our study, even focusing on ground-dwelling mammals, it is important to have in mind
452 that species with small home ranges have a higher detection probability, and are recorded more often
453 than species with large territories or seasonal migrants. We highlighted that our sampling effort
454 provided satisfactory estimates of species composition (Ahumada et al., 2011; Beaudrot et al., 2016)
455 and that a standardized and replicable method, as adopted in this study, is crucial to obtain reliable
456 results and provide quality information to institutions and government authorities about priority areas
457 for conservation.

458

459 4.1 Conservation implications

460

461 From a biodiversity conservation perspective, our study provides a way to identify local sites
462 (and at finer scales, each camera trap point) associated with ecological uniqueness in terms of
463 community composition. This finding suggests that species contributions to β -diversity differ in terms
464 of abundance and occupancy between fragmented and continuous forest landscapes. Most of the
465 differences among mammal communities were determined by richness differences rather than species
466 replacements, which may be caused by different historical and ecological processes leading to local
467 extinctions of specialist and rare species and compensatory increases in habitat generalists.
468 Monitoring mammal communities through LCBD and SCBD metrics may provide useful insights to
469 identify changes in the variation of community structure across spatial and temporal scales. Thus, to
470 maintain a complete regional pool of species, it is important to design management plans covering
471 both ecologically unique and species-rich sites.

472 SCBD was an important indicator of which of these species contributed most to the total
473 variation among sites, ensuring a better understanding of the processes behind β -diversity patterns.

474 We emphasize the importance of SCBD in this context, as conservation efforts can be targeted to
475 species presenting intermediate to low occupancy of sites. We thus highlight that other studies would
476 be useful to further investigate the role of environmental and spatial factors influencing the
477 uniqueness of vertebrate communities.

478

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680

SUPPORTING INFORMATION

Ecospecies	Species	BCI	CAX	CSN	COU	MAN	VB	YAN	YAS
Atelocynus microtis	Atelocynus microtis	-	X	-	X	-	-	X	X
Cabassous	Cabassous centralis	X	-	-	-	-	-	-	-
	Cabassous unicinctus	-	X	X	-	X	-	X	-
Canis latrans	Canis latrans	X	-	-	-	-	-	-	-
Coendou	Coendou prehensilis	-	-	-	-	-	-	X	-
	Coendou rothschildi	X	-	-	-	-	-	-	-
Cuniculus paca	Cuniculus paca	X	X	X	X	X	X	X	X
Dasyprocta	Dasyprocta fuliginosa	-	-	-	-	-	-	X	X
	Dasyprocta leporina	-	X	X	-	X	-	-	-
	Dasyprocta punctata	X	-	-	X	-	X	-	-
Dasypus	Dasypus kappleri	-	X	X	X	-	-	X	X
	Dasypus novemcinctus	X	X	X	X	X	X	X	X
Didelphis marsupialis	Didelphis marsupialis	X	X	X	X	X	X	X	X
Eira barbara	Eira barbara	X	X	X	X	X	X	X	X
Galictis vittata	Galictis vittata	X	-	-	-	-	-	-	X
Herpailurus yagouaroundi	Herpailurus yagouaroundi	X	X	X	X	X	-	X	X
Leopardus pardalis	Leopardus pardalis	X	X	X	X	X	X	X	X
Leopardus tigrinus	Leopardus tigrinus	-	-	X	X	-	-	-	-
Leopardus wiedii	Leopardus wiedii	X	X	X	X	X	X	X	X
Mazama	Mazama americana	-	X	X	X	X	-	X	X
	Mazama temama	X	-	-	-	-	X	-	-
Mazama nemorivaga	Mazama nemorivaga	-	X	X	-	X	-	-	X
Myoprocta	Myoprocta acouchy	-	-	X	-	X	-	-	-
	Myoprocta pratti	-	-	-	X	-	-	-	X
Myrmecophaga tridactyla	Myrmecophaga tridactyla	-	X	X	X	X	-	X	X
Nasua	Nasua narica	X	-	-	-	-	X	-	-
	Nasua nasua	-	X	X	X	X	-	X	X
Odocoileus virginianus	Odocoileus virginianus	X	-	-	-	-	X	-	-
Panthera onca	Panthera onca	-	X	X	X	X	X	X	X
Pecari tajacu	Pecari tajacu	X	X	X	X	X	X	X	X
Priodontes maximus	Priodontes maximus	-	X	X	X	-	-	-	X
Procyon cancrivorus	Procyon cancrivorus	X	-	X	X	-	-	X	X
Puma concolor	Puma concolor	-	X	X	X	X	X	X	X
Sciurus	Sciurus aestuans	-	X	X	-	X	-	-	-
	Sciurus granatensis	X	-	-	-	-	X	-	-
	Sciurus ignitus	-	-	-	X	-	-	-	-
	Sciurus igniventris	-	-	-	X	-	-	-	X
Speothos venaticus	Speothos venaticus	-	-	X	-	-	-	X	X
Sylvilagus brasiliensis	Sylvilagus brasiliensis	X	-	-	X	-	-	-	X
Tamandua	Tamandua mexicana	X	-	-	-	-	X	-	-
	Tamandua tetradactyla	-	X	X	X	X	-	X	X
Tapirus	Tapirus bairdii	X	-	-	-	-	X	-	-
	Tapirus terrestris	-	X	X	X	X	-	X	X
Tayassu pecari	Tayassu pecari	-	X	X	X	X	-	-	X
Tremarctos ornatus	Tremarctos ornatus	-	-	-	-	-	-	X	-
Urosciurus spadiceus	Urosciurus spadiceus	-	-	-	X	-	-	X	-
Species richness		21	23	26	27	21	16	24	27
Number of images		9622	3419	2918	2932	1244	1621	1945	7169
Sampling effort		7312	9175	8009	6882	3738	6232	6762	9022

Table S2 – Species recorded at eight Neotropical forest sites and its biological traits (Order, trophic guild and body mass), species metrics (Naïve occupancy and relative abundance [RAI]), and ‘species contribution to β -diversity’ (SCBD) index. Values of SCBD in bold identify the taxa that were the most important contributors to BD_{Total} (i.e., index was higher than the mean of SCBD).

Species	Order	Trophic guild	Body mass			
			(Kg)	Naive Occ	RAI	SCBD
<i>Atelocynus microtis</i>	Carnivora	Carnivore	7749.97	0.100	0.98	0.0036
<i>Cabassous spp</i>	Cingulata	Insectivore	3809.96	0.022	0.23	0.0009
<i>Canis latrans</i>	Carnivora	Carnivore	13406.33	0.018	0.03	0.0001
<i>Coendou spp</i>	Rodentia	Herbivore-browser	2000	0.017	0.03	0.0002
<i>Cuniculus paca</i>	Rodentia	Herbivore-browser	8172.55	0.533	52.40	0.1096
<i>Dasyprocta spp</i>	Rodentia	Herbivore-frugivore	2674.98	0.700	135.73	0.1094
<i>Dasytus spp</i>	Cingulata	Insectivore	6850	0.283	28.39	0.0667
<i>Didelphis marsupialis</i>	Didelphimorphia	Omnivore	1091.16	0.237	14.97	0.0540
<i>Eira barbara</i>	Carnivora	Carnivore	3910.03	0.133	3.80	0.0180
<i>Gallictis vittata</i>	Carnivora	Carnivore	3200	0.017	0.03	0.0001
<i>Herpailurus yagouaroundi</i>	Carnivora	Carnivore	6875	0.057	0.92	0.0052
<i>Leopardus pardalis</i>	Carnivora	Carnivore	11900.08	0.265	8.92	0.0324
<i>Leopardus tigrinus</i>	Carnivora	Carnivore	2250	0.054	0.09	0.0008
<i>Leopardus wiedii</i>	Carnivora	Carnivore	3249.97	0.061	1.02	0.0088
<i>Mazama nemorivaga</i>	Cetartiodactyla	Herbivore-browser	16633.17	0.373	8.01	0.0373
<i>Mazama spp</i>	Cetartiodactyla	Herbivore-frugivore	22799.75	0.512	36.02	0.0919
<i>Myoprocta spp</i>	Rodentia	Herbivore-frugivore	600	0.605	40.25	0.1408
<i>Myrmecophaga tridactyla</i>	Pilosa	Insectivore	22333.15	0.124	2.43	0.0147
<i>Nasua spp</i>	Carnivora	Herbivore-frugivore	3793.85	0.214	10.14	0.0336
<i>Odocoileus virginianus</i>	Cetartiodactyla	Herbivore-browser	55508.56	0.247	2.62	0.0049
<i>Panthera onca</i>	Carnivora	Carnivore	100000	0.073	1.68	0.0116
<i>Pecari tajacu</i>	Cetartiodactyla	Herbivore-browser	21266.69	0.456	42.52	0.0943
<i>Priodontes maximus</i>	Cingulata	Insectivore	45359.68	0.078	1.08	0.0065
<i>Procyon spp</i>	Carnivora	Omnivore	6949.92	0.033	0.49	0.0022
<i>Puma concolor</i>	Carnivora	Carnivore	51600.04	0.093	2.08	0.0171
<i>Sciurus spp</i>	Rodentia	Herbivore-granivore	330	0.196	6.68	0.0230
<i>Speothos venaticus</i>	Carnivora	Carnivore	5999.98	0.025	0.08	0.0005
<i>Sylvilagus brasiliensis</i>	Lagomorfa	Herbivore-browser	949.99	0.028	0.54	0.0017
<i>Tamandua spp</i>	Pilosa	Insectivore	4209.98	0.099	2.10	0.0109
<i>Tapirus spp</i>	Perissodactyla	Herbivore-browser	299999.13	0.286	11.99	0.0760
<i>Tayassu pecari</i>	Cetartiodactyla	Herbivore-frugivore	32233.69	0.167	3.66	0.0161
<i>Tremarctos ornatus</i>	Carnivora	Herbivore-frugivore	140000.63	0.018	0.01	0.0001
<i>Urosciurus spadiceus</i>	Rodentia	Herbivore-granivore	403.33	0.171	0.96	0.0070

3. Sessão II

Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests

A segunda sessão desta tese foi elaborada e formatada conforme as normas da publicação científica *Plos One*, disponível em: <https://journals.plos.org/plosone/s/submission-guidelines>. O artigo foi publicado em março/2019, disponível em: <https://doi.org/10.1371/journal.pone.0213671>

1 Prey availability and temporal partitioning modulate felid 2 coexistence in Neotropical forests

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32 **Abstract**

33 Carnivores have long been used as model organisms to examine mechanisms that allow coexistence
34 among ecologically similar species. Interactions between carnivores, including competition and
35 predation, comprise important processes regulating local community structure and diversity. We use
36 data from an intensive camera-trapping monitoring program across eight Neotropical forest sites to
37 describe the patterns of spatiotemporal organization of a guild of five sympatric cat species: jaguar
38 (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus*
39 *yagouaroundi*) and margay (*Leopardus wiedii*). For the three largest cat species, we developed multi-
40 stage occupancy models accounting for habitat characteristics (landscape complexity and prey
41 availability) and models accounting for species interactions (occupancy estimates of potential
42 competitor cat species). Patterns of habitat-use were best explained by prey availability, rather than
43 habitat structure or species interactions, with no evidence of negative associations of jaguar on puma
44 and ocelot occupancy or puma on ocelot occupancy. We further explore temporal activity patterns
45 and overlap of all five felid species. We observed a moderate temporal overlap between jaguar, puma
46 and ocelot, with differences in their activity peaks, whereas higher temporal partitioning was observed
47 between jaguarundi and both ocelot and margay. Lastly, we conducted temporal overlap analysis and
48 calculated species activity levels across study sites to explore if shifts in daily activity within species
49 can be explained by varying levels of local competition pressure. Activity patterns of ocelots,
50 jaguarundis and margays were similarly bimodal across sites, but pumas exhibited irregular activity
51 patterns, most likely as a response to jaguar activity. Activity levels were similar among sites and
52 observed differences were unrelated to competition or intraguild killing risk. Our study reveals
53 apparent spatial and temporal partitioning for most of the species pairs analyzed, with prey abundance
54 being more important than species interactions in governing the local occurrence and spatial
55 distribution of Neotropical forest felids.

56

57 **Introduction**

58 Species interactions comprise one of the most important processes maintaining the structure of
59 local biological diversity, including how species with similar ecological requirements can coexist [1].
60 Among various existing interspecific ecological relationships, competitive and predation interactions,
61 and their reciprocal effects, have the potential to affect diversity patterns equally, each of which could
62 either limit or promote coexistence [2].

63 Following the competitive exclusion principle, if two or more species locally compete for the
64 same limiting resource, then interspecific competition may exclude a particular species from the
65 community, suggesting an upper boundary in the number of species that can be accommodated within
66 a niche space [3,4]. However, competing species can coexist when diverging in their niche space,
67 partitioning one or more niche axes: space, time and food resources [5]. Although, whether the
68 ultimate outcome is either coexistence or exclusion is primarily determined by whether partitioning
69 of the dominant interactions occurs — be that competition or predation [2].

70 In mammalian communities, carnivore species are a model group to study mechanisms of
71 coexistence, because they occupy higher trophic levels and exhibit greater similarity in morphology
72 and ecological requirements [6–9]. Niche differentiation has been well documented as a mechanism
73 allowing coexistence between sympatric carnivores, for which responses to competition have been
74 attributed to their prey size spectrum [10–12], habitat preferences [13–15] and daily activity rhythms
75 [6,16–18]. Competition between carnivores and their spatial distribution may be determined by not
76 only predation on non-carnivore prey, but also the perceived or real risk of intraguild killing. Much
77 evidence is available on interspecific killing involving different pairs of coexisting carnivore species
78 [19–22], especially felids, which may have sweeping effects on carnivore community structure.
79 Carnivores' body size and morphological similarity have a strong influence on interspecific
80 competition and killing, and it is expected that interspecific interactions should be higher when
81 species pairs are closer in size [23].

82 Carnivore population density scales to prey productivity [24,25], but the high expansion of
83 human activities, conducting to habitat loss, landscape modification, poaching and human-carnivore
84 conflicts, are leading carnivores populations to decline worldwide [26–28]. As a consequence of
85 altered anthropogenic landscapes, reductions in both carnivores and prey abundance may have an
86 impact on carnivores' mechanisms of resource selection, temporal activity patterns, and space use
87 [6,26,27,29].

88 Despite the key role of trophic interactions in carnivore species coexistence, understanding how
89 much competition and risk of intraguild killing influence large carnivore assemblages remains a
90 challenge. This is mainly due to the difficulty in obtaining data across broad spatial scales required
91 to study these ecological processes, as well as sufficient records of species that frequently occur at
92 low densities and/or exhibit elusive behavior. Most studies discuss species interactions at local scales
93 (e.g.,[11,15,30]), but how predators change their behavior as they move through heterogeneous
94 landscapes remains largely unexplored. Conducting multi-site comparisons of spatial distributions
95 and activity budgets of co-existing wild cats will be important to improve understanding of
96 mechanisms of coexistence.

97 In this study, we combine data from long-term camera trap monitoring at eight protected forest
98 sites across the Neotropics. Up to six cat species could be found within each study site [31–33]: jaguar
99 (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus*
100 *yagouaroundi*), margay (*Leopardus wiedii*) and oncilla (*Leopardus tigrinus*). These species spanning
101 a wide range in bodies sizes, with jaguar and puma being the large predators (31-158 kg and 29-120
102 kg, respectively) and ocelot, jaguarundi, margay and oncilla figuring as smaller cat species (8-15 kg,
103 4.5-9 kg, 3-9 kg, and 1.5-3kg, respectively) [13,34–38].

104 We investigated patterns of niche differentiation between five of the six cat species (excluding
105 oncilla due to limited records) occurring at our Neotropical forest sites (Fig 1), focusing on
106 mechanisms of coexistence at sites under varying levels of integrity. Our study areas are under
107 different landscape contexts (i.e. fragmented or intact forests), and contain different species

108 compositions and abundances of felids and their prey base [31,33]. We used the following
109 approaches: (1) occupancy modelling, as a measure of habitat use, to identify which characteristics
110 (landscape complexity and prey availability) influence habitat use of jaguar, puma and ocelot; (2)
111 occupancy modelling incorporating occupancy estimates of potential competitive cat species to
112 explore spatial co-occurrence among the same three largest Neotropical cats; (3) modelling of
113 temporal activity patterns of the five species (jaguar, puma, ocelot, jaguarundi and margay) to assess
114 and quantify overlaps in temporal activity between felids pairs that are more closely matched in size;
115 (4) modelling of temporal activity patterns within Neotropical cat species to compare temporal
116 activity patterns and activity levels across study sites with differing felid assemblages and potential
117 levels of competition.

118

119 **Fig 1. Target Neotropical cat species and summary hypotheses.** From large to smaller species: A
120 – Jaguar, B – Puma; C – Ocelot, D – Jaguarundi, and E – Margay. Spatial partitioning hypothesis
121 (including jaguar, puma and ocelot): 1) prey availability would be more important in determining
122 felid habitat use than landscape covariates; 2) based on body weight ratios, jaguar exert negative
123 effects on puma and ocelot, and puma exerts negative effects on ocelot. Temporal partitioning
124 hypothesis (including all five species): higher temporal segregation between species pairs
125 experiencing higher chances of competition. Black arrows indicate strong relationship and grey
126 arrows indicate weaker relationship. Photos by: CAX (A, C and E), COU (B) and YAN (D).

127

128 Competition and interspecific killing are predicted according to body weight relationships.
129 Food competition should be higher when the larger species was less than twice the size of the smaller
130 one [23], while the intensity of interspecific killing should reach a maximum when the larger species
131 is 2.0 - 5.4 times as large as the smaller one [21]. Based on that, pumas and jaguars are more likely
132 to compete for food as they have similar body sizes and their distribution are modulated by similar
133 prey [6,11]. The same relationship is expected among ocelot, jaguarundi and margay [6,8]. In

134 addition, jaguars and pumas should exert a strong killing pressure on the ocelot and, in turn, ocelots
135 on the two smaller species, jaguarundi and margay [6].

136 We hypothesized that there would be spatial segregation among the three largest cats, with
137 large-bodied prey availability being a key factor for jaguar and puma, and small-bodied prey
138 availability for ocelot; but we expected that puma, being a subordinate competitor of jaguar, will vary
139 in its selection of optimal habitat as an avoidance response to jaguar [39]. We therefore hypothesized
140 negative effects of jaguar on puma and ocelot occupancy, negative effects of puma on ocelot, and
141 neutral effects of either puma or ocelot on jaguar occupancy. Regarding temporal interactions, we
142 hypothesized, all else being equal, higher temporal segregation between species pairs experiencing
143 higher chances of competition and intraguild killing (i.e., jaguar-puma and puma-ocelot higher than
144 jaguar-ocelot; and ocelot-jaguarundi and jaguarundi-margay higher than ocelot-margay). Lastly, we
145 are interested if differences within species across sites would be explained by competition pressure,
146 and we hypothesized that there would be temporal shifts, on both activity patterns and activity levels,
147 within the same species between study sites due to low or high occurrence of large predators.

148

149 **Methods**

150 **Study Sites**

151 We used data from eight Neotropical forest sites distributed across six countries in Central and
152 South America (Table 1; Fig 2). Data are part of the Tropical Ecology Assessment and Monitoring
153 (TEAM) Network, a global standardized monitoring program for terrestrial vertebrates based on
154 camera-trapping.

155 **Table 1. Location and area of the eight Neotropical forest sites analysed in this paper.**

Code	Study site, Country	Longitude, Latitude	Area (ha)	Landscape type ^a
BCI	Barro Colorado Nature Monument, Panama	-79.851, 9.092	32631.22	FR
CAX	Caxiuanã National Forest, Brazil	-51.534, -1.775	471192.63	CF
COU	Cocha Cashu - Manu National Park, Peru	-71.409, -11.843	1704505.53	CF
CSN	Central Suriname Nature Reserve, Suriname	-56.207, 4.741	1630233.61	CF
MAN	Manaus, Brazil	-59.935, -2.415	1198944.01	FR
VB	Volcan Barva Transect, Costa Rica	-84.021, 10.422	49502.04	FR
YAN	Yanachaga National Park, Peru	-75.303, -10.316	293234.07	FR
YAS	Yasuni Research Station, Ecuador	-76.458, -0.609	1040686.74	CF

156 ^aClassification based on [33]: FR – fragmented forest and CF – continuous forest.

157

158 **Fig 2. Location of the eight Neotropical study sites and a map of a typical camera trap array at**
 159 **Caxiuanã National Forest (CAX), Brazil.** Each point represents a camera trap location. Camera
 160 traps are distributed in two sampling arrays of 30 camera traps each (North and South of Caxiuanã
 161 River) See site codes on Table 1.

162

163 Our study sites consist of intact protected forest landscapes, in which formal protected areas
 164 were either indistinguishable from the continuous forest in surrounding areas (i.e., CAX, COU, CSN,
 165 and YAS) or fragmented forest landscapes in which protected areas were embedded within a
 166 patchwork mosaic of forest and non-forest areas (i.e., BCI, MAN, VB, and YAN) (See categorization
 167 criteria for landscapes in [33]).

168

169 **Data collection**

170 We collected data on five Neotropical cats, *Panthera onca* (jaguar), *Puma concolor* (puma),
 171 *Leopardus pardalis* (ocelot), *Herpailurus yagouaroundi* (jaguarundi), and *Leopardus wiedii*
 172 (margay), following the standardized TEAM protocol for monitoring terrestrial vertebrates [40,41].

173 The sampling design consisted of a set of regular grids of 60 camera trap stations at a density of one
174 camera per 2 km² (spaced approx. 1.4 km apart), corresponding to a sampling area of \approx 120 km² at
175 each site (Fig 2). Camera traps were deployed once a year at the same camera trap station, remaining
176 in the field for at least 30 days (ranged 30-60 days) during the dry season at each site (or months with
177 <200 mm mean rainfall). Each year of survey (i.e, 60 camera traps X 30 days) was defined as a
178 sampling period.

179 The total number of sampling period varies between study sites (2 – 10 years of data), because
180 monitoring protocol was implemented in different moments at each site. Therefore for occupancy
181 modeling, we performed exploratory analysis to select the ideal time interval to group the data for
182 analysis, and then used five sampling periods at each study site (except for Manaus where only two
183 surveys were available) (Table 2, See Data Analysis for details). Camera traps (Models RM45 and
184 HC500, Reconyx Inc.) were setup to take three pictures per trigger with no delay between photos,
185 working 24 hours/day. No baits were used to attract animals (Detailed information about the
186 implementation protocol is available on [40,41]).

187 In addition to the target species' data, we collected information on prey species of jaguar, puma,
188 and ocelot using the images from the camera traps. The use of camera trap images to assess prey
189 availability has been adopted in previous carnivore studies, for both occupancy [8,42,43] and
190 detection probabilities [44]. This was possible because the method allows recording a wide range of
191 ground-dwelling mammals and birds, most of them medium to large-sized species. Data from
192 mammals and birds with body size < 1Kg, recognized as jaguarundis and margays' prey [8,10,34],
193 were not recorded because their occurrence would be probably under-represented given the method
194 used [40].

195 **Covariates**

196 For each camera trap station we recorded variables associated with landscape complexity
197 (elevation range, distance to the nearest water source, slope and the Normalized Difference Vegetation
198 Index - NDVI), food resources (prey availability) and species interactions (occupancy estimates of
199 potentially competing cat species). Elevation and slope data were calculated using a digital elevation
200 model (DEM) based on the NASA Shuttle Radar Topographic Mission (SRTM), with spatial
201 resolution of one arc-second ($\approx 30\text{m}$). Elevation range was obtained by the difference between the
202 higher and lower elevation of camera traps station within each study site. Normalized Difference of
203 Vegetation Index (NDVI), was generated from eMODIS NDVI scenes (Vegetation monitoring). We
204 obtained the mean NDVI at a buffer of a 500 meters radius around each camera trap point. Data of
205 DEM and eMODIS were downloaded from the U.S. Geological Survey [45] and the estimates were
206 made using QGIS software [46]. Distance to the nearest water source (river/streams) was estimated
207 using hydrological shapefiles from HydroSHEDS [47] in QGIS software [46] and the R package
208 *Fossil* [48].

209 Prey availability at each camera trap station was inferred using the camera data of potential
210 prey species (ground-dwelling mammals and birds; See S1 Table for prey species list at each site).
211 Firstly, prey images were separated assuming a 1-hour interval between consecutive photos to ensure
212 the records were independent [49,50]. Prey availability was defined as the ratio between the total
213 number of prey records and the sampling effort for each camera trap station in each sampling period
214 [51–53]. We subdivided prey species into two categories [44]: 1) Large-bodied prey: mammals and
215 birds with a body mass greater than 15 kg, and 2) Small-bodied prey, mammals and birds with a body
216 mass less than 15 kg. These categories are based on dietary preferences of jaguar and puma (which
217 mostly consume medium to large-bodied prey [54,55]), and ocelot (which consume small to medium-
218 bodied prey [10,18]). Prey body mass data were obtained from the EltonTraits1.0 database that
219 includes information on key descriptors of the foraging ecology of birds and mammals [56]. We

220 normalized all covariates and used Spearman's rank correlations to test for collinearity. Only
 221 covariates with low correlation ($\rho > 0.70$) were used (S2 Table).

222

223 Data analysis

224

225 Spatial partitioning

226 We used single-species occupancy models with a likelihood-based approach to estimate the
 227 occupancy (ψ) of jaguar, puma and ocelot, and assess habitat use and intraguild interactions, while
 228 accounting for detection probability [57,58]. Because data for jaguarundi, margay, and oncilla were
 229 restrict to few records in most of the study sites and/or species were not recorded during consecutive
 230 sampling periods (preventing species pairs comparisons), we did not perform occupancy analysis for
 231 these three smaller cats (Information about detections and relative abundance were given at Table 2).

232

Table 2. Sampling period analysed, sampling effort, number of detections (Detc), records per 100 CT/days (RAI), and estimated occupancy probability¹ (ψ) from single-season models of the Neotropical cats' species in eight protected forest sites.

Site	Number of Sampling periods (years)	Effort	Jaguar			Puma			Ocelot			Jaguarundi			Margay			Oncilla		
			Detc	RAI	Ψ (\pm SE)	Detc	RAI	Ψ (\pm SE)	Detc	RAI	Ψ (\pm SE)	Detc	RAI	Ψ	Detc	RAI	ψ	Detc	RAI	ψ
BCI	5 (2010–2014)	9199	0	-	-	0	-	-	196	2.13	0.74 (0.17)	10	0.11	-	4	0.04	-	0	-	-
CAX	5 (2010–2015)	11395	36	0.32	0.45 (0.14)	58	0.51	0.43 (0.03)	43	0.38	0.57 (0.09)	2	0.02	-	28	0.25	-	0	-	-
COU	5 (2011–2015)	9481	46	0.49	0.50 (0.16)	45	0.47	0.46 (0.03)	283	2.98	0.67 (0.14)	9	0.09	-	9	0.09	-	6	0.06	-
CSN	5 (2008–2012)	11107	39	0.35	0.47 (0.16)	39	0.35	0.43 (0.04)	127	1.14	0.60 (0.10)	22	0.20	-	33	0.30	-	2	0.02	-
MAN	2 (2010–2011)	4600	10	0.22	0.34 (0.09)	5	0.11	0.37 (0.06)	18	0.39	0.63 (0.09)	4	0.09	-	0	0	-	0	-	-
VB	5 (2012–2016)	6971	2	0.03	-	37	0.53	-	21	0.30	0.62 (0.11)	0	-	-	1	0.01	-	1	0.01	-
YAN	5 (2011–2015)	8249	23	0.28	0.37 (0.08)	17	0.21	0.47 (0.03)	60	0.73	0.60 (0.09)	16	0.19	-	7	0.08	-	0	-	-
YAS	5 (2012–2016)	11833	30	0.25	0.62 (0.18)	54	0.46	0.43 (0.04)	167	1.41	0.66 (0.12)	18	0.15	-	17	0.14	-	0	-	-

¹Occupancy probability and standard deviation estimated by model averaging.

233

234 We organized the detection histories of each species by dividing each of the sampling periods
235 into sampling occasions of five days each [53]. We adopted a single-season analytical approach,
236 wherein data from five sampling periods at each study site were stacked, as independent surveys in
237 modelling procedures. Single-season modelling was chosen because our data were too sparse to fit
238 multi-season occupancy models, which estimates additional parameters (colonization/extinction).
239 Also, this was based on the assumption that annual variation in detection probability and occupancy
240 (and the relationship between occurrence and habitat covariates) would be minimal over the time-
241 frame of the study. We therefore developed models to formally assess the effect of time (multiple
242 sampling periods) in occupancy and detection. We allowed ψ (ψ) to be constant and to vary
243 according to study site and time (i.e., sampling period) or a combination of both, and then we assumed
244 the same for detection probability (p) using all possible combinations between parameters and
245 covariates. Model selection results provided no evidence that time had a marked influence on
246 occupancy and detection probabilities (S3 Table). From this, we relaxed the basic occupancy
247 modelling assumption that sites are closed to population changes [58,59] and broadly interpreted
248 occupancy as a measure of local habitat use, instead to “true occupancy”, considering that the
249 presence of a species at a camera trap station occurs completely by chance [57].

250 We used a multi-stage approach while modelling the occupancy of each cat species (similar to
251 [9,60]). We first built models to find the main covariates influencing for detection probability prior
252 to performing model selection to investigating habitat use [57]. We constrained occupancy to be
253 constant (ψ (.)) and allowed p to vary by a single covariate or a combination of covariates (additive
254 effects) [57]. The covariates used in detection (p) models reflect habitat characteristics and/or access
255 to resources that likely to affect animal behavior and, consequently, species’ detection. We also
256 introduced a categorical variable, referring to “study site”, which account for factors that can
257 influence detection due to slightly different field procedures and local habitat characteristics.
258 Covariates for p were: elevation range, NDVI, large-bodied prey availability for jaguar and puma
259 models, and small-bodied prey availability for ocelot models, and study site.

260 For the next stage, we developed a second model set to determine the most influential habitat
261 factors for occupancy. We allowed ψ to vary by a single covariate or a combination of two covariates,
262 and fixed detection covariate(s) to those selected from the previous step for each species. We selected
263 covariates for occupancy models that may reflect habitat preferences: elevation range, distance to the
264 nearest water source, NDVI, availability of small-bodied prey and large-bodied prey. We
265 hypothesized that prey availability would have a positive effect on habitat use, with large-bodied prey
266 being a key factor for jaguar and puma, and small-bodied prey for ocelot. We were interested in the
267 possible difference between the two most similar species (jaguar and puma), so we expected that
268 puma will vary in its selection of optimal habitat.

269 Finally, in a third step we used single-species occupancy models to examine species co-
270 occurrence by including occupancy estimates of jaguar, puma and ocelot from previous step as a
271 potential covariate in predicting occupancy. By assuming that the influence of larger-bodied species
272 is more intense on smaller ones, either by interference competition or interspecific killing [6,19,23],
273 we built models to examine if habitat use is significantly influenced by the occurrence of a reciprocal
274 competitor. In this way, for example, if jaguar are significantly influencing the spatial distribution
275 (and hence habitat use) of puma or ocelot, then we would expect a significant association in the model.
276 We therefore hypothesized negative effects of jaguar on puma and ocelot, negative effects of puma
277 on ocelot, and neutral effects of either puma or ocelot on jaguar occupancy. We evaluated species
278 interactions models including the most supported habitat models ($\Delta AIC < 2$ from step 2) in the model
279 set for each species, and comparing AIC values and models weights [9,61].

280 We assessed candidate models and estimated parameters for each modelling step using the R
281 package *Unmarked* [62,63]. We performed a multi-model selection procedure based in Akaike's
282 Information Criterion (AIC) and model fits were evaluated using the overdispersion parameter (\hat{c}) on
283 the saturated model (including all covariates, e.g., ψ (small+large+elevation+dist.water+ndvi)) by
284 running a goodness-of-fit test [57,61]. Models with $\Delta AIC < 2$ were considered to have substantial
285 support and \hat{c} was used to correct AIC for overdispersion (QAIC) [61]. When several models

286 obtained AIC support, we applied model averaging to obtain occupancy and detection estimates,
287 using the R package *AICcmodavg* [61,64].

288 Additionally, we assessed the relative importance of each covariate by summing the Akaike
289 weights ($AIC_{wt}/QAIC_{wt}$) of all the models in which that covariate was present [61]. When models set
290 do not contain the same number of each covariate, we divided the cumulative model weights for a
291 particular variable by the number of models containing that variable to get an average weight
292 ($AIC_{wt}/QAIC_{wt}$) [61]. We used beta coefficients to determine whether the influence of a covariate
293 was negative or positive and calculated the 95% confidence intervals for the model averaged
294 estimates to discriminate the importance of individual variables [57,61,64]. When 95% CIs of beta
295 estimates did not include 0, we concluded that the given covariate has a strong effect on habitat use
296 [61].

297

298 **Temporal partitioning**

299 We used time and date recorded in the images of all camera traps and surveys to describe daily
300 activity patterns, activity levels and temporal overlap. Analyses were performed when species
301 presented a minimum of ten images at each study site [65]. Time of day was converted to solar time
302 (i.e., adjusted according to sunrise and sunset) and anchored in the equinoctial algorithm ($\pi/2$ and
303 $\pi*3/2$) for all study sites, allowing the comparison between different time zones [66,67], using the
304 *Insol* package in R [66].

305 Activity pattern (i.e., distribution of activity of an animal throughout the day) was estimated
306 using the Kernel circular density function [68,69]. To quantify overlap between daily activities we
307 used the overlap coefficient (Δ), which varies from 0 (no overlap) to 1 (total overlap). We used Δ_1
308 and Δ_4 estimators when the number of images was <75 and ≥ 75 , respectively [69,70]. Confidence
309 intervals were obtained from 999 smoothed bootstrap samples. Analyses were conducted using the
310 *Overlap* and *Activity* packages in R [70,71]. As the overlap coefficient is a descriptive method, we

311 compared the activity patterns of each species pairs using Watson's two-sample test (U^2) in the
312 *Circular* package, which is a homogeneity test for circular data, where values for U^2 inform if two
313 samples belong to the same parent population (H_0) or differ significantly [65,72]. Based on
314 morphometric similarity and greater probability of competition and intraguild killing [23], we
315 hypothesized higher temporal segregation between species pairs experiencing higher chances of
316 competition.

317 Finally, we investigated whether activity patterns and activity levels (i.e., proportion of
318 hours/day that an animal is active) within the same species across study sites can be explained by
319 competitive pressure. We expected temporal shifts within the same species between study sites due
320 to low or high occupancy of large predators. We then assumed that the pressure of competition and/or
321 killing risk would be determined by a ranking based on occupancy estimates of jaguar, puma and
322 ocelot from previous spatial analyses (and camera trap rates for jaguarundi and margay). Intra- and
323 inter-specific comparisons of activity levels were implemented using a Wald test in the *Activity*
324 package [71].

325

326 **Results**

327 Five years of camera-trapping at each of the eight study sites amounted to a total sampling effort
328 of 72,835 camera trap days across 480 camera trap stations, yielding 186 records of jaguar (*Panthera*
329 *onca*), 255 of puma (*Puma concolor*), 915 of ocelot (*Leopardus pardalis*), 81 of jaguarundi
330 (*Herpailurus yagouaroundi*), 99 of margay (*Leopardus wiedii*) and nine of oncilla (*Leopardus*
331 *tigrinus*) (Table 2).

332

333 **Spatial partitioning**

334 Detection probability – Two ‘best’ models supported large-bodied prey, study site and elevation
335 as the main predictors for jaguar detection probability, while highest-ranking models indicated large-

336 bodied prey and elevation as important in explaining puma detectability (S4 Table). For ocelot, the
337 two top-ranked models for detectability included all possible predictors. On the basis of AIC/QAIC
338 and model weights, we selected the most parsimonious model of each species while running
339 occupancy models, capturing the main features of the data [57] (S4 Table).

340 Occupancy probability - Two occupancy models were supported for jaguar in habitat models
341 set ($AIC < 2$), with a significant positive effect of large-bodied prey availability (Fig 3A and 4A; S5
342 Table). As expected, adding puma and ocelot occupancy estimates had no influence on jaguars'
343 habitat use (Fig 3B and 4B; S6 Table). Even with the covariate 'puma occupancy' being first-ranked
344 in the models set accounting for species interactions, only large-bodied prey strongly affected jaguars'
345 habitat use (based on 95% IC; Fig 4B and S6 Table).

346

347 **Fig 3 – Relative importance of environmental and interaction covariates on the habitat use of**
348 **three Neotropical forest cats:** row A – Sum of models weights ($AIC_{wt}/QAIC_{wt}$) of occupancy
349 models to assess habitat factors; row B – Sum of models weights ($AIC_{wt}/QAIC_{wt}$) of occupancy
350 models to assess both habitat factors and species interactions.

351

352 **Fig 4 - Covariates effect on habitat use of jaguar, puma and ocelot.** Beta estimates with 95% of
353 confidence interval estimated from single-season species models: row A - Beta estimates from
354 occupancy models to assess habitat factors; row B – Beta estimates from occupancy models to assess
355 both habitat factors and species interactions (The beta estimates has an effect on the dependent
356 variable when confidence interval do not include 0).

357

358 For puma, five models received support, but none of the best-ranked covariates (distance to the
359 nearest water source, NDVI, and elevation) represented a strong effect on habitat use (Fig 3A and
360 4A; S5 Table). Adding jaguar and ocelot occupancy estimates improved the fit of puma models

361 incorporating habitat covariates (Fig 3B), but both species had no significant influence on pumas'
362 habitat use (Fig 4B and S6 Table).

363 Five models had substantial support for ocelot occupancy with a positive effect of small prey
364 availability emerging as the most important predictor. Elevation, large-bodied prey, NDVI and
365 distance to nearest water source were also ranked highly, but only small-bodied prey had a significant
366 effect (Fig 3A and 4A; S5 Table). Model set accounting for species interactions also supported five
367 models, but only small-bodied prey had a large effect on ocelot occupancy, contradicting our
368 hypothesis (Fig 3B and 4B; S6 Table).

369

370 Temporal partitioning

371 There was a moderate degree of temporal overlap between jaguar, puma and ocelot activity
372 patterns, with the peaks of activity differing between most of the analyzed species pairs (Fig 5; S7
373 Table). We observed an overlap average of $\Delta = 0.69$ for jaguar-puma, $\Delta = 0.63$ for jaguar-ocelot, and
374 $\Delta = 0.66$ for puma-ocelot. Higher coefficients of overlap were observed for jaguar-puma and jaguar-
375 ocelot pairs at CSN ($\Delta > 0.79$) and lower overlap was observed for jaguar-puma at YAN ($\Delta = 0.50$)
376 and jaguar-ocelot at YAN and YAS ($\Delta < 0.50$). Considering the smaller cats, pairwise activity overlap
377 in ocelot-jaguarundi were low for all sites (average of $\Delta = 0.39$), while ocelot-margay on average
378 overlapped by $\Delta = 0.69$. Jaguarundis and margays could only be compared across two sites, but
379 showed the lowest activity overlap (mean $\Delta = 0.20$), due to their nearly opposite temporal activity
380 (Fig 6; S7 Table). Low numbers of jaguarundi and margay photographic detections prohibited
381 detailed analysis of overlap activity for all study sites, but we observed from other 6 records of
382 jaguarundi (CAX: 2; MAN: 4) and 21 records of margay (BCI: 4; COU: 9; VB: 1; YAN: 7) that
383 species were active in the same time period observed during overlap analysis described above (Fig
384 6), with jaguarundi active during daylight and margay being more active during night time.

385

386 **Fig 5. Coefficient of overlap in daily activity patterns between jaguar, puma and ocelot in**
387 **Neotropical forest sites.** X and Y axis represent time of the day and activity density, respectively.
388 Overlap is represented by blue shaded areas and Δ is the coefficient of overlap (varying from 0 – no
389 overlap to 1 – total overlap). (*) indicates significant differences. Study site is indicated in the top left
390 corner.

391

392 **Fig 6. Coefficient of overlap in daily activity patterns between ocelot, jaguarundi and margay**
393 **in Neotropical forest sites.** X and Y axis represent time of the day and activity density, respectively.
394 Overlap is represented by blue shaded areas and Δ is the coefficient of overlap (varying from 0 – no
395 overlap to 1 – total overlap). (*) indicates significant differences. Study site is indicated in the top left
396 corner.

397

398 Examining temporal shifts within the same species across study sites, we observed that jaguars
399 were mainly active during the day at CAX, YAN and YAS sites (>60% of activity between 06:00h
400 and 18:00h), but exhibited a cathemeral activity pattern at CSN. Nevertheless, differences were only
401 significant when these sites were compared with COU, where jaguar exhibited a nocturnal peak (40%
402 of activity between 18:00h – 00:00h) (Fig 7; S8 Table). Puma showed a non-uniform pattern, showing
403 different activity peaks across sites (Fig 7). Overlap within puma populations was on average $\Delta =$
404 0.71 (range = 0.50 – 0.88) and activity pattern differed significantly (S8 Table).

405

406 **Fig 7. Intraspecific variation in daily activity patterns in felid species across eight Neotropical**
407 **forest sites.** X and Y axis represent time of the day and activity density, respectively.

408

409 Ocelots were mainly active during crepuscular and nocturnal periods (>60% of activity between
410 18:00h and 06:00h). The only exception was CSN, where ocelots showed a cathemeral pattern.
411 Temporal overlap within ocelots across sites was high (mean $\Delta = 0.79$; range = 0.67 – 0.88).

412 Jaguarundis exhibited a completely diurnal pattern across all sites with a bimodal activity peaks
413 around dawn and dusk, while margays were strictly nocturnal (~70% of activity between 18:00h and
414 06:00h). Both species showed no significant differences in their activity period across sites (Fig 7; S8
415 Table).

416 The overall activity levels (proportion of time spent active) were 0.58 (SE = 0.09) for jaguar,
417 0.47 (SE = 0.09) for puma, 0.45 (SE = 0.07) for ocelot, 0.32 (SE = 0.07) for jaguarundi and 0.33 (SE
418 = 0.07) for margay (Fig 8). Considering the effect of predator pressure, activity level of puma was
419 higher at VB, where jaguar had the lowest abundance. However, differences are statistically
420 significant only between VB and YAN sites (Wald $\chi^2 = 4.67$, $df = 1$, $p = 0.03$; S9 Table).

421 Ocelot daily activity levels were higher at CSN, which differed significantly to other sites
422 (except when compared with CAX and BCI). Ocelot activity level was also higher at BCI, where
423 large-bodied cats are missing and ocelots are essentially the top-predator. Differences were
424 statistically significant between BCI and three other sites: MAN (Wald $\chi^2 = 5.66$, $df = 1$, $p = 0.01$),
425 VB (Wald $\chi^2 = 6.30$, $df = 1$, $p = 0.01$) and YAS (Wald $\chi^2 = 10.03$, $df = 1$, $p < 0.01$).

426 Jaguarundis and margays were active for a similar proportion of time, regardless of ocelot
427 occupancy patterns. Margay activity was higher at CAX, where ocelot occupancy was lower, but
428 differences were not significant (Fig 8; S9 Table).

429

430 **Fig 8. Daily activity level of felid species across the eight Neotropical forest sites.** Proportion of
431 active hours per day. Error bars represent the standard error.

432

433 Discussion

434 Our study explored how environmental and species interactions affect the habitat use and
435 activity patterns of forest felid assemblages in the New World tropics. The patterns and assemblage
436 structure observed at our eight study sites are congruent with previous studies in Neotropical forests

437 [6,29,31], with the two large-bodied cats consistently showing their highest abundances in large tracts
438 of protected forests, the ocelots being numerically dominant at most of the sites, regardless of their
439 conservation status and forest extent, and the smaller cats appearing as less abundant species.

440

441 Species habitat use and spatial partitioning

442 Occupancy models accounting for detection probability showed evidence that niche
443 differentiation between jaguar, puma, and ocelot according to prey preferences is a potential
444 mechanism of coexistence. Jaguars and ocelots occupancy was closely related to prey availability
445 [24,55], which helps explain differences across sites. Large-bodied prey were more abundant at sites
446 where jaguar occupancy estimates were higher (e.g. YAS and COU). Conversely, low incidence of
447 large-bodied prey abundance matched low rates of jaguar occupancy (e.g. MAN and YAN). At YAN
448 site, for example, two important ungulate prey species of jaguar — brown brocket deer (*Mazama*
449 *nemorivaga*) and white-lipped peccary (*Tayassu pecari*) — failed to be recorded during the entire
450 camera trapping monitoring.

451 Even though models reflected some well-known relationships, like jaguars and pumas
452 presenting positive associations with water bodies [14,73], only prey availability emerged as an
453 important covariate in determining jaguars' space use. Puma was not significantly influenced by any
454 covariates. Also, models evaluating species interactions showed no evidence of avoidance of puma
455 to the jaguar, and vice-versa. These findings agree with other studies that shown no spatial segregation
456 between jaguars and pumas [44,74], and potentially species may adopt other mechanisms to allow
457 coexistence, as the use of different food resources and/or partitioning of their activity period
458 [6,67,75].

459 Our hypothesis that smaller-bodied predators behaviorally evade larger apex predators was
460 framed based on the notion that the local distribution of a top predator may be shaped by resource
461 availability, while the distribution of a mesopredator is largely related to predation risk [76]. Although

462 we did not find a significant influence of jaguar on the spatial distribution of puma, our results suggest
463 that jaguar selects habitats based on high prey abundance, whereas puma display sufficient plasticity
464 in habitat use, indicated by the lack of significance for any covariates in the top-ranked models, and
465 this probably reduces convergence in the use of similar resources with jaguar [15,77]. Pumas are
466 considered to be more opportunistic predators, being observed at fragmented and human-modified
467 forest landscapes, which have a heavier impact on jaguars [15,73,77].

468 Regarding ocelots, its distributions were strongly influenced by small-bodied prey rather than
469 other habitat covariates or by occupancy estimates of the two largest predators. These findings
470 supported the idea that ocelot does not meaningfully compete for food resources with either jaguar or
471 puma [18]. Competition between puma and ocelot is expected to be higher when jaguar is relatively
472 abundant [78], but competitive exclusion between these species is at best unlikely given the lack of
473 interaction we observed. Our results agree with other studies showing spatial co-occurrence between
474 pumas and ocelots [6,74], and observing that detection probability can be higher when the other
475 species were present in the same camera trap station [6]. Furthermore, ocelot occupancy was high
476 both at sites where the two largest-bodied felids were either absent (BCI) or rare (YAN and MAN),
477 but also at sites where these apex predators were relatively common (YAS and COU).

478 Our results are according with studies involving other sympatric mammalian carnivores. In
479 general, species with similar ecological requirements were often more likely to overlap spatially [7],
480 and habitat features were more important in maintaining the distribution and structure of carnivore
481 guild than species interactions [9].

482

483 Temporal partitioning

484 Another coexistence mechanism explored in our study was temporal partitioning [6,79]. In
485 support of our temporal segregation hypothesis, we observed that the activity patterns of species pairs
486 (i.e. jaguar-puma, jaguar-ocelot and puma-ocelot) overlapped to a moderate degree, and were

487 significantly different in pairwise comparisons of activity at most sites. Because of the greater
488 morphological similarity between jaguar and puma, we expected a lower degree of overlap between
489 them compared to jaguar-ocelot and puma-ocelot pairs, but this was not confirmed. However, other
490 studies observed that top predators exhibit similar daily activity cycles [44,80,81], indicating that
491 some degree of temporal overlap would be expected from the similar dietary profiles of jaguars and
492 pumas. It is more likely that the general temporal patterns can be related to the attractiveness of food
493 resources, rather than avoidance of a larger predator [11,67].

494 Jaguar and puma are able to adjust their activity to reduce their foraging energy expenditure,
495 by matching their activity to that of their main prey species [30,67]. We cannot rule out the option
496 that prey abundance and some other habitat characteristics affects temporal activity [29], and
497 consequently temporal partitioning between apex predators. Indeed, the lowest overlap between
498 jaguar and puma was observed at the Ecuadorian site (YAN, $\Delta = 0.51$). Perhaps this is likely
499 associated with the absence of some species and low abundance of large-bodied prey, as stated above.
500 Further analysis considering more detailed habitat characteristics and human disturbance factors are
501 required to understand the relationship between the daily activities of predators facing differences in
502 prey availability.

503 Considering the smaller felids, our hypotheses of low overlap in activity patterns were
504 confirmed for both the ocelot-jaguarundi and jaguarundi-margay species pairs, which are closest in
505 terms of body weights [34]. This is consistent with a study in the Brazilian Atlantic Forest [6], which
506 suggested that jaguarundis reduce interference competition with the larger ocelots, and avoid
507 competition with similarly-sized margays, by selecting opposite time-periods for their activities.
508 Also, even with ocelots and margays overlapping in their activity patterns, some adaptations for an
509 arboreal life permit the margays to explore a different niche from ocelots [34,36]. A study in Atlantic
510 forest remnant using co-occurrence analysis found no evidence that ocelot have a negative influence
511 on how the margay use the habitat [8].

512 A final approach in our activity pattern analysis was to investigate if competitive pressure, here
513 measured as occupancy of larger-bodied predators (or abundance for jaguarundi *vs* margay), could
514 explain shifts in activity patterns and levels across study sites. Daily activity patterns within pumas
515 across sites reinforced the notion that temporal shifts in jaguar activities have an impact on sympatric
516 pumas, which tends to concentrate its activities away from the peak of jaguar activity. Moreover,
517 when jaguars are virtually absent, as in VB, pumas extended their activity, with diurnal peaks between
518 mid-day and dusk. Similar results were observed in daily activities patterns of puma and leopard in
519 areas with high or low abundances of apex predators (jaguar and tiger, respectively), likely as an
520 evasive response in side-stepping direct encounters when dominant species are most active [29,82].

521 Ocelots showed temporal segregation in relation to jaguars and pumas, but temporal activities
522 were unlikely modulated by intraguild killing pressure, and nocturnal activity was also observed
523 across several Neotropical landscapes [6,12,83–85]. Degree of overlap between ocelot populations
524 did not support our hypothesis of competitive pressure, and ocelots were active during similar periods
525 of the day at BCI, where large cats are absent, VB and MAN, where detection rates were low, and
526 YAS and COU, where large cats were far more common.

527 Jaguar was active for the same proportion of time in most of the sites, as well as pumas,
528 jaguarundis and margays, and differences in activity across sites were mostly not significant. These
529 felid species were therefore active during similar amounts of time regardless of the occurrence of
530 larger predators. Despite significant differences in activity levels of ocelots, no clear pattern could be
531 identified across sites with either higher or lower occurrence of top predators. Due to the large effect
532 found between ocelots' habitat use and small-bodied prey in our occupancy analysis, we expect that
533 further studies evaluating factors other than competition pressure of a larger predator may explain
534 differences on activity levels.

535 **Conclusions**

536 This is the first study providing a large-scale insights into the co-occurrence of five forest hyper-
537 carnivore species throughout the Neotropical region, assessing patterns across protected areas of
538 differing size and intactness. We have shown that jaguar, puma and ocelot exhibit clear spatial
539 preferences at local to landscape scales according to prey availability. We found that prey availability
540 is more important for felid space-use than either landscape variables or species interactions, which
541 likely supports the notion of multi-species convergence on productive prey sites, rather than
542 competitive interactions.

543 Competition was more important in explaining spatial and temporal segregation among jaguars
544 and pumas, than between either of these apex predators and ocelot. Otherwise, interspecific
545 competition played an important role between ocelot and smaller sympatric cats [18], since both the
546 local occupancy and circadian activity rhythms of ocelots affect jaguarundi and margay.

547 A recent global-scale study of co-occurrence of sympatric carnivores found that similar-sized
548 species sharing the same temporal activity patterns and dietary habits were more likely to co-occur
549 than expected by chance [7]. Although, the study used a categorization to describe general activity
550 patterns and diet, not capturing variations on carnivores' behaviour at a particular study area. Indeed,
551 our results showed that some spatial and temporal overlapping may occur, mainly between the three
552 largest species, but go further assessing finer-scale of resource availability and diurnal rhythms,
553 detecting niche partitioning in a local scale and differences in felids' behaviour across study sites. In
554 this paper, we highlight the importance of understanding the implications of interspecific interactions
555 to conservation and management strategies, particularly in terms of rapidly declining carnivore
556 populations, which may have major impacts on the diversity of lower trophic levels [2].

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562

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773 **Supporting information list**

774 **S1 Table – Prey species list and relative abundance index (images/100 ctdays) of small (< 15 Kg)**
775 **and large prey (> 15Kg) of carnivores in our eight Neotropical study sites.**

776 **S2 Table – Spearman’s rank correlation to test for collinearity among continuous covariates**
777 **($\rho > 0.70$).**

778 **S3 Table - Model selection analysis for occupancy (Ψ) and detection probability (p) used to**
779 **evaluate the effect of time (sampling period) and study site on the habitat use of three sympatric**
780 **felids, the jaguar (*Panthera onca*), puma (*Puma concolor*) and ocelot (*Leopardus pardalis*) in**
781 **Neotropical forests.**

782 **S4 Table - Single-species detection models used to evaluate the effects of covariates on the**
783 **detection probability (p) of three sympatric felids, the jaguar (*Panthera onca*), puma (*Puma***
784 ***concolor*) and ocelot (*Leopardus pardalis*) in Neotropical forests. Detection probability was**
785 **modelled as a function of elevation, NDVI, study site (site), large prey availability (large) for jaguar**
786 **and puma models and small prey availability (small) for ocelot models, or as a constant ($p(\cdot)$).**

787 **S5 Table - Single-species occupancy models used to evaluate the effects of elevation (Elev.),**
788 **distance to nearest water source (water), NDVI (ndvi), small prey’s availability (small) and**
789 **large prey’s availability (large) on the habitat use of jaguar (*Panthera onca*), puma (*Puma***
790 ***concolor*) and ocelot (*Leopardus pardalis*) in Neotropical forests.**

791 **S6 Table - Single-species occupancy models used to evaluate best habitat factors and species**
792 **interactions. Occupancy probability was modelled as a function of elevation (Elev.), distance to**
793 **water (water), NDVI (ndvi), small prey’s availability (small), large prey’s availability (large) and**
794 **occupancy estimates of each cat species (jaguar, puma and ocelot).**

795 **S7 Table - Coefficient of overlap (Δ) with confidence intervals (CI lower/CI upper) and**
796 **Watson's two-sample test (two-sample U_2) performed on pairwise comparisons between cat**
797 **species per site.**

798 **S8 Table - Coefficient of overlap (Δ_1) with confidence intervals (CI lower/CI upper) and**
799 **Watson's two-sample test (two-sample U_2) performed on pairwise comparisons between study**
800 **sites.**

801 **S9 Table - Differences in the daily activity level (*i. e.*, proportion of hours per day that an animal**
802 **is active), standard errors (SE), Wald test (W) of Neotropical cats across the eight study sites**
803 **(*Significant difference <0.05).**

FIGURES

Fig 1

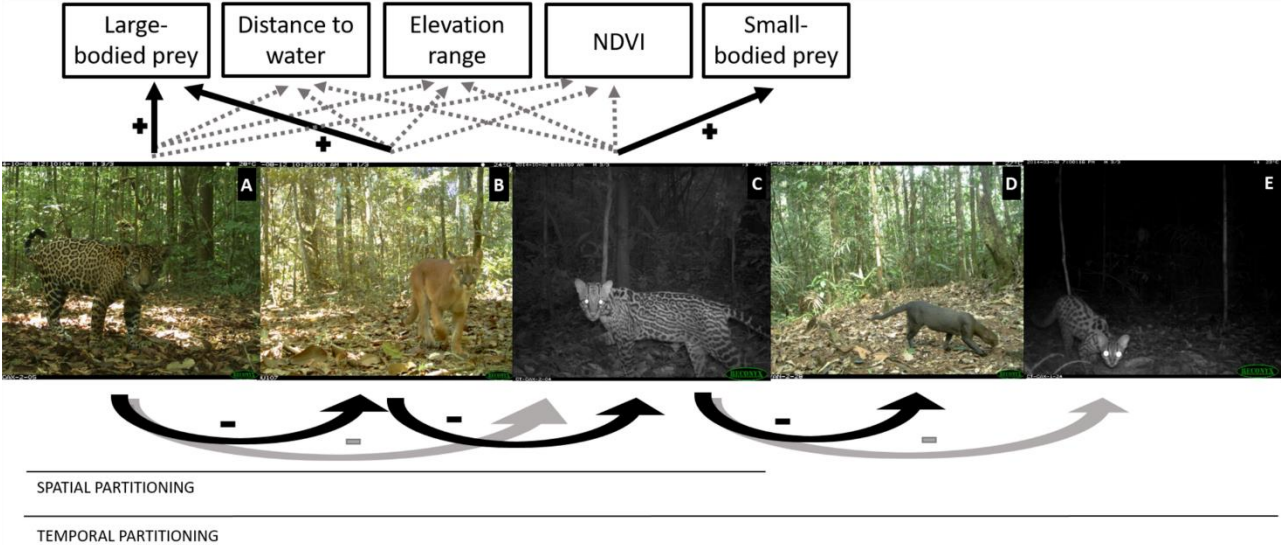


Fig 2

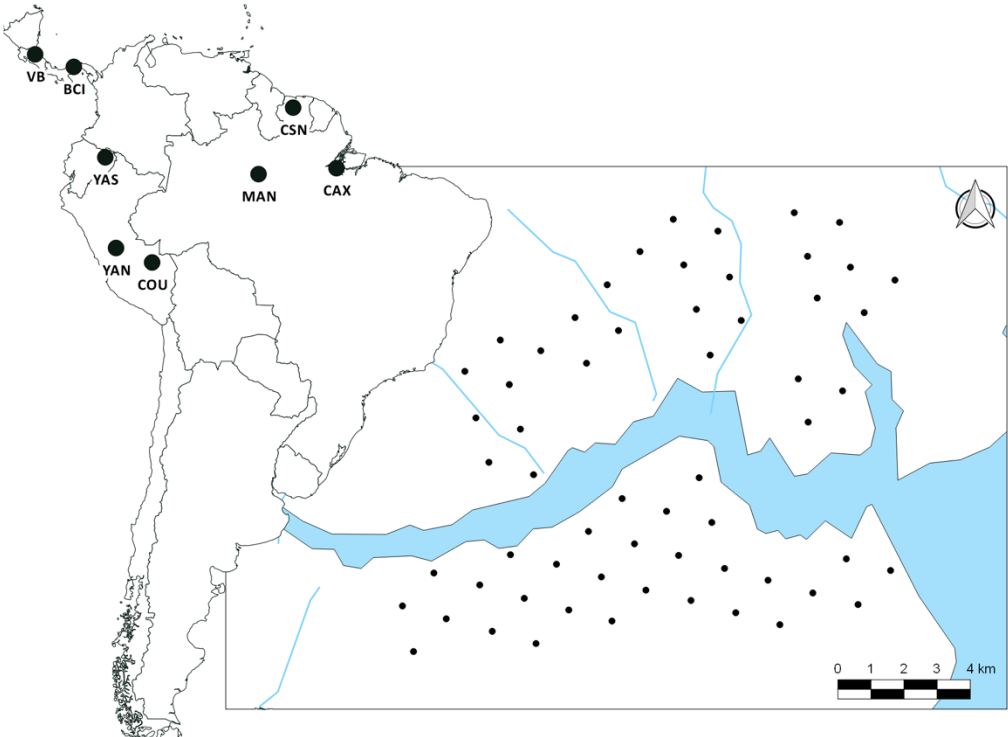


Fig 3

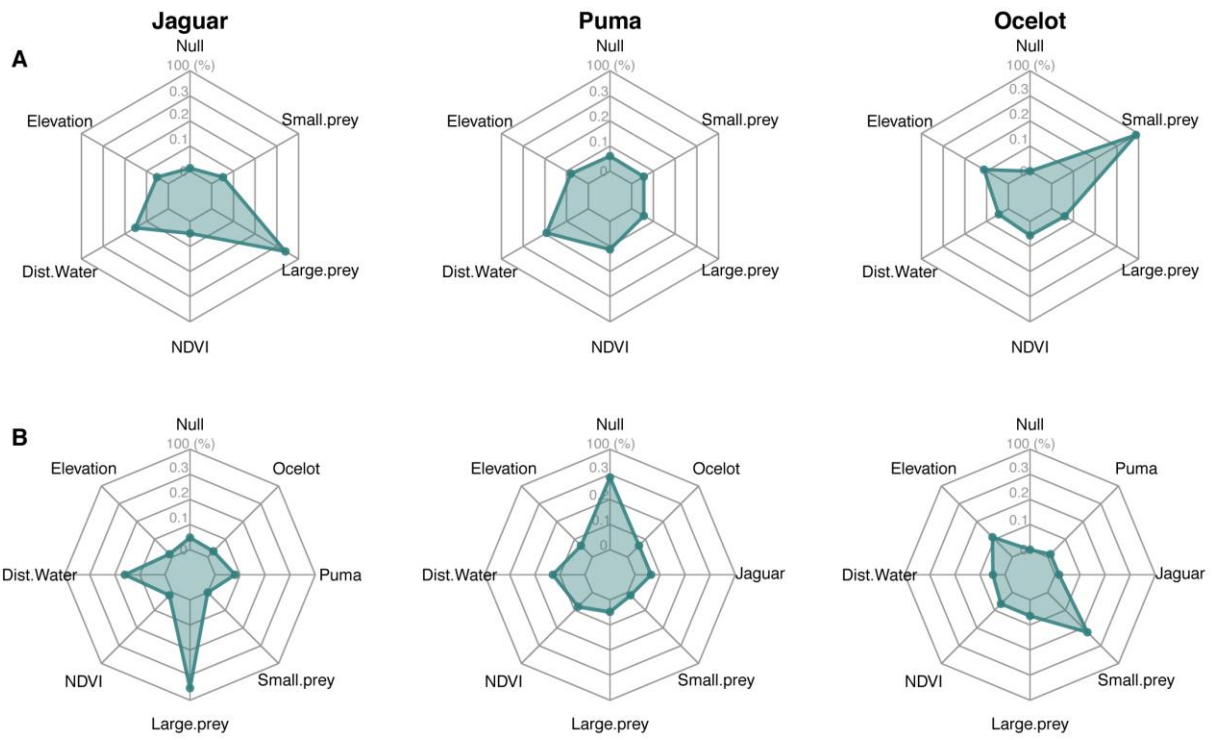


Fig 4

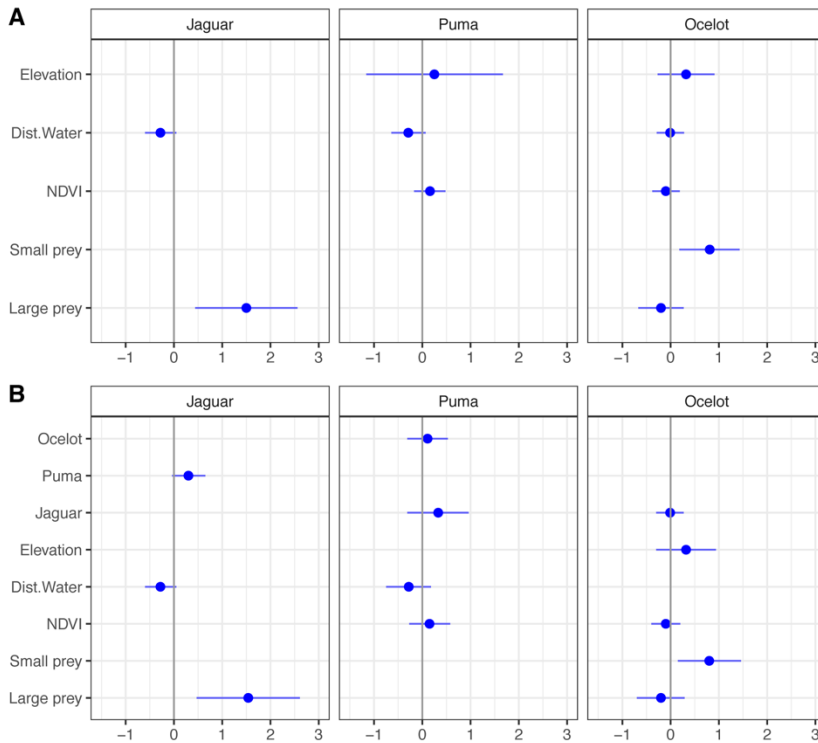


Fig 5

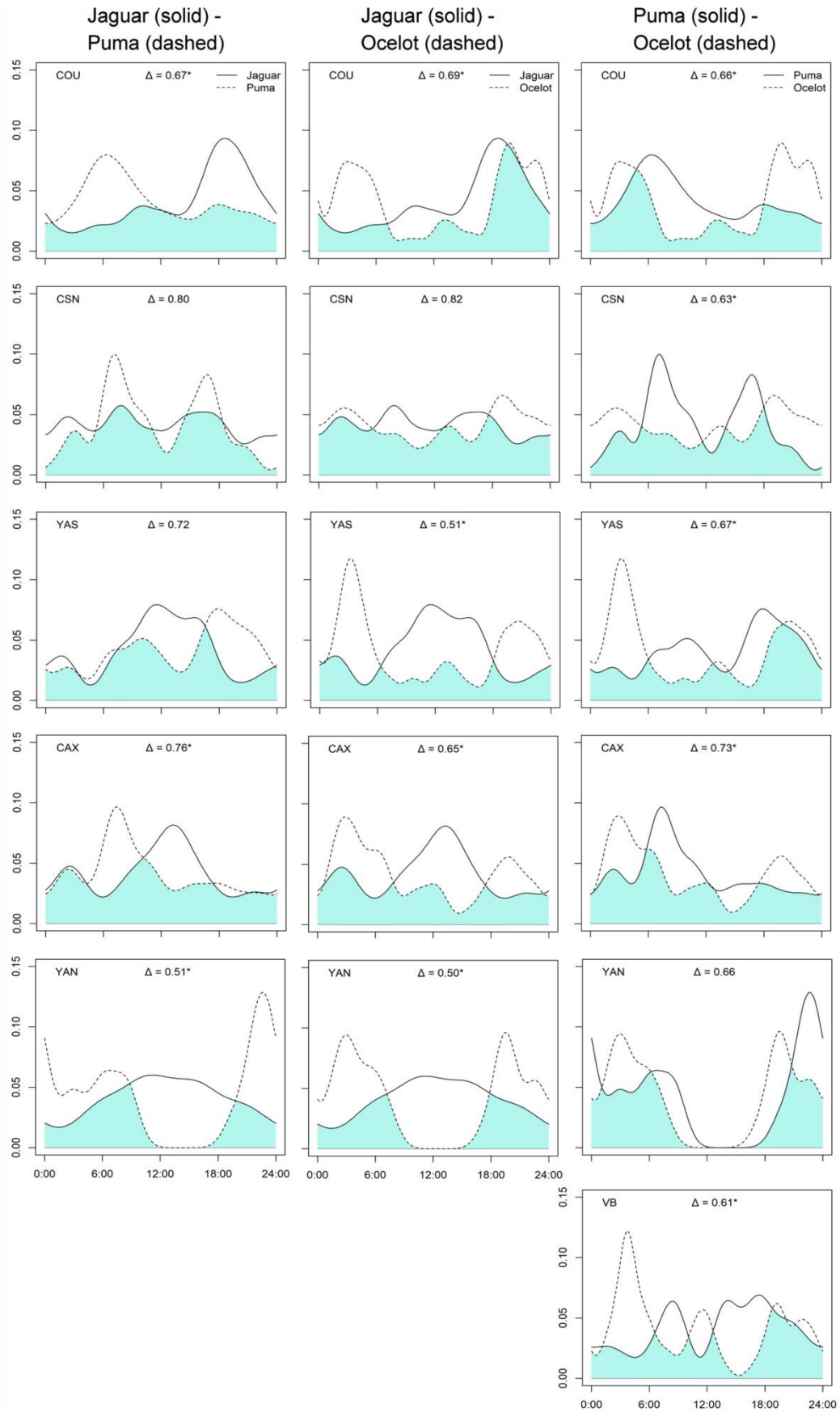


Fig 6

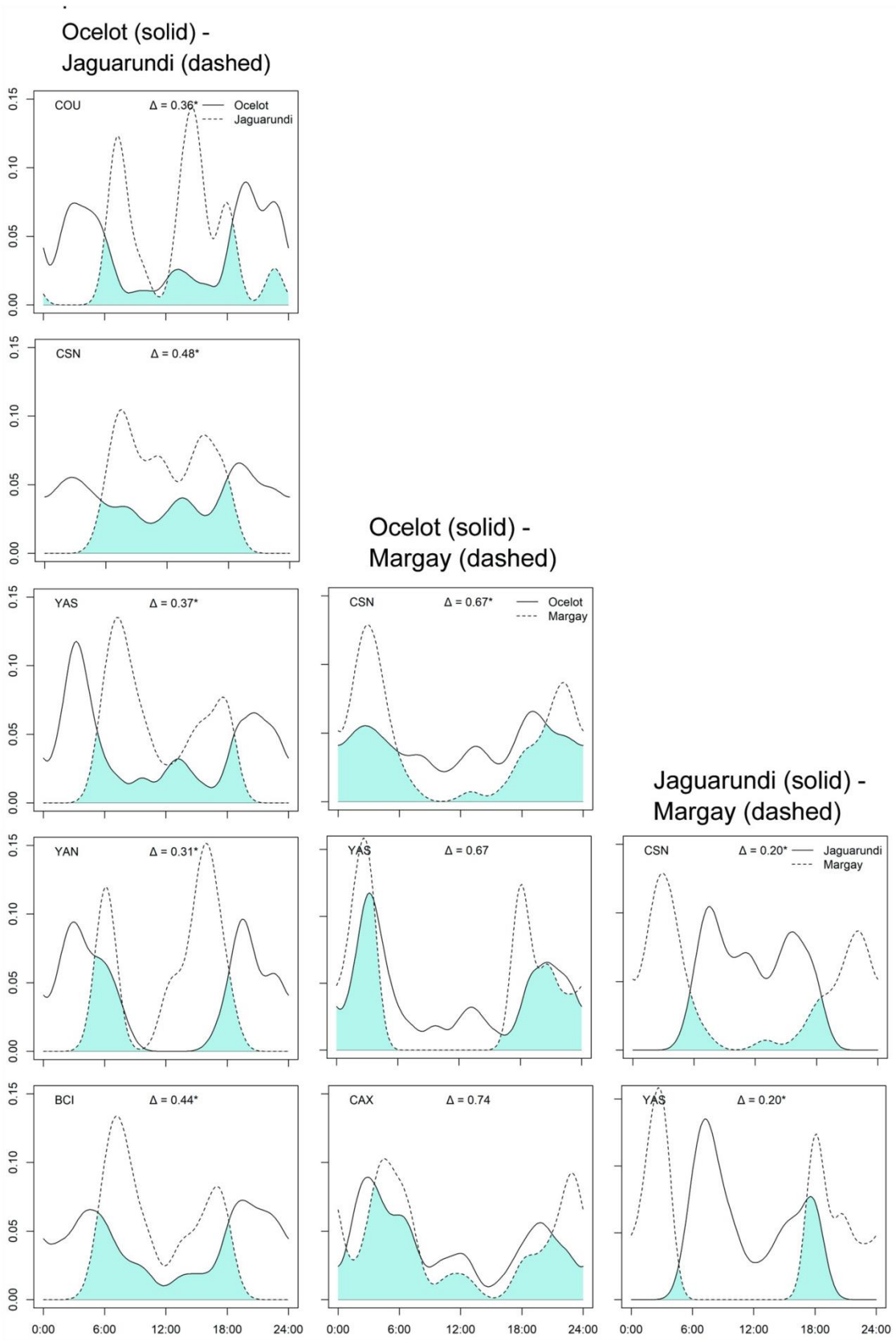


Fig 7

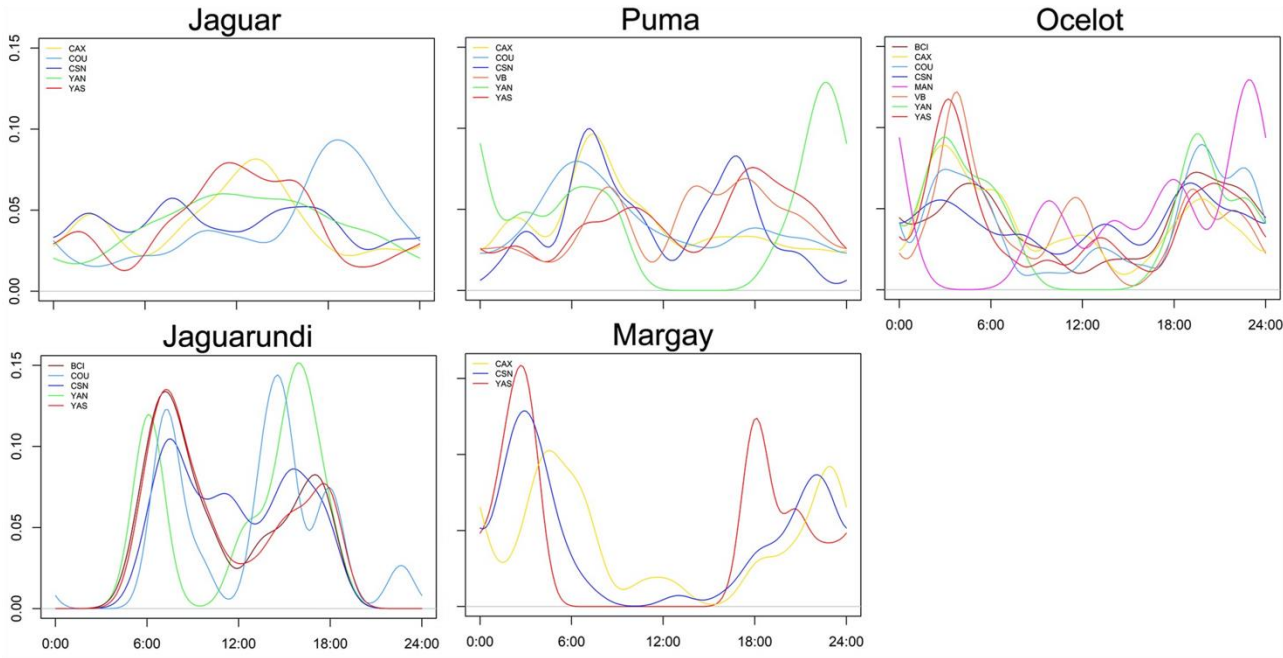
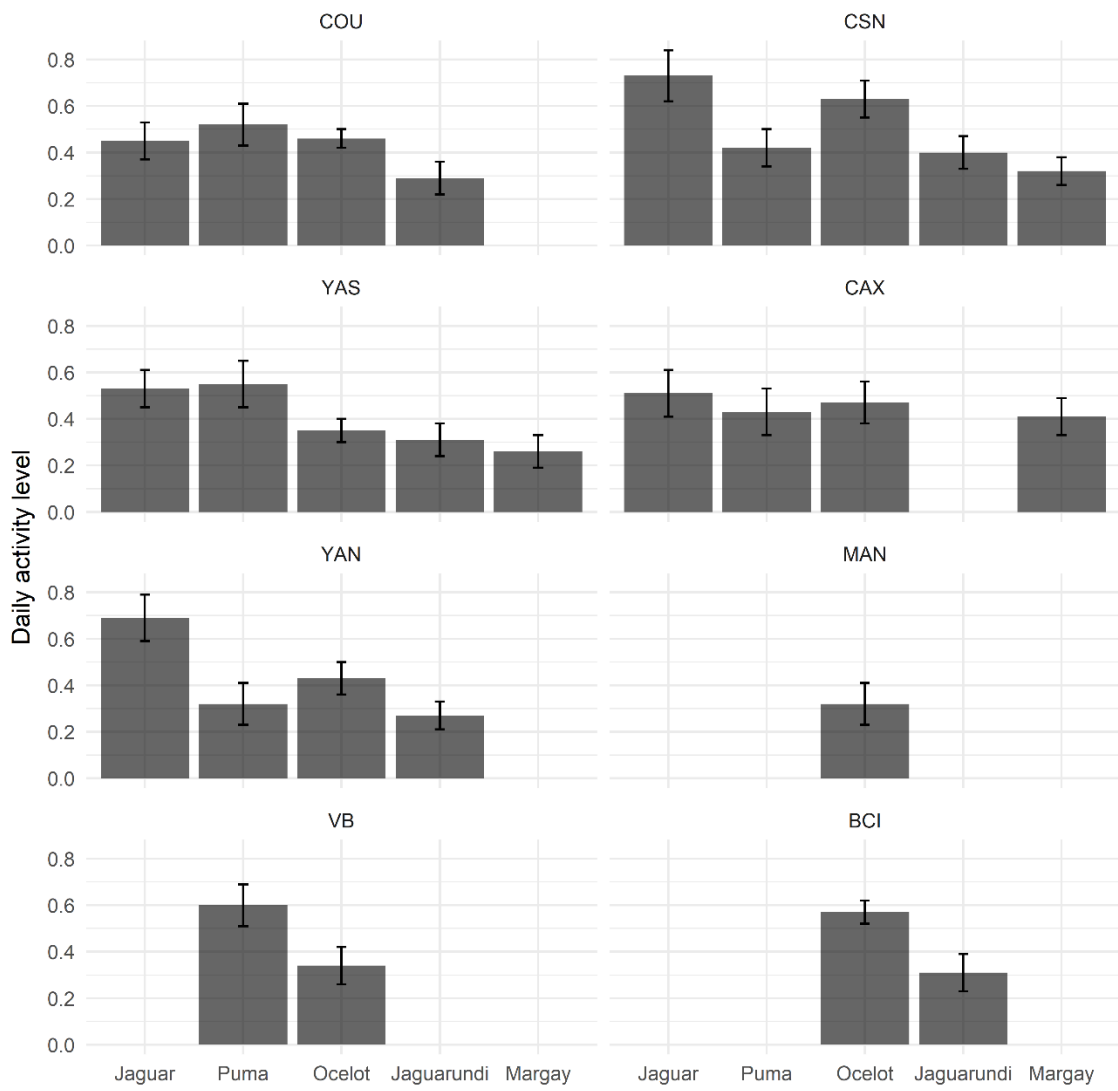


Fig 8



SUPPORTING INFORMATION

S1 Table – Prey species list and relative abundance index (images/100 ctdays) of small-bodied prey (< 15 Kg) and large-bodied prey (> 15Kg) of carnivores in our eight Neotropical forest study sites. Site codes: BCI - Barro Colorado Nature Monument, CAX - Caxiuanã National Forest, COU - Cocha Cashu - Manu National Park, CSN - Central Suriname Nature Reserve, MAN – Manaus, VB - Volcan Barva Transect, YAN - Yanachaga National Park, YAS - Yasuni Research Station.

Species	BCI	CAX	COU	CSN	MAN	VB	YAN	YAS
<i>Small prey - mammals</i>								
<i>Cabassous centralis</i>	0.13	-	-	-	-	-	-	-
<i>Cabassous unicinctus</i>	-	0.02	-	-	0.02	-	0.01	-
<i>Caluromys derbianus</i>	-	-	-	-	-	0.03	-	-
<i>Cuniculus paca</i>	8.27	2.79	7.55	3.45	2.63	3.36	12.83	8.59
<i>Dasyprocta fuliginosa</i>	-	-	-	-	-	-	6.46	15.13
<i>Dasyprocta leporina</i>	-	13.60	-	10.53	5.76	-	-	-
<i>Dasyprocta punctata</i>	52.67	-	9.93	-	-	2.93	-	-
<i>Dasypus kappleri</i>	-	2.74	0.37	1.30	-	-	0.36	1.36
<i>Dasypus novemcinctus</i>	3.96	2.21	1.11	2.27	3.09	1.45	2.44	4.10
<i>Didelphis marsupialis</i>	3.27	1.61	2.36	1.66	3.74	0.20	0.48	0.29
<i>Marmosa demerarae</i>	-	0.01	-	-	0.02	-	-	-
<i>Marmosa murina</i>	-	-	-	0.02	-	-	-	-
<i>Marmosa regina</i>	-	-	0.02	-	-	-	-	-
<i>Marmosa robinsoni</i>	0.03	-	-	-	-	-	-	-
<i>Metachirus nudicaudatus</i>	0.26	0.96	-	1.34	5.57	-	0.01	0.19
<i>Monodelphis breviceaudata</i>	-	-	-	0.01	-	-	-	-
<i>Monodelphis glirina</i>	-	-	0.13	-	-	-	-	-
<i>Myoprocta acouchy</i>	-	-	-	6.17	17.52	-	-	-
<i>Myoprocta pratti</i>	-	-	4.86	-	-	-	-	11.38
<i>Nasua narica</i>	4.92	-	-	-	-	0.30	-	-
<i>Nasua nasua</i>	-	0.73	0.23	0.08	0.15	0.00	1.29	0.58
<i>Philander opossum</i>	0.18	-	0.75	1.27	0.78	0.03	-	-
<i>Proechimys breviceauda</i>	-	-	12.48	-	-	-	-	-
<i>Proechimys guyannensis</i>	-	-	-	1.24	-	-	-	-

<i>Proechimys semispinosus</i>	3.87	-	0.02	-	-	0.01	-	-
<i>Proechimys sp</i>	-	0.30	2.63	-	0.07	-	0.22	0.11
<i>Sciurus aestuans</i>	-	0.03	-	0.07	0.09	-	-	-
<i>Sciurus granatensis</i>	0.93	-	-	-	-	-	-	-
<i>Sciurus ignitus</i>	-	-	2.08	-	-	-	0.01	-
<i>Sciurus igniventris</i>	-	-	0.01	-	-	-	-	2.19
<i>Sciurus spadiceus</i>	-	-	0.27	-	-	-	0.59	-
<i>Sciurus variegatoides</i>	-	-	-	-	-	0.01	-	-
<i>Sylvilagus brasiliensis</i>	0.13	-	0.49	-	-	-	-	0.18
<i>Tamandua mexicana</i>	0.92	-	-	-	-	-	-	-
<i>Tamandua tetradactyla</i>	-	0.19	0.08	0.04	0.13	-	0.07	0.19
<i>Tylomys watsoni</i>	-	-	-	-	-	-	0.24	-
Small prey - birds								
<i>Crax alector</i>	-	-	-	2.30	1.39	-	-	-
<i>Crax rubra</i>	0.50	-	-	-	-	0.53	-	-
<i>Crypturellus atrocapillus</i>	-	-	0.03	-	-	-	-	-
<i>Crypturellus bartletti</i>	-	-	0.77	-	-	-	-	0.02
<i>Crypturellus cinereus</i>	-	-	0.19	0.04	-	-	-	0.02
<i>Crypturellus soui</i>	-	-	1.02	0.02	-	-	0.01	0.06
<i>Crypturellus strigulosus</i>	-	0.04	-	-	-	-	-	-
<i>Crypturellus undulatus</i>	-	-	0.17	-	-	-	-	0.01
<i>Crypturellus variegatus</i>	-	0.19	0.21	0.36	0.87	-	-	0.32
<i>Geotrygon frenata</i>	-	-	-	-	-	-	0.15	-
<i>Geotrygon montana</i>	0.43	0.05	0.15	0.37	1.65	-	-	1.34
<i>Geotrygon saphirina</i>	-	-	-	-	-	-	-	0.02
<i>Geotrygon violacea</i>	-	-	0.02	0.11	-	-	-	-
<i>Leptotila cassini</i>	0.93	-	-	-	-	-	-	-
<i>Leptotila rufaxilla</i>	-	-	1.11	0.51	-	-	-	0.13
<i>Leptotila verreauxi</i>	0.03	-	-	-	0.11	-	-	0.03
<i>Mitu salvini</i>	-	-	-	-	-	-	-	0.98
<i>Mitu tuberosum</i>	-	1.23	5.32	-	-	-	4.56	-
<i>Odontophorus gujanensis</i>	0.02	-	-	0.09	0.04	-	-	0.16

<i>Odontophorus stellatus</i>	-	-	0.50	-	-	-	-	-
<i>Penelope jacquacu</i>	-	-	0.25	0.05	-	-	0.19	0.37
<i>Penelope marail</i>	-	-	-	0.01	-	-	-	-
<i>Penelope pileata</i>	-	0.04	-	-	-	-	-	-
<i>Penelope purpurascens</i>	0.05	-	-	-	-	-	-	-
<i>Penelope superciliaris</i>	-	0.06	-	-	-	-	-	-
<i>Pipile cumanensis</i>	-	-	0.01	-	-	-	-	-
<i>Pipile pipile</i>	-	-	-	-	-	-	-	0.03
<i>Psophia crepitans</i>	-	-	-	5.19	4.59	-	-	7.32
<i>Psophia leucoptera</i>	-	-	7.97	-	-	-	-	-
<i>Psophia viridis</i>	-	3.48	-	-	-	-	-	-
<i>Tinamus guttatus</i>	-	0.10	0.06	-	-	-	0.05	0.08
<i>Tinamus major</i>	2.34	0.05	2.12	2.00	1.91	-	0.06	1.66
<i>Tinamus tao</i>	-	0.18	0.70	-	-	-	0.99	-
SMALL PREY - SUB-TOTAL	83.86	30.59	65.96	40.47	50.13	8.85	31.03	56.82
Large prey - mammals								
<i>Hydrochoerus hydrochaeris</i>	-	-	0.02	-	-	-	-	-
<i>Hydrochoerus isthmus</i>	0.01	-	-	-	-	-	-	-
<i>Mazama americana</i>	-	4.67	6.28	6.69	1.96	-	1.01	9.57
<i>Mazama nemorivaga</i>	-	2.85	-	1.42	1.33	-	-	2.80
<i>Mazama temama</i>	3.32	-	-	-	-	2.34	-	-
<i>Myrmecophaga tridactyla</i>	-	0.57	0.51	0.42	0.28	-	0.15	0.59
<i>Odocoileus virginianus</i>	1.64	-	-	0.04	-	0.10	-	-
<i>Pecari tajacu</i>	9.31	1.82	2.77	1.49	1.96	14.53	0.64	8.80
<i>Priodontes maximus</i>	-	0.11	0.36	0.42	-	-	-	0.30
<i>Tapirus bairdii</i>	0.01	-	-	-	-	2.01	-	-
<i>Tapirus terrestris</i>	-	0.90	2.87	2.58	0.41	-	1.90	2.61
<i>Tayassu pecari</i>	-	0.18	0.57	0.23	0.15	-	-	2.28
LARGE PREY SUB-TOTAL	14.30	11.09	13.37	13.29	6.09	18.98	3.70	26.94
TOTAL	98.16	41.68	79.34	53.76	56.22	27.83	34.73	83.76

S2 Table – Spearman’s rank correlation to test for collinearity among continuous covariates ($\rho > 0.70$).

	Small prey	Large prey	Elevation range	Dist.to water	NDVI	Slope
Small prey	1	0.55	-0.11	-0.01	0.00	-0.13
Large prey	0.55	1	-0.16	0.00	-0.03	-0.16
Elevation range	-0.11	-0.16	1	-0.07	-0.10	0.86
Distance to water	-0.01	0.00	-0.07	1	-0.07	-0.11
NDVI	0.00	-0.03	-0.10	-0.07	1	-0.11
Slope	-0.13	-0.16	0.86	-0.11	-0.11	1

S3 Table - Model selection analysis for occupancy (Ψ) and detection probability (p) used to evaluate the effect of time (sampling period) and study site on the habitat use of three sympatric felids, the jaguar (*Panthera onca*), the puma (*Puma concolor*) and the ocelot (*Leopardus pardalis*) in Neotropical forests.

Models						
Jaguar	K	AIC	ΔAIC	AIC_{wt}	CumltvWt	Rsqr
$\Psi(\cdot)p(\cdot)$	2	1824.31	0	0.50	0.5	0.00
$\Psi(\text{site})p(\cdot)$	7	1824.58	0.27	0.43	0.93	0.01
$\Psi(\text{time})p(\cdot)$	28	1828.79	4.48	0.05	0.98	0.04
$\Psi(\cdot)p(\text{time})$	28	1831.61	7.3	0.01	0.99	0.04
$\Psi(\text{site})p(\text{site})$	12	1833.3	8.99	0.01	1	0.01
$\Psi(\text{time})p(\text{site})$	33	1837.32	13.01	0.00	1	0.05
$\Psi(\text{time})p(\text{time})$	54	1860.46	36.15	0.00	1	0.06
Puma	K	QAIC	ΔQAIC	QAIC_{wt}	Cum.Wt	Quasi.LL
$\Psi(\text{site})p(\cdot)$	8	1102.06	0.00	0.87	0.87	-543.03
$\Psi(\text{site})p(\text{site})$	13	1106.83	4.78	0.08	0.95	-540.42
$\Psi(\cdot)p(\cdot)$	3	1107.62	5.56	0.05	1.00	-550.81
$\Psi(\text{time})p(\cdot)$	29	1133.97	31.91	0.00	1.00	-537.98
$\Psi(\cdot)p(\text{time})$	29	1135.39	33.33	0.00	1.00	-538.69
$\Psi(\text{time})p(\text{site})$	34	1138.75	36.69	0.00	1.00	-535.37
Ocelot	K	QAIC	ΔQAIC	QAIC_{wt}	Cum.Wt	Quasi.LL
$\Psi(\text{site})p(\text{site})$	17	4816.73	0.00	1.00	1.00	-2391.36
$\Psi(\cdot)p(\text{time})$	39	4833.67	16.95	0.00	1.00	-2377.84
$\Psi(\text{time})p(\text{site})$	46	4842.27	25.54	0.00	1.00	-2375.13
$\Psi(\text{site})p(\cdot)$	10	4869.07	52.34	0.00	1.00	-2424.53
$\Psi(\text{time})p(\text{time})$	75	4886.52	69.79	0.00	1.00	-2368.26
$\Psi(\text{time})p(\cdot)$	39	4895.88	79.16	0.00	1.00	-2408.94
$\Psi(\cdot)p(\cdot)$	3	5016.47	199.75	0.00	1.00	-2505.24

S4 Table - Single-species detection models used to evaluate the effects of covariates on the detection probability (p) of three sympatric felids, the jaguar (*Panthera onca*), puma (*Puma concolor*) and ocelot (*Leopardus pardalis*) in Neotropical forests. Detection probability was modelled as a function of elevation range (elevation), NDVI (ndvi), study site (site), large-bodied prey availability (large) for jaguar and puma models and small-bodied prey availability (small) for ocelot models, or as a constant ($p(\cdot)$).

Models	Beta estimates (\pm SE)						
	K	AIC	Δ AIC	AICwt	Large prey	Elev.	NDVI
JAGUAR							
$\psi(\cdot)p(\text{site+large})$	8	1816.89	0	0.42	0.44 (0.14)	-	-
$\psi(\cdot)p(\text{large+elevation})$	4	1818.45	1.57	0.19	0.30 (0.12)	-0.19 (0.12)	-
$\psi(\cdot)p(\text{large})$	3	1819.28	2.4	0.13	0.33 (0.11)	-	-
$\psi(\cdot)p(\text{large+elevation+site+ndvi})$	10	1819.91	3.03	0.09	0.45 (0.14)	0.16 (0.18)	-0.04 (0.09)
$\psi(\cdot)p(\text{large+ndvi})$	4	1820.73	3.84	0.06	0.34 (0.11)	-	0.06 (0.08)
$\psi(\cdot)p(\text{elevation})$	3	1821.36	4.47	0.05	-	-0.24 (0.12)	-
$\psi(\cdot)p(\text{elevation+ndvi})$	4	1823.2	6.31	0.02	-	-0.24 (0.12)	0.03 (0.08)
$\psi(\cdot)p(\text{site})$	7	1823.99	7.1	0.01	-	-	-
$\psi(\cdot)p(\cdot)$	2	1824.31	7.42	0.01	-	-	-
$\psi(\cdot)p(\text{site+elevation})$	8	1825.13	8.24	0.01	-	-0.15 (0.17)	-
$\psi(\cdot)p(\text{site+ndvi})$	8	1825.94	9.06	0.00	-	-	-0.02 (0.09)
$\psi(\cdot)p(\text{ndvi})$	3	1825.98	9.1	0.00	-	-	0.05 (0.08)
PUMA							
$\psi(\cdot)p(\text{large+elevation})$	5	982.39	0.00	0.31	0.33 (0.11)	-0.36 (0.14)	-

$\psi(.)p(\text{elevation})$	4	984.05	1.66	0.14	-	-0.41 (0.14)	-
$\psi(.)p(\text{large})$	4	984.56	2.17	0.11	0.39 (0.11)	-	-
$\psi(.)p(\text{site+large})$	9	984.67	2.28	0.10	0.36 (0.13)	-	-
$\psi(.)p(\text{elevation+ndvi})$	5	985.07	2.68	0.08	-	-0.41 (0.14)	0.12 (0.09)
$\psi(.)p(\text{large+ndvi})$	5	985.17	2.78	0.08	0.39 (0.10)	-	0.14 (0.09)
$\psi(.)p(\text{site})$	8	985.96	3.57	0.05	-	-	-
$\psi(.)p(\text{site+ndvi})$	9	986.79	4.40	0.03	-	-	0.14 (0.10)
$\psi(.)p(\text{site+elevation})$	9	986.96	4.57	0.03	-	-0.27 (0.20)	-
$\psi(.)p(\text{large+elevation+site+ndvi})$	11	987.05	4.66	0.03	0.34 (0.12)	-0.24 (0.20)	0.11 (0.10)
$\psi(.)p(.)$	3	988.05	5.66	0.02	-	-	-
$\psi(.)p(\text{ndvi})$	4	988.76	6.37	0.01	-	-	0.14 (0.09)

OCELOT	K	AIC	ΔAIC	AICwt	Small prey	Elev.	NDVI
$\psi(.)p(\text{site+small})$	8	4663.65	0	0.67	0.14 (0.04)	-	-
$\psi(.)p(\text{small+elevation+site+ndvi})$	10	4665.12	1.47	0.32	0.14 (0.04)	0.13 (0.10)	-0.03 (0.05)
$\psi(.)p(\text{site+elevation})$	8	4673.25	9.6	0.01	-	0.14 (0.10)	-
$\psi(.)p(\text{site})$	7	4673.38	9.73	0.01	-	-	-
$\psi(.)p(\text{site+ndvi})$	8	4674.83	11.17	0.00	-	-	-0.04 (0.05)
$\psi(.)p(\text{small+elevation})$	4	4817.44	153.79	0.00	0.28 (0.05)	-0.11 (0.06)	-
$\psi(.)p(\text{small})$	3	4818.82	155.16	0.00	0.30 (0.05)	-	-
$\psi(.)p(\text{small+ndvi})$	4	4820.78	157.12	0.00	0.30 (0.05)	-	-0.01 (0.05)

$\Psi(\cdot)p(\text{elevation})$	3	4857.68	194.03	0.00	-	-0.15 (0.06)	-
$\Psi(\cdot)p(\text{elevation}+\text{ndvi})$	4	4859.62	195.97	0.00	-	-0.15 (0.06)	-0.01 (0.05)
$\Psi(\cdot)p(\cdot)$	2	4862.87	199.22	0.00	-	-	-
$\Psi(\cdot)p(\text{ndvi})$	3	4864.87	201.22	0.00	-	-	0.00 (0.05)

S5 Table - Single-species occupancy models used to evaluate the effects of elevation (Elev.), distance to nearest water source (water), NDVI (ndvi), small-bodied prey's availability (small) and large-bodied prey's availability (large) on the habitat use of jaguar (*Panthera onca*), puma (*Puma concolor*) and ocelot (*Leopardus pardalis*) in Neotropical forests.

Models		Beta estimates (\pm SE)								
Jaguar	K	AIC	Δ AIC	AIC _{w_t}	Elev.	Dist. Water	NDVI	Large prey	Small prey	
$\psi(\text{large+water})\rho(\text{large+site})$	10	1812.13	0	0.34	-	-0.28 (0.17)	-	1.54 (0.54)	-	
$\psi(\text{large})\rho(\text{large+site})$	9	1813.02	0.89	0.21	-	-	-	1.42 (0.53)	-	
$\psi(\text{large+small})\rho(\text{large+site})$	10	1814.41	2.29	0.11	-	-	-	1.38 (0.53)	0.14 (0.18)	
$\psi(\text{large+elevation})\rho(\text{large+site})$	10	1814.63	2.5	0.10	-0.14 (0.21)	-	-	1.42 (0.54)	-	
$\psi(\text{large+ndvi})\rho(\text{large+site})$	10	1814.7	2.57	0.09	-	-	0.09 (0.15)	1.49 (0.55)	-	
$\psi(\cdot)\rho(\text{large+site})$	8	1816.89	4.76	0.03	-	-	-	-	-	
$\psi(\text{global})\rho(\text{large+site})$	13	1817.01	4.88	0.03	-0.09 (0.22)	-0.27 (0.17)	0.09 (0.15)	1.55 (0.55)	0.13 (0.19)	
$\psi(\text{water})\rho(\text{large+site})$	9	1817.52	5.39	0.02	-	-0.19 (0.16)	-	-	-	
$\psi(\text{elevation})\rho(\text{large+site})$	9	1818.4	6.28	0.01	-0.18 (0.24)	-	-	-	-	
$\psi(\text{small})\rho(\text{large+site})$	9	1818.74	6.61	0.01	-	-	-	-	-0.03 (0.08)	

$\psi(\text{ndvi})p(\text{large+site})$	9	1818.82	6.69	0.01	-	-	-0.04 (0.15)	-	-
$\psi(\text{water+elevation})p(\text{large+site})$	10	1819.15	7.02	0.01	-0.17 (0.25)	-0.18 (0.16)	-	-	-
$\psi(\text{water+ndvi})p(\text{large+site})$	10	1819.45	7.32	0.01	-	-0.19 (0.16)	-0.04 (0.14)	-	-
$\psi(\text{elevation+small})p(\text{large+site})$	10	1820.22	8.1	0.01	-0.19 (0.24)	-	-	-	-0.03 (0.08)
$\psi(\text{elevation+ndvi})p(\text{large+site})$	10	1820.31	8.18	0.01	-0.19 (0.24)	-	-0.04 (0.15)	-	-
$\psi(\text{water+small})p(\text{large+site})$	10	1824.03	11.9	0.00	-	-0.20 (0.17)	-	-	0.27 (0.24)
$\psi(\text{small+ndvi})p(\text{large+site})$	10	1825.46	13.33	0.00	-	-	-0.02 (0.15)	-	0.25 (0.23)
Puma	K	QAIC	ΔQAIC	QAIC_wt	Elev.	Dist. Water	NDVI	Large prey	Small prey
$\psi(\text{water})p(\text{large+elevation})$	10	521.67	0.00	0.19	-	-0.21 (0.15)	-	-	-
$\psi(.)p(\text{large+elevation})$	11	522.58	0.92	0.12	-	-	-	-	-
$\psi(\text{water+ndvi})p(\text{large+elevation})$	11	523.26	1.59	0.09	-	-0.21 (0.15)	0.15 (0.13)	-	-
$\psi(\text{ndvi})p(\text{large+elevation})$	11	523.38	1.71	0.08	-	-	0.16 (0.13)	-	-
$\psi(\text{water+elevation})p(\text{large+elevation})$	11	523.61	1.94	0.07	-0.24 (0.23)	-0.20 (0.15)	-	-	-

$\psi(\text{elevation})p(\text{large+elevation})$	11	523.62	1.95	0.07	-0.27 (0.22)	-	-	-	-
$\psi(\text{small})p(\text{large+elevation})$	12	524.28	2.61	0.05	-	-	-	-	-0.02 (0.08)
$\psi(\text{large+water})p(\text{large+elevation})$	12	524.38	2.72	0.05	-	-0.18 (0.16)	-	0.38 (0.32)	-
$\psi(\text{large})p(\text{large+elevation})$	12	524.50	2.83	0.05	-	-	-	0.45 (0.36)	-
$\psi(\text{elevation+ndvi})p(\text{large+elevation})$	12	524.57	2.90	0.04	-0.25 (0.23)	-	0.15 (0.13)	-	-
$\psi(\text{water+small})p(\text{large+elevation})$	12	524.97	3.30	0.04	-	-0.21 (0.16)	-	-	0.24 (0.22)
$\psi(\text{large+ndvi})p(\text{large+elevation})$	12	525.21	3.54	0.03	-	-	0.17 (0.14)	0.44 (0.37)	-
$\psi(\text{elevation+small})p(\text{large+elevation})$	12	525.22	3.56	0.03	-0.27 (0.22)	-	-	-	-0.02 (0.08)
$\psi(\text{large+small})p(\text{large+elevation})$	12	525.29	3.62	0.03	-	-	-	0.41 (0.36)	0.20 (0.19)
$\psi(\text{large+elevation})p(\text{large+elevation})$	12	525.35	3.68	0.03	-0.27 (0.21)	-	-	0.45 (0.37)	-
$\psi(\text{small+ndvi})p(\text{large+elevation})$	12	525.49	3.82	0.03	-	-	0.17 (0.13)	-	0.23 (0.22)
$\psi(\text{global})p(\text{large+elevation})$	15	529.95	8.28	0.00	-0.24 (0.22)	-0.17	0.16 (0.13)	0.35 (0.33)	0.20 (0.20)

Ocelot	K	QAIC	ΔQAIC	QAIC _w	Elev.	Dist. Water	NDVI	Large prey	Small prey
ψ(small)p(site+small)	10	3549.98	0.00	0.29	-	-	-	-	0.77 (0.27)
ψ(small+elevation)p(site+small)	11	3550.10	0.11	0.28	0.32 (0.26)	-	-	-	0.85 (0.29)
ψ(small+large)p(site+small)	11	3551.34	1.36	0.15	-	-	-	-0.20 (0.21)	0.84 (0.29)
ψ(small+ndvi)p(site+small)	11	3551.46	1.48	0.14	-	-	-0.10 (0.13)	-	0.79 (0.27)
ψ(small+water)p(site+small)	11	3551.98	2.00	0.11	-	-0.01 (0.13)	-	-	0.77 (0.27)
ψ(global)p(site+small)	14	3555.21	5.22	0.02	0.31 (0.28)	-0.03 (0.14)	-0.07 (0.12)	-0.20 (0.21)	0.92 (0.31)
ψ(.)p(site+small)	9	3560.69	10.71	0.00	-	-	-	-	-
ψ(elevation)p(site+small)	10	3562.13	12.15	0.00	0.20 (0.28)	-	-	-	-
ψ(large)p(site+small)	10	3562.24	12.26	0.00	-	-	-	0.07 (0.13)	-
ψ(ndvi)p(site+small)	10	3562.40	12.42	0.00	-	-	-0.08 (0.14)	-	-
ψ(water)p(site+small)	10	3562.69	12.70	0.00	-	0.01 (0.14)	-	-	-
ψ(elevation+large)p(site+small)	11	3563.65	13.66	0.00	0.20 (0.27)	-	-	0.08 (0.14)	-

$\psi(\text{elevation+ndvi})p(\text{site+small})$	11	3563.93	13.94	0.00	0.19 (0.28)	-	-0.07 (0.14)	-	-
$\psi(\text{large+ndvi})p(\text{site+small})$	11	3563.93	13.94	0.00	-	-	-0.08 (0.14)	0.08 (0.14)	-
$\psi(\text{water+elevation})p(\text{site+small})$	11	3564.13	14.14	0.00	0.20 (0.28)	-0.01 (0.14)	-	-	-
$\psi(\text{water+large})p(\text{site+small})$	11	3564.23	14.25	0.00	-	0.02 (0.14)	-	0.08 (0.14)	-
$\psi(\text{water+ndvi})p(\text{site+small})$	11	3564.36	14.38	0.00	-	0.03 (0.15)	-0.09 (0.16)	-	-

S6 Table - Single-species occupancy models used to evaluate best habitat factors and species interactions. Occupancy probability (Ψ) was modelled as a function of elevation (Elev.), distance to the nearest water source (water), NDVI (ndvi), small-bodied prey's availability (small), large-bodied prey's availability (large) and occupancy estimates of each cat species (jaguar, puma and ocelot).

Models	Beta estimates (\pm SE)											
	Jaguar	K	AIC	Δ AIC	AIC _{wt}	Elev.	Dist. Water	NDVI	Large prey	Small prey	Puma	Ocelot
$\psi(\text{puma+large})\rho(\text{large+site})$		10	1811.85	0	0.33	-	-	-	1.60 (0.55)	-	0.30 (0.18)	-
$\psi(\text{large+water})\rho(\text{large+site})$		10	1812.13	0.28	0.29	-	-0.28 (0.17)	-	1.54 (0.54)	-	-	-
$\psi(\text{large})\rho(\text{large+site})$		9	1813.02	1.17	0.19	-	-	-	1.42 (0.54)	-	-	-
$\psi(\text{ocelot+large})\rho(\text{large+site})$		10	1814.88	3.03	0.07	-	-	-	1.40 (0.53)	-	-	0.06 (0.15)
$\psi(\cdot)\rho(\text{large+site})$		8	1816.89	5.04	0.03	-	-	-	-	-	-	-
$\psi(\text{puma})\rho(\text{large+site})$		9	1817.86	6.01	0.02	-	-	-	-	-	0.17 (0.16)	-
$\psi(\text{ocelot})\rho(\text{large+site})$		9	1818.46	6.61	0.01	-	-	-	-	-	-	0.09 (0.14)
$\psi(\text{global})\rho(\text{large+site})$		15	1819	7.15	0.01	0.38 (1.02)	2.63 (4.37)	-0.91 (1.25)	1.43 (0.64)	8.86 (7.76)	3.18 (4.62)	-5.87 (5.03)
$\psi(\text{ocelot+water})\rho(\text{large+site})$		10	1819.04	7.19	0.01	-	-0.19 (0.16)	-	-	-	-	0.10 (0.14)
$\psi(\text{puma+ocelot})\rho(\text{large+site})$		10	1819.37	7.52	0.01	-	-	-	-	-	0.17 (0.16)	0.10 (0.14)

$\psi(\text{puma}+\text{elevation})\rho(\text{large}+\text{site})$	10	1819.38	7.53	0.01	-0.19 (0.24)	-	-	-	-	0.17 (0.16)	-
$\psi(\text{puma}+\text{water})+\rho(\text{large}+\text{site})$	10	1819.42	7.57	0.01	-	-0.35 (0.55)	-	-	-	-0.17 (0.56)	-
$\psi(\text{puma}+\text{ndvi})+\rho(\text{large}+\text{site})$	10	1819.5	7.65	0.01	-	-	-0.09 (0.15)	-	-	0.20 (0.17)	-
$\psi(\text{ocelot}+\text{elevation})\rho(\text{large}+\text{site})$	10	1819.98	8.13	0.01	-0.18 (0.24)	-	-	-	-	-	0.09 (0.14)
$\psi(\text{ocelot}+\text{ndvi})\rho(\text{large}+\text{site})$	10	1820.4	8.55	0.00	-	-	-0.03 (0.15)	-	-	-	0.09 (0.14)
$\psi(\text{ocelot}+\text{small})\rho(\text{large}+\text{site})$	10	1822.82	10.97	0.00	-	-	-	-	2.56 (1.85)	-	-1.67 (1.23)
$\psi(\text{puma}+\text{small})\rho(\text{large}+\text{site})$	10	1824.29	12.44	0.00	-	-	-	-	0.27 (0.24)	0.19 (0.17)	-
Puma	K	QAIC	ΔQAIC	QAIC_{wt}	Elev.	Dist. Water	NDVI	Large prey	Small prey	Jaguar	Ocelot
$\psi(\cdot)\rho(\text{large}+\text{elevation})$	5	664.24	0.00	0.19	-	-	-	-	-	-	-
$\psi(\text{water})\rho(\text{large}+\text{elevation})$	6	664.69	0.46	0.15	-	-0.29 (0.14)	-	-	-	-	-
$\psi(\text{ndvi})\rho(\text{large}+\text{elevation})$	6	665.65	1.41	0.09	-	-	0.16 (0.12)	-	-	-	-
$\psi(\text{jaguar})\rho(\text{large}+\text{elevation})$	6	665.92	1.69	0.08	-	-	-	-	-	0.32 (0.18)	-
$\psi(\text{ocelot})\rho(\text{large}+\text{elevation})$	6	665.99	1.75	0.08	-	-	-	-	-	-	0.10 (0.12)

$\psi(\text{water}+\text{ndvi})\text{p}(\text{large}+\text{elevation})$	7	666.19	1.96	0.07	-	-0.28 (0.14)	0.15 (0.12)	-	-	-	-
$\psi(\text{water}+\text{elevation})\text{p}(\text{large}+\text{elevation})$	7	666.62	2.39	0.06	0.25 (0.54)	-0.29 (0.14)	-	-	-	-	-
$\psi(\text{jaguar}+\text{water})+\text{p}(\text{large}+\text{elevation})$	7	667.10	2.86	0.05	-	-0.22 (0.14)	-	-	-	0.21 (0.22)	-
$\psi(\text{jaguar}+\text{ndvi})+\text{p}(\text{large}+\text{elevation})$	7	667.29	3.06	0.04	-	-	0.18 (0.13)	-	-	0.34 (0.18)	-
$\psi(\text{jaguar}+\text{large})\text{p}(\text{large}+\text{elevation})$	7	667.43	3.19	0.04	-	-	-	-0.32 (0.39)	-	0.32 (0.28)	-
$\psi(\text{jaguar}+\text{small})\text{p}(\text{large}+\text{elevation})$	7	667.65	3.41	0.03	-	-	-	-	0.16 (0.17)	0.32 (0.17)	-
$\psi(\text{jaguar}+\text{ocelot})\text{p}(\text{large}+\text{elevation})$	7	667.65	3.42	0.03	-	-	-	-	-	0.30 (0.18)	0.11 (0.13)
$\psi(\text{jaguar}+\text{elevation})\text{p}(\text{large}+\text{elevation})$	7	667.91	3.67	0.03	0.11 (0.51)	-	-	-	-	0.32 (0.18)	-
$\psi(\text{ocelot}+\text{elevation})\text{p}(\text{large}+\text{elevation})$	7	667.95	3.72	0.03	0.16 (0.52)	-	-	-	-	-	0.10 (0.12)
$\psi(\text{ocelot}+\text{large})\text{p}(\text{large}+\text{elevation})$	7	668.28	4.04	0.03	-	-	-	0.43 (0.32)	-	-	0.13 (0.13)
$\psi(\text{ocelot}+\text{ndvi})\text{p}(\text{large}+\text{elevation})$	7	673.63	9.39	0.00	-	-	-26.22 (22.56)	-	-	-	4.76 (3.36)
$\psi(\text{ocelot}+\text{water})\text{p}(\text{large}+\text{elevation})$	7	673.68	9.44	0.00	-	68.27 (80.56)	-	-	-	-	3.49 (4.87)

$\psi(\text{ocelot+small})p(\text{large+elevation})$	7	675.26	11.02	0.00	-	-	-	-	9.26 (39.79)	-	-10.16 (41.61)
$\psi(\text{global})p(\text{large+elevation})$	12	675.34	11.10	0.00	0.09 (0.59)	-0.30 (0.17)	0.16 (0.13)	-0.10 (0.34)	-0.11 (0.55)	0.03 (0.30)	0.22 (0.45)
Ocelot	K	QAIC	ΔQAIC	QAIC_{wt}	Elev.	Dist. Water	NDVI	Large prey	Small prey	Jaguar	Puma
$\psi(\text{small})p(\text{site+small})$	10	3196.69	0.00	0.25	-	-	-	-	0.77 (0.27)	-	-
$\psi(\text{small+elevation})p(\text{site+small})$	11	3197.00	0.30	0.22	0.32 (0.26)	-	-	-	0.85 (0.29)	-	-
$\psi(\text{small+large})p(\text{site+small})$	11	3198.11	1.42	0.12	-	-	-	-0.20 (0.21)	0.84 (0.29)	-	-
$\psi(\text{small+ndvi})p(\text{site+small})$	11	3198.22	1.53	0.12	-	-	-0.10 (0.13)	-	0.79 (0.27)	-	-
$\psi(\text{jaguar+small})p(\text{site+small})$	11	3198.68	1.99	0.09	-	-	-	-	0.78 (0.28)	-0.01 (0.12)	-
$\psi(\text{puma+small})p(\text{site+small})$	11	3198.69	2.00	0.09	-	-	-	-	0.77 (0.27)	-	-0.01 (0.14)
$\psi(\text{small+water})p(\text{site+small})$	11	3198.69	2.00	0.09	-	-0.01 (0.13)	-	-	0.77 (0.27)	-	-
$\psi(\text{global})p(\text{site+small})$	16	3203.55	6.86	0.01	0.68 (0.46)	-2.09 (2.28)	0.54 (0.64)	-0.71 (0.28)	1.01 (0.33)	0.36 (0.18)	-2.29 (2.44)
$\psi(.)p(\text{site+small})$	9	3206.13	9.43	0.00	-	-	-	-	-	-	-

$\psi(\text{jaguar})p(\text{site+small})$	10	3207.78	11.09	0.00	-	-	-	-	-	0.09 (0.13)	-
$\psi(\text{puma})p(\text{site+small})$	10	3208.10	11.41	0.00	-	-	-	-	-	-	-0.03 (0.15)
$\psi(\text{jaguar+elevation})p(\text{site+small})$	11	3209.20	12.50	0.00	0.21 (0.27)	-	-	-	-	0.10 (0.13)	-
$\psi(\text{jaguar+ndvi})p(\text{site+small})$	11	3209.52	12.83	0.00	-	-	-0.08 (0.14)	-	-	0.09 (0.13)	-
$\psi(\text{puma+elevation})p(\text{site+small})$	11	3209.61	12.91	0.00	0.19 (0.27)	-	-	-	-	-	-0.03 (0.16)
$\psi(\text{jaguar+large})p(\text{site+small})$	11	3209.62	12.93	0.00	-	-	-	0.05 (0.12)	-	0.06 (0.15)	-
$\psi(\text{jaguar+puma})p(\text{site+small})$	11	3209.64	12.95	0.00	-	-	-	-	-	0.11 (0.14)	-0.07 (0.17)
$\psi(\text{puma+large})p(\text{site+small})$	11	3209.68	12.98	0.00	-	-	-	0.08 (0.14)	-	-	-0.04 (0.16)
$\psi(\text{jaguar+water})p(\text{site+small})$	11	3209.72	13.02	0.00	-	0.05 (0.15)	-	-	-	0.11 (0.14)	-
$\psi(\text{puma+ndvi})p(\text{site+small})$	11	3209.85	13.15	0.00	-	-	-0.08 (0.15)	-	-	-	-0.03 (0.16)
$(\text{puma+water})p(\text{site+small})$	11	3209.98	13.29	0.00	-	-0.17 (0.43)	-	-	-	-	-0.21 (0.47)

S7 Table - Coefficient of overlap (Δ) with confidence intervals (CI lower/CI upper) and Watson's two-sample test (two-sample U_2) performed on pairwise comparisons between cat species per site.

Site	Species	Coefficient of Overlap			Watson's Two-Sample Test	
		Δ	CI lower	CI upper	U^2	P value
BCI	Ocelot vs Jaguarundi	0.436	0.274	0.598	0.3895	< 0.001
CAX	Jaguar vs Puma	0.763	0.586	0.875	0.1964	< 0.05
	Jaguar vs Ocelot	0.645	0.559	0.918	0.2255	< 0.05
	Puma vs Ocelot	0.731	0.593	0.885	0.2053	< 0.05
	Ocelot vs Margay	0.741	0.578	0.876	0.0641	ns
CSN	Jaguar vs Puma	0.798	0.668	0.906	0.0814	ns
	Jaguar vs Ocelot	0.823	0.717	0.915	0.1564	ns
	Puma vs Ocelot	0.634	0.520	0.747	0.4759	< 0.001
	Ocelot vs Jaguarundi	0.484	0.378	0.588	0.8492	< 0.001
	Ocelot vs Margay	0.669	0.556	0.773	0.5277	< 0.001
	Jaguarundi vs Margay	0.197	0.091	0.304	1.5352	< 0.001
COU	Jaguar vs Puma	0.670	0.535	0.810	0.3866	< 0.001
	Jaguar vs Ocelot	0.687	0.579	0.789	0.5393	< 0.001
	Puma vs Ocelot	0.662	0.557	0.770	0.7369	< 0.001
	Ocelot vs Jaguarundi	0.360	0.214	0.518	0.6856	< 0.001
	Ocelot vs Margay	0.828	0.589	0.990	0.0248	ns
	Jaguarundi vs Margay	0.337	0.121	0.587	0.1578	ns
VB	Puma vs Ocelot	0.606	0.476	0.733	0.3839	< 0.01
	Ocelot vs Margay	0.588	0.362	0.791	0.1114	ns
YAN	Jaguar vs Puma	0.508	0.317	0.704	0.3244	< 0.01
	Jaguar vs Ocelot	0.497	0.317	0.686	0.4877	< 0.001
	Puma vs Ocelot	0.659	0.451	0.835	0.0563	ns
	Ocelot vs Jaguarundi	0.314	0.164	0.475	0.7318	< 0.001
	Ocelot vs Margay	0.635	0.368	0.876	0.0725	ns
	Jaguarundi vs Margay	0.325	0.125	0.525	0.2159	< 0.05

YAS	Jaguar vs Puma	0.720	0.581	0.859	0.23	< 0.05
	Jaguar vs Ocelot	0.506	0.360	0.655	0.5508	< 0.001
	Puma vs Ocelot	0.668	0.559	0.772	0.5311	< 0.001
	Ocelot vs Jaguarundi	0.365	0.239	0.494	0.826	< 0.001
	Ocelot vs Margay	0.668	0.487	0.813	0.1229	ns
	Jaguarundi vs Margay	0.202	0.059	0.340	0.6889	< 0.001

S8 Table - Coefficient of overlap ($\Delta 1$) with confidence intervals (CI lower/CI upper) and Watson's two-sample test (two-sample U_2) performed on pairwise comparisons between study sites (ns – non-significant).

Species	Sites	Coefficient of Overlap			Watson's Two-Sample Test	
		$\Delta 1$	CI lower	CI upper	U^2	P value
Jaguar	CAX - CSN	0.824	0.679	0.945	0.111	ns
	CAX - COU	0.650	0.490	0.796	0.288	< 0.01
	CAX - YAN	0.827	0.666	0.962	0.036	ns
	CAX - YAS	0.874	0.733	0.989	0.025	ns
	CSN - COU	0.731	0.579	0.859	0.225	< 0.05
	CSN - YAN	0.856	0.711	0.985	0.056	ns
	CSN - YAS	0.788	0.637	0.914	0.123	ns
	COU - YAN	0.731	0.544	0.886	0.148	ns
	COU - YAS	0.642	0.489	0.790	0.319	< 0.01
	YAN - YAS	0.838	0.672	0.972	0.031	ns
Puma	CAX - CSN	0.841	0.722	0.948	0.066	ns
	CAX - COU	0.885	0.773	0.973	0.047	ns
	CAX - VB	0.727	0.572	0.855	0.229	< 0.05
	CAX - YAN	0.613	0.405	0.812	0.224	< 0.05
	CAX - YAS	0.748	0.604	0.893	0.232	< 0.05
	CSN - COU	0.795	0.665	0.909	0.132	ns
	CSN - VB	0.760	0.629	0.878	0.102	ns
	CSN - YAN	0.506	0.316	0.689	0.364	< 0.01
	CSN - YAS	0.728	0.586	0.847	0.195	< 0.05
	COU - VB	0.745	0.601	0.869	0.226	< 0.05
	COU - YAN	0.635	0.438	0.815	0.195	< 0.05
	COU - YAS	0.758	0.613	0.885	0.205	< 0.05
	VB - YAN	0.537	0.366	0.698	0.338	< 0.01
	VB - YAS	0.842	0.714	0.945	0.051	ns
	YAN - YAS	0.552	0.380	0.721	0.333	< 0.01

Ocelot	BCI - CAX	0.826	0.709	0.928	0.081	ns
	BCI - CSN	0.866	0.792	0.929	0.139	ns
	BCI - COU	0.876	0.825	0.924	0.126	ns
	BCI - MAN	0.866	0.792	0.929	0.138	ns
	BCI - VB	0.774	0.661	0.876	0.109	ns
	BCI - YAN	0.835	0.740	0.915	0.141	ns
	BCI - YAS	0.818	0.750	0.881	0.202	< 0.05
	CAX - CSN	0.819	0.684	0.925	0.123	ns
	CAX - COU	0.795	0.680	0.894	0.128	ns
	CAX - MAN	0.727	0.510	0.874	0.071	ns
	CAX - VB	0.849	0.736	0.942	0.031	ns
	CAX - YAN	0.819	0.705	0.912	0.092	ns
	CAX - YAS	0.837	0.725	0.924	0.070	ns
	CSN - COU	0.796	0.728	0.861	0.369	< 0.01
	CSN - MAN	0.758	0.543	0.849	0.092	ns
	CSN - VB	0.772	0.668	0.873	0.192	< 0.05
	CSN - YAN	0.739	0.645	0.830	0.300	< 0.01
	CSN - YAS	0.811	0.731	0.881	0.318	< 0.01
	COU - MAN	0.739	0.544	0.841	0.065	ns
	COU - VB	0.783	0.671	0.879	0.228	< 0.05
	COU - YAN	0.836	0.745	0.903	0.058	ns
	COU - YAS	0.860	0.794	0.917	0.160	ns
	MAN - VB	0.716	0.529	0.864	0.093	ns
	MAN - YAN	0.670	0.525	0.878	0.079	ns
	MAN - YAS	0.712	0.547	0.849	0.085	ns
	VB - YAN	0.752	0.640	0.857	0.176	ns
	VB - YAS	0.831	0.741	0.911	0.138	ns
	YAN - YAS	0.800	0.709	0.872	0.068	ns
Jaguarundi	BCI - CSN	0.837	0.609	1.008	0.049	ns
	BCI - COU	0.701	0.451	0.898	0.041	ns
	BCI - YAN	0.690	0.425	0.904	0.100	ns

	BCI - YAS	0.951	0.730	1.110	0.015	ns
	CSN - COU	0.727	0.533	0.880	0.067	ns
	CSN - YAN	0.683	0.496	0.851	0.184	ns
	CSN - YAS	0.827	0.657	0.966	0.066	ns
	COU - YAN	0.627	0.423	0.815	0.138	ns
	COU - YAS	0.720	0.508	0.899	0.045	ns
	YAN - YAS	0.655	0.437	0.850	0.152	ns
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Margay	CAX - CSN	0.718	0.570	0.862	0.158	ns
	CAX - YAS	0.499	0.311	0.694	0.165	ns
	CSN - YAS	0.743	0.553	0.899	0.038	ns
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S9 Table - Differences in the daily activity level (*i. e.*, proportion of hours per day that an animal is active), standard errors (SE), Wald test (W) of Neotropical cats across the eight study sites (*Significant difference <0.05).

Species	Site	Difference	SE	W	<i>p</i>
Jaguar	CAX-COU	0.06	0.13	0.25	0.62
	CAX-CSN	0.21	0.15	2.12	0.15
	CAX-YAN	0.18	0.14	1.64	0.20
	CAX-YAS	0.01	0.13	0.01	0.91
	COU-CSN	0.28	0.13	4.32	0.04*
	COU-YAN	0.25	0.13	3.69	0.05*
	COU-YAS	0.08	0.11	0.48	0.49
	CSN-YAN	0.03	0.15	0.05	0.83
	CSN-YAS	0.20	0.13	2.22	0.14
	YAN-YAS	0.17	0.13	1.71	0.19
Puma	CAX-COU	0.09	0.14	0.45	0.50
	CAX-CSN	0.01	0.13	0.01	0.91
	CAX-VB	0.17	0.13	1.64	0.20
	CAX-YAN	0.11	0.14	0.61	0.44
	CAX-YAS	0.12	0.14	0.71	0.40
	COU-CSN	0.11	0.12	0.76	0.38
	COU-VB	0.08	0.13	0.39	0.53
	COU-YAN	0.20	0.13	2.29	0.13
	COU-YAS	0.03	0.13	0.04	0.85
	CSN-VB	0.19	0.12	2.44	0.12
	CSN-YAN	0.09	0.12	0.57	0.45
	CSN-YAS	0.13	0.13	1.11	0.29
	VB-YAN	0.28	0.13	4.67	0.03*
	VB-YAS	0.05	0.13	0.17	0.68
YAN-YAS	0.22	0.13	2.78	0.10	
Ocelot	BCI - CAX	0.11	0.11	1.04	0.31
	BCI - CSN	0.06	0.09	0.40	0.53
	BCI - COU	0.11	0.07	2.84	0.09

BCI - MAN	0.25	0.11	5.66	0.02*	
BCI - VB	0.23	0.09	6.30	0.01*	
BCI - YAN	0.14	0.09	2.75	0.10	
BCI - YAS	0.22	0.07	10.03	0.00*	
CAX - CSN	0.17	0.12	1.94	0.16	
CAX - COU	0.00	0.10	0.00	0.99	
CAX - MAN	0.14	0.13	1.21	0.27	
CAX - VB	0.13	0.12	1.07	0.30	
CAX - YAN	0.03	0.12	0.09	0.77	
CAX - YAS	0.11	0.10	1.17	0.28	
CSN - COU	0.17	0.09	3.87	0.05*	
CSN - MAN	0.31	0.12	6.74	0.01*	
CSN - VB	0.29	0.11	7.27	0.01*	
CSN - YAN	0.20	0.10	3.86	0.05*	
CSN - YAS	0.28	0.09	9.84	0.00*	
COU - MAN	0.14	0.10	2.00	0.16	
COU - VB	0.12	0.09	2.01	0.16	
COU - YAN	0.03	0.08	0.17	0.68	
COU - YAS	0.11	0.06	3.23	0.07	
MAN - VB	0.02	0.12	0.03	0.87	
MAN - YAN	0.11	0.12	0.92	0.34	
MAN - YAS	0.03	0.10	0.10	0.75	
VB - YAN	0.09	0.10	0.78	0.38	
VB - YAS	0.01	0.09	0.02	0.89	
YAN - YAS	0.08	0.08	0.89	0.35	
Jaguarundi	BCI - CSN	0.09	0.11	0.66	0.42
	BCI - COU	0.02	0.11	0.04	0.84
	BCI - YAN	0.04	0.10	0.12	0.72
	BCI - YAS	0.00	0.11	0.00	0.98
	CSN - COU	0.11	0.10	1.16	0.28
	CSN - YAN	0.12	0.09	1.75	0.19

	CSN - YAS	0.09	0.10	0.84	0.36
	COU - YAN	0.01	0.10	0.02	0.88
	COU - YAS	0.02	0.10	0.03	0.85
	YAN - YAS	0.03	0.09	0.12	0.72
Margay	CAX - CSN	0.08	0.10	0.71	0.40
	CAX - YAS	0.14	0.11	1.85	0.17
	CSN - YAS	0.06	0.09	0.48	0.49

4. Sessão III

Dinâmica sazonal de mamíferos terrestres em uma floresta na Amazônia Oriental

A terceira sessão desta tese foi elaborada e formatada conforme as normas da publicação científica *Plos One*, disponível em: <https://journals.plos.org/plosone/s/submission-guidelines>

1 Dinâmica sazonal de mamíferos terrestres em uma floresta na
2 Amazônia Oriental

3
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33 **Resumo**

34 As florestas tropicais possuem uma sazonalidade pronunciada, alternando entre períodos secos e
35 chuvosos em diversos níveis. Tais mudanças têm diversas implicações em relação a disponibilidade
36 de recursos necessários para os mamíferos terrestres (por exemplo, água e frutos) e,
37 conseqüentemente, podem influenciar nos padrões de atividade e movimentação de diversas espécies.
38 Neste estudo nós utilizamos 60 *camera traps* distribuídas numa área de aproximadamente 120 km²
39 para avaliar o efeito da variação sazonal na comunidade de mamíferos terrestres em uma floresta de
40 terra firme na Amazônia Oriental. Nós testamos a hipótese de que existe uma movimentação sazonal
41 dos mamíferos terrestres, principalmente de espécies frugívoras e granívoras, em resposta às
42 mudanças na disponibilidade de água e de recursos alimentares. Utilizamos a abordagem de análise
43 de ocupação, contabilizando a probabilidade de detecção, para examinar a influência de seis variáveis
44 (estação, precipitação, temperatura, elevação, distância ao rio principal e distância vertical à
45 drenagem) na distribuição espacial das espécies. Totalizamos um esforço amostral de 7.564 *camera*
46 *traps*/dia, obtendo 3.019 registros independentes (1.591 na estação chuvosa e 1.428 na estação seca)
47 de 24 espécies de mamíferos. A sazonalidade influenciou a probabilidade de detecção apenas de
48 *Cuniculus paca* e *Dasyprocta leporina*, enquanto a temperatura foi importante para *C. paca* e as
49 espécies do gênero *Dasybus*. Com relação à ocupação, apenas *D. leporina* e *Mazama americana*
50 apresentaram uma maior estimativa de ocupação durante a estação chuvosa. A elevação foi uma
51 preditora significativa para *C. paca*, *Mazama americana*, *Dasybus* spp e *Tapirus terrestris*, enquanto
52 que a distância vertical à drenagem influenciou a ocupação de grandes felinos (*Panthera onca* + *Puma*
53 *concolor*). Nenhuma variável apresentou efeito robusto nos modelos realizados para *Mazama*
54 *nemorivaga* e *Pecari tajacu* (com base em 95% IC). Nosso estudo demonstrou que o efeito da
55 sazonalidade pode ser limitado para mamíferos residentes na área, mas ressalta a importância de
56 considerar mudanças ao longo do ano para o melhor entendimento da dinâmica de mamíferos

57 terrestres, a fim de traçar estratégias efetivas de manejo e preservação destas espécies em unidades
58 de conservação na Amazônia.

59

60 **Introdução**

61 As florestas neotropicais são reconhecidas por sua alta diversidade de espécies de mamíferos [1–
62 4], sendo a Amazônia uma das áreas que apresenta maior riqueza e endemismo para esse grupo [5].
63 A distribuição e abundância de mamíferos são influenciadas por diversos fatores, relacionados à
64 disponibilidade de recursos, heterogeneidade do habitat, interações interespecíficas, bem como por
65 fatores antrópicos [6–9].

66 Grande parte dos fatores que influenciam na ocorrência dos mamíferos são conduzidos por
67 mudanças sazonais em seu ambiente. Isso pode ser observado nas florestas tropicais, as quais
68 possuem uma sazonalidade pronunciada em termos de precipitação, alternando entre períodos secos
69 e chuvosos em diversos níveis [10]. Tais mudanças resultam em diversas implicações relacionadas à
70 disponibilidade de recursos, como água e alimento, e, conseqüentemente, nos padrões de atividade e
71 movimentação de diversas espécies terrestres [11–15].

72 A movimentação lateral de mamíferos e aves foi observada em diversos estudos conduzidos em
73 área alagáveis na Amazônia, as quais constituem uma barreira física para muitas espécies durante o
74 período de inundação das florestas, mas também provêm uma abundante quantidade de frutos e
75 sementes no solo após a vazão das águas no período da seca [11,16]. Estudos confirmam que a
76 variação espaço-temporal na floração e frutificação das espécies vegetais nos diferentes tipos
77 florestais tem uma grande influência na área de uso e no comportamento de forrageamento de animais
78 frugívoros e granívoros [11,16,17]. No entanto, os efeitos das variações sazonais da precipitação e
79 temperatura sobre a mastofauna ainda são pouco estudados e a maioria deles não considera que a
80 probabilidade de detecção das espécies pode variar entre as estações (mas veja [18]).

81 Em geral, estudos envolvendo mamíferos utilizam metodologias e esforços amostrais variados,
82 o que torna difícil a comparação e o entendimento dos processos que conduzem a dinâmica espaço-
83 temporal das espécies [19]. A estação chuvosa em florestas tropicais, por exemplo, foi poucas vezes
84 contemplada em estudos com mamíferos terrestres [20], devido às dificuldades de acesso em algumas
85 áreas e potenciais danos que a alta umidade pode causar às armadilhas fotográficas [18]. Entretanto,
86 estes dados são necessários para identificar, planejar e implementar estratégias eficazes de
87 conservação. Uma amostragem padronizada e replicada ao longo do tempo possibilita compreender
88 e diferenciar flutuações naturais das populações e respostas às mudanças causadas pelas atividades
89 humanas [9,21–23].

90 Neste estudo, nós avaliamos o efeito da sazonalidade sobre a comunidade de mamíferos terrestres
91 em uma floresta de terra firme na Amazônia Oriental. Nós testamos a hipótese de que há uma
92 movimentação sazonal dos mamíferos terrestres, principalmente de espécies frugívoras e granívoras,
93 em resposta às mudanças na disponibilidade de água e de recursos alimentares. Utilizamos a
94 abordagem de modelagem de ocupação, contabilizando a probabilidade de detecção, para avaliar os
95 efeitos da sazonalidade considerando uma maior oferta de frutos e flores durante a estação seca e as
96 mudanças climatológicas (precipitação e temperatura) associadas. Para os modelos de ocupação
97 também testamos os efeitos da disponibilidade de água, relacionado às medidas de distância ao rio
98 principal e a distância vertical à drenagem (HAND), e da elevação do terreno. Estas variáveis
99 contemplam diferentes ambientes entre igapós, baixios e platôs na floresta de terra firme, enquanto
100 que a medida de elevação também está associada às diferenças no solo.

101

102 **Métodos**

103 **Área de estudo e sazonalidade**

104 A área de estudo foi a Floresta Nacional (FLONA) de Caxiuanã (Decreto-Lei 209 em
105 28/11/1961) situada em parte dos municípios de Portel e Melgaço, no Estado do Pará, Brasil. Esta é

106 a maior unidade de conservação no interflúvio dos rios Xingu e Tocantins, abrangendo uma área de
107 317.946,37 hectares (Fig 1) [24]. Distante cerca de 400 km de Belém, a capital do Estado, a FLONA
108 de Caxiuanã é considerada bastante preservada, sobretudo pelo seu difícil acesso e baixa densidade
109 populacional. A vegetação é representada quase que em sua totalidade por Floresta Ombrófila Densa
110 de Terras Baixas (região de platôs: 60,1%; e região de baixios: 30,1%), além de áreas de Floresta
111 Ombrófila Densa Aluvial (floresta de igapó e várzea: 8,7%) e campinarana (1,1%) [24,25].

112

113 **Fig 1. Localização da área de estudo e das matrizes de armadilhas fotográficas na Floresta**
114 **Nacional de Caxiuanã, Estado do Pará, Brasil.** FLONA de Caxiuanã detalhada em vermelho. As
115 armadilhas foram instaladas em duas matrizes de 30 pontos amostrais cada ao Norte e Sul do Rio
116 Caxiuanã.

117

118 No aspecto climático, a região apresenta o clima tropical quente e úmido (subtipo **Am**, segundo
119 a classificação de Köppen) [14]. A sazonalidade na área é bem caracterizada pela precipitação, sendo
120 o período chuvoso compreendido entre dezembro e maio (1.871,2 mm, cerca de 85% da precipitação
121 anual total) e o período seco entre junho e novembro (340,4 mm, representando 15% da precipitação
122 anual total) [14]. A temperatura média do ar oscila em torno de 26,7°C, apresentando temperaturas
123 mínimas de 22°C e máximas de 32°C [14].

124 A sazonalidade ocorre também em relação a queda de detritos vegetais no solo, como folhas,
125 caules, flores e frutos. Um monitoramento mensal de liteira na FLONA de Caxiuanã indicou que a
126 maior deposição de flores e frutos no solo, os quais constituem a base alimentar de uma grande parcela
127 dos mamíferos terrestres, ocorre entre os meses de julho e novembro, coincidindo com a época menos
128 chuvosa [14,26]. A média de flores e frutos contabilizados para o período de maior precipitação na
129 FLONA foi de 49.33 Kg.ha⁻¹, enquanto que no período de menor precipitação foi de 100.16 Kg.ha⁻¹
130 [14].

131

132 **Amostragem de mamíferos terrestres**

133 Os mamíferos terrestres foram amostrados através do uso de armadilhas fotográficas (*camera*
134 *traps*). Para isso, nós instalamos 60 pontos amostrais divididos em duas matrizes de trinta armadilhas
135 fotográficas cada, as quais foram distribuídas na porção norte e sul do Rio Caxiuanã, equidistantes
136 por 1.4 km e abrangendo uma área total de cerca de 120 km² (Fig 1). A cada período amostral as
137 armadilhas fotográficas foram instaladas em duas campanhas sequenciais de 30 pontos amostrais
138 (nomeadas matriz norte e matriz sul), ficando ativas em média por 37 dias consecutivos (± 8 dias). Os
139 equipamentos foram configurados para efetuar três fotos por disparo, sem intervalos entre os disparos
140 e nenhum tipo de isca foi utilizado.

141 Nós realizamos a coleta de dados durante quatro períodos amostrais nos mesmos 60 pontos,
142 totalizando duas amostras para cada estação: 1) entre dezembro de 2010 e fevereiro de 2011; 2) entre
143 agosto e novembro de 2012; 3) entre fevereiro e abril de 2014; e 4) entre agosto e novembro de 2014
144 (Fig 2). Apenas durante o terceiro período de amostragem (fevereiro-abril/2014) não foi possível
145 monitorar a segunda matriz (matriz sul) devido aos danos causados aos equipamentos pela intensa
146 precipitação durante a primeira parte da amostragem. Portanto, tivemos apenas 30 pontos de
147 monitoramento na estação chuvosa deste ano.

148

149 **Fig 2 – Médias mensais de precipitação e temperatura durante os períodos amostrais na área**
150 **de estudo.** Os períodos amostrais durante a estação chuvosa compreenderam de dezembro/2010 a
151 fevereiro/2011 e fevereiro a abril/2014, enquanto que na estação seca foram realizados de agosto a
152 novembro de 2012 e agosto a outubro de 2014.

153

154 **Variáveis**

155 Nós extraímos variáveis relacionadas ao habitat para cada ponto amostral: elevação, distância
156 vertical à drenagem mais próxima (*Vertical Distance to the Nearest Drainage* [HAND]) e a menor

157 distância em linha reta ao rio principal, o Rio Caxiuanã. Estas variáveis são comumente associadas à
158 distribuição de mamíferos [16,27,28] e discriminam as regiões de platôs e baixios na floresta de terra
159 firme, bem como as áreas de igapó na FLONA de Caxiuanã. Além disso, nós calculamos a média da
160 temperatura (°C) e a soma da precipitação (mm) durante o período em que cada armadilha fotográfica
161 esteve ativa.

162 A elevação foi calculada usando um modelo de elevação digital (DEM) da missão topográfica
163 do radar de transferência da NASA (SRTM), com resolução espacial de 1 arco segundo (cerca de 30
164 metros). As imagens DEM foram obtidas a partir da base de dados U.S. Geological Survey [29]. O
165 algorítmico HAND está relacionado a disponibilidade de água no solo, ou seja, valores próximos a
166 zero indicam que o lençol freático está próximo à superfície e valores mais altos indicam áreas bem
167 drenadas [30]. O valor de HAND foi obtido com base nos arquivos asc-grid produzidos a partir de
168 SRTM DEM, seguindo Rennó et al [30] (disponível em <http://www.dpi.inpe.br/Ambdata>). Já a
169 distância para o rio principal, o Rio Caxiuanã, foi calculada com base nos shapefiles hidrológicos da
170 Base de Dados HydroSHEDS [31]. Todas as estimativas foram geradas no programa QGis [32]. Os
171 dados de temperatura e precipitação foram retirados da base de dados do projeto *Tropical Ecology*
172 *Assessment and Monitoring (TEAM) Network*, o qual mantém uma torre de monitoramento climático
173 na área da Floresta Nacional de Caxiuanã. A base de dados climáticos do projeto reúne dados de
174 monitoramento entre os anos de 2002 e 2017 [33].

175

176 **Análise de dados**

177 Todas as análises foram realizados na linguagem de programação R [34]. Para comparar se o
178 esforço amostral entre períodos amostrais e estações foi satisfatório para registrar a maioria das
179 espécies na área, nós construímos curvas de acumulação de espécies, separadamente para cada
180 período amostral, usando o método de rarefação e o estimador Jackknife de primeira ordem através
181 da função *specaccum* do pacote ‘vegan’ [35]. Também estimamos o número potencial de espécies

182 não detectadas por período amostral através da função *specpool* [35]. Todas as imagens de uma
183 mesma espécie em uma mesma armadilha fotográfica foram separadas por um intervalo de uma hora
184 entre elas para garantir a independência das mesmas [36]. A abundância das espécies foi expressa
185 pela relação entre o número de imagens de uma espécie e o esforço amostral realizado (i.e., imagens
186 por 100 *camera trap*-dia), permitindo a comparação entre os diferentes períodos amostrais [37,38].
187 Nós examinamos as diferenças na abundância total e de cada espécie entre as estações seca e chuvosa
188 através de testes t de Student e teste t pareado (utilizando o critério de correção de Bonferroni), usando
189 um nível de significância de $p < 0.05$ (Os dados foram testados previamente e quando não atenderam
190 as premissas de normalidade e homogeneidade foram utilizados testes não paramétricos
191 correspondentes).

192 O padrão de distribuição espacial dos pontos amostrais da mastofauna entre as estações seca e
193 chuvosa foi evidenciado pela Análise de Coordenadas Principais (PCoA) [39] e testado através de
194 uma ANOVA Multivariada Permutacional (PERMANOVA) [40]. Para isso, os dados de abundância
195 das espécies foram padronizados e uma matriz de distância de Bray-Curtis foi utilizada para a análise.
196 Posteriormente, a variância das amostras foi testada pelo método da dispersão permutacional
197 (PERMDISP) [40]. Este método é um teste multivariado análogo ao teste de Levene de
198 homogeneidade das variâncias, no qual são obtidas as distâncias médias dos pontos amostrais em
199 relação ao centroide de seu respectivo tratamento (estação seca/chuvosa) em um espaço multivariado
200 de coordenadas principais [35]. Adicionalmente, utilizamos a matriz de dissimilaridade para verificar
201 o grau de concordância na composição de espécies entre as duas estações através de uma análise de
202 Procrustes. Este teste estatístico (m^2) mede o quão divergente são as ordenações de cada estação,
203 testando-se a significância através de 10.000 permutações [41]. PERMANOVA e Procrustes foram
204 realizados utilizando-se o pacote ‘vegan’ (funções *adonis*, *procrustes* e *protest*) [35].

205 Utilizamos o valor de VIF (*Variance Inflation Factor*) para avaliar a existência de
206 multicolinearidade entre as variáveis de habitat selecionadas. VIF foi calculado usando o pacote ‘car’

207 [42] através de um modelo de regressão. Todas as variáveis numéricas apresentaram VIF <3 e foram
208 retidas para uso nos modelos de ocupação.

209 Para testar a hipótese de que existe um efeito sazonal na ocupação e detectabilidade das
210 espécies, nós utilizamos a modelagem de ocupação para as espécies que apresentaram um número
211 suficiente de registros para a análise (i.e., > 10 imagens por período amostral) [43,44]. Além disso,
212 nós agrupamos os registros dos dois maiores felinos presentes na área (*Panthera onca* e *Puma*
213 *concolor*) na tentativa de superar o baixo número de detecções individuais de cada espécie e
214 incorporá-los na análise. A ocupação (Ψ) é definida como a proporção de sítios aonde é esperado que
215 a espécie ocorra, enquanto que a detectabilidade (p) refere-se a probabilidade de a espécie ser
216 detectada dada a sua presença [43,45].

217 Nós organizamos o histórico de detecção de cada espécie separadamente dividindo cada período
218 amostral em ocasiões de 10 dias cada. Utilizamos uma abordagem de modelagem de ocupação
219 dinâmica implícito, ou seja, cada período amostral foi modelado através de uma análise *single-season*,
220 ignorando a auto-correlação temporal [43]. A escolha pelo método foi realizada com base em análises
221 exploratórias as quais indicaram que a probabilidade de detecção das espécies não foi influenciada
222 pelo período de amostragem em anos diferentes (i.e., modelos nulos e/ou incorporando as estações
223 [seca/chuvosa] obtiveram maior suporte do que os modelos que consideraram os diferentes períodos
224 amostrais). Além disso, o grande número de ausências (zeros) no histórico de detecção prejudica uma
225 análise *multi-season* na qual um número maior de parâmetros são estimados (colonização/extinção)
226 [46]. A partir da abordagem *single-season*, nós combinamos os dados dos quatro períodos e
227 construímos modelos para acessar o efeito da sazonalidade na detectabilidade e ocupação das espécies
228 utilizando o pacote ‘unmarked’ [47].

229 Para diminuir o número de combinações possíveis e um grande número de modelos, nós
230 dividimos o procedimento de modelagem em duas etapas. Primeiramente, nós investigamos a
231 influência da sazonalidade na probabilidade de detecção (p) das espécies, mantendo a ocupação
232 constante ($\Psi(\cdot)$). Assim, p variou em função da variável categórica principal “estação”

233 (seca/chuvosa), representando as épocas do ano com maior e menor disponibilidade de recursos
234 alimentares. Outras duas variáveis numéricas também foram utilizadas: a precipitação e a temperatura
235 média no período de amostragem. Estas variáveis podem influenciar tanto na movimentação dos
236 animais quanto na sensibilidade da armadilha fotográfica e, conseqüentemente, na detecção. Para
237 avaliar os melhores modelos utilizamos o Critério de Informação de Akaike (AIC). Os modelos foram
238 considerados bem suportados quando o valor de AIC foi menor que dois [48]. Para avaliar os modelos
239 selecionados realizamos um teste de ajuste (*Godness-of-fit test*) no modelo com maior número de
240 parâmetros, ou seja, o modelo que inclui todas as variáveis (i.e., modelo global), e corrigimos a
241 seleção de modelos em caso de alta dispersão dos dados utilizando o valor de *c-hat* (QAIC) [45,48].
242 O modelo mais parcimonioso, considerando o menor valor de AIC e o peso (AICwt) foi retido para
243 a modelagem de ocupação.

244 Na segunda etapa, nós desenvolvemos um segundo conjunto de modelos para avaliar a
245 influência da sazonalidade e de outros fatores do habitat na ocupação das espécies. Além da variável
246 categórica “estação”, foram selecionadas variáveis que poderiam influenciar na movimentação dos
247 mamíferos dentro da área de estudo devido à mudanças sazonais no habitat de acordo com a estação
248 (por ex., áreas inundáveis de igapó durante a estação chuvosa, disponibilidade de água na estação
249 seca). Desta maneira, fixamos em p a variável escolhida na primeira etapa e Ψ variou em função da
250 elevação, da distância vertical à drenagem (HAND) e da distância ao rio principal. A seleção de
251 modelos seguiu o mesmo critério descrito acima para os modelos de detecção ($AIC < 2$). Quando
252 mais de um modelo obteve suporte, realizamos a média dos modelos para obter as estimativas para a
253 ocupação e os parâmetros através do pacote ‘AICcmodavg’ [49].

254 Nós utilizamos os valores do coeficiente beta para avaliar se a influência da variável foi positiva
255 ou negativa e calculamos o intervalo de confiança a 95% para avaliar a importância das variáveis.
256 Quando o intervalo de confiança não incluiu o zero, concluímos que a variável tem um efeito
257 significativo na ocupação da espécie [45,48,49].

258 **Resultados**

259 O esforço amostral totalizou 7.564 *camera traps*/dia, obtendo 3.019 registros independentes
260 (1.591 na estação chuvosa e 1.428 na estação seca). Foram registradas 24 espécies para as duas
261 estações (22 e 24 espécies por estação), representando sete ordens (Tabela 1). Apenas as espécies
262 *Cabassous unicinctus* e *Herpailurus yagouaroundi* foram registradas exclusivamente na estação seca.

263 Comparações entre as curvas de rarefação e as estimativas de riqueza de espécies demonstram
264 que o esforço foi suficiente para amostrar a comunidade de mamíferos, registrando entre 88 e 96%
265 do total de espécies estimadas para a área (Jackknife I = 22 – 26 espécies) (Fig 3). Embora a abundância
266 total tenha sido maior na estação chuvosa, não houve diferença significativa entre as estações (Teste
267 U de Mann-Whitney = 1172, $p=0.592$). Apenas três espécies apresentaram um aumento significativo
268 na taxa de detecção durante a estação chuvosa, *D. leporina*, *M. americana* e *M. tridactyla* (Tabela 1).

269

270 **Fig 3. Curvas de rarefação de espécies para a comunidade de mamíferos terrestres na Floresta**
271 **Nacional de Caxiuanã, Pará, Brasil.** Detecção de espécies por *camera trap* em cada período
272 amostral: linhas nas cores azul (estação chuvosa) e laranja (estação seca) representam a média
273 derivada de 1.000 aleatorizações, enquanto que as respectivas áreas sombreadas representam 95% de
274 intervalo de confiança.

Tabela 1 – Mamíferos terrestres registrados na Floresta Nacional de Caxiuanã, Pará – Brasil e abundância relativa (imagens/100 camera traps-dia) das espécies durante as estações seca e chuvosa. (* indica $p < 0.05$ - diferença significativa na taxa de detecção das espécies entre as estações através do teste de Mann-Whitney usando o critério de correção de Bonferroni).

Ordem	Espécies	Nome comum	Abundância relativa	
			Chuvosa	Seca
Carnivora	<i>Atelocynus microtis</i> (Sclater, 1883)	Cachorro do mato de orelha curta	0.05	0.09
	<i>Eira barbara</i> (Linnaeus, 1758)	Irara	0.58	0.85
	<i>Herpailurus yagouaroundi</i> (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi	0.18	-
	<i>Leopardus pardalis</i> (Linnaeus, 1758)	Jaguaritica	1.25	0.71
	<i>Leopardus wiedii</i> (Schinz, 1821)	Gato maracajá	0.58	0.39
	<i>Nasua nasua</i> (Linnaeus, 1766)	Quati	1.61	1.20
	<i>Panthera onca</i> (Linnaeus, 1758)	Onça pintada	0.76	0.56
	<i>Puma concolor</i> (Linnaeus, 1771)	Onça parda	0.76	0.94
	Cingulata	<i>Cabassous unicinctus</i> (Linnaeus, 1758)	Tatu-de-rabo-mole	0.05
<i>Dasyopus spp</i> (Linnaeus, 1758)		Tatu galinha/quinze quilos	12.22	7.93
<i>Priodontes maximus</i> (Kerr, 1792)		Tatu canastra	0.31	0.14
Cetartiodactyla	<i>Mazama americana</i> (Erxleben, 1777)	Veado vermelho	9.37	9.11*
	<i>Mazama nemorivaga</i> (F. Cuvier, 1817)	Veado fuboca	5.32	4.97
	<i>Pecari tajacu</i> (Linnaeus, 1758)	Caititu	4.46	4.15
	<i>Tayassu pecari</i> (Link, 1795)	Queixada	0.71	0.38
Didelphimorphia	<i>Didelphis marsupialis</i> Linnaeus, 1758	Gambá comum	3.36	2.32
	<i>Metachirus nudicaudatus</i> (É. Geoffroy, 1803)	Cuíca de quatro olhos	0.72	1.40
Perissodactyla	<i>Tapirus terrestres</i> (Linnaeus, 1758)	Anta	1.52	1.54
Pilosa	<i>Myrmecophaga tridactyla</i> (Linnaeus, 1758)	Tamanduá bandeira	1.66	1.05*
	<i>Tamandua tetradactyla</i> (Linnaeus, 1758)	Tamanduá-mirim	0.40	0.48
Rodentia	<i>Cuniculus paca</i> (Linnaeus, 1766)	Paca	7.40	4.62
	<i>Dasyprocta leporina</i> (Linnaeus, 1758)	Cotia	42.27	23.91*
	<i>Proechimys spp</i> Tomes, 1860	Rato de espinho	1.24	0.83
	<i>Sciurus aestuans</i> Linnaeus, 1766	Quatipuru	0.13	0.04
Esforço amostral			3.342	4.222
Riqueza de espécies			24	22

275 Em relação a composição de espécies, observamos que houve diferença significativa entre as
276 estações seca e chuvosa (PERMANOVA; $F = 2.624$, $p = 0.007$), porém a análise *a posteriori* indicou
277 que há homogeneidade na variância das ordenações entre as estações ($F = 6.723$, $p = 0.009$). Esse
278 resultado confirma o padrão de ordenação espacial visualizado através da PCoA (Fig 4A), na qual se
279 observa a similaridade na composição das espécies entre as estações. Além disso, o teste de rotação
280 de Procruste indicou alta concordância entre a comunidade de mamíferos nas estações seca e chuvosa
281 ($m^2 = 0.806$, $r = 0.440$, $p = 0.035$; Fig 4B).

282

283 **Fig 4 – Composição de mamíferos terrestres durante as estações seca e chuvosa na área da**
284 **Floresta Nacional de Caxiuanã, Pará, Brasil.** (A) Análise de Coordenadas Principais (PCoA) para
285 a comunidade de mamíferos terrestres nas estações seca (cor laranja) e chuvosa (cor azul); (B) Análise
286 de *Procrustes Rotation*. As setas indicam a migração das espécies no espaço multivariado entre as
287 estações seca (círculos laranjas) e chuvosa (círculos azuis).

288

289 Detectabilidade e ocupação das espécies

290 Probabilidade de detecção - para os oito taxa que obtiveram o número suficiente de registros
291 em cada período amostral (> 10 imagens), apenas os modelos para as espécies *C. paca* e *D. leporina*
292 indicaram que a estação influenciou significativamente a detectabilidade destas espécies (Fig 5,
293 Tabela S1). O efeito da estação chuvosa foi negativo para *C. paca* e positivo para *D. leporina*, ou
294 seja, a probabilidade de detecção durante a estação chuvosa diminuiu para *C. paca* e aumentou para
295 *D. leporina*. Além disso, a temperatura também foi um importante preditor para *C. paca* e as espécies
296 do gênero *Dasybus*, apresentando um efeito negativo para ambas. Para *M. americana*, *M. nemorivaga*,
297 *P. tajacu*, os grandes felinos (*P. onca* + *P. concolor*) e *T. terrestris* o modelo nulo ($p(.)$) foi o mais
298 parcimonioso, não indicando influência da sazonalidade, precipitação ou temperatura na
299 probabilidade de detecção das mesmas (Tabela S1).

300 **Fig 5 – Efeitos da sazonalidade, precipitação e temperatura na probabilidade de detecção de**
301 ***Cuniculus paca*, *Dasyprocta leporina* e *Dasypus* spp.** Estimativas do valor de beta com 95% de
302 intervalo de confiança (As estimativas beta afetam a variável dependente quando o intervalo de
303 confiança não inclui o zero).

304

305 Probabilidade de ocupação – a sazonalidade foi um fator significativo apenas na ocupação de *D.*
306 *leporina* e *M. americana*, indicando que a ocupação destas espécies aumenta durante a estação
307 chuvosa (Fig 6; Tabela 2). Com relação as variáveis de habitat, a elevação foi uma preditora
308 significativa para *C. paca* (efeito negativo), *M. americana*, *Dasypus* spp e *T. terrestris* (efeito positivo
309 para todas as três). Entre três e cinco modelos obtiveram suporte substancial ($AIC < 2$) para *M.*
310 *nemorivaga*, *P. tajacu* e os grandes felinos (*P. onca* + *P. concolor*), elegendo todas as variáveis
311 (estação, HAND, distância para o rio e elevação; Tabela 2). Entretanto, nenhuma variável foi
312 considerada significativa para a ocupação destas espécies (Fig 6; Lista completa dos modelos em
313 Tabela S2).

314

315 **Fig 6 – Efeitos da sazonalidade, distância ao rio Caxiuanã, elevação e distância vertical à**
316 **drenagem (HAND) na ocupação de *Cuniculus paca*, *Dasyprocta leporina* e *Dasypus* spp, *Mazama***
317 ***americana*, *Mazama nemorivaga*, *Pecari tajacu*, *Panthera onca* + *Puma concolor* e *Tapirus***
318 ***terrestris*.** Estimativas do valor de beta com 95% de intervalo de confiança (As estimativas beta
319 afetam a variável dependente quando o intervalo de confiança não inclui o zero).

Tabela 2 – Melhores modelos de ocupação (AIC < 2) para os oito taxa avaliados (*Cuniculus paca*, *Dasyprocta leporina*, *Dasytus spp*, *Mazama americana*, *Mazama nemorivaga*, *Pecari tajacu*, *Panthera onca* + *Puma concolor* e *Tapirus terrestris*). A ocupação foi modelada em função da sazonalidade (estação), elevação (elev), distância ao rio Caxiuaná (rio) e distância vertical à drenagem (hand). As variáveis de detecção foram retidas na etapa anterior na qual a probabilidade de detecção foi avaliada em função da sazonalidade (estação), temperatura (temp) e precipitação (precip).

Espécies	Modelos	K	AIC/QAIC	Δ	Wt	CumltvWt
<i>C. paca</i>	$\Psi(\text{hand}+\text{elev})\text{p}(\text{estação}+\text{temp})$	7	643.77	0.00	0.55	0.55
<i>D. leporina</i>	$\Psi(\text{elev})\text{p}(\text{estação}+\text{precip})$	6	756.26	0.00	0.16	0.16
	$\Psi(\text{estação})\text{p}(\text{estação}+\text{precip})$	6	756.26	0.00	0.16	0.32
	$\Psi(\text{elev}+\text{estação})\text{p}(\text{estação}+\text{precip})$	7	756.47	0.21	0.14	0.46
	$\Psi(\cdot)\text{p}(\text{estação}+\text{precip})$	5	756.94	0.68	0.11	0.57
	$\Psi(\text{hand}+\text{estação})\text{p}(\text{estação}+\text{precip})$	7	757.60	1.34	0.08	0.66
	$\Psi(\text{rio}+\text{estação})\text{p}(\text{estação}+\text{precip})$	7	757.72	1.46	0.08	0.73
	$\Psi(\text{rio}+\text{elev})\text{p}(\text{estação}+\text{precip})$	7	758.08	1.82	0.06	0.80
	$\Psi(\text{hand}+\text{elev})\text{p}(\text{estação}+\text{precip})$	7	758.26	2.00	0.06	0.86
<i>Dasytus spp</i>	$\Psi(\text{hand}+\text{elev})\text{p}(\text{temp})$	6	798.44	0.00	0.66	0.66
<i>M. americana</i>	$\Psi(\text{elev}+\text{estação})\text{p}(\cdot)$	5	779.74	0.00	0.59	0.59
<i>M. nemorivaga</i>	$\Psi(\text{elev})\text{p}(\cdot)$	4	481.20	0.00	0.23	0.23
	$\Psi(\text{rio}+\text{elev})\text{p}(\cdot)$	5	481.94	0.74	0.16	0.38
	$\Psi(\cdot)\text{p}(\cdot)$	3	482.32	1.12	0.13	0.51
	$\Psi(\text{elev}+\text{estação})\text{p}(\cdot)$	5	482.62	1.42	0.11	0.62
	$\Psi(\text{hand}+\text{elev})\text{p}(\cdot)$	5	483.01	1.81	0.09	0.72
<i>P. tajacu</i>	$\Psi(\cdot)\text{p}(\cdot)$	3	275.76	0.00	0.26	0.26
	$\Psi(\text{hand})\text{p}(\cdot)$	4	277.15	1.39	0.13	0.40
	$\Psi(\text{elev})\text{p}(\cdot)$	4	277.40	1.63	0.12	0.51
	$\Psi(\text{rio})\text{p}(\cdot)$	4	277.51	1.75	0.11	0.62
	$\Psi(\text{estação})\text{p}(\cdot)$	4	277.76	2.00	0.10	0.72
<i>P. onca</i> + <i>P. concolor</i>	$\Psi(\text{hand}+\text{elev})\text{p}(\cdot)$	4	411.59	0	0.3873	0.39
	$\Psi(\text{rio}+\text{elev})\text{p}(\cdot)$	4	412.4	0.81	0.2578	0.65
	$\Psi(\text{global})\text{p}(\cdot)$	6	412.96	1.38	0.1946	0.84
<i>T. terrestris</i>	$\Psi(\text{elev})\text{p}(\cdot)$	3	388.92	0	0.33	0.33
	$\Psi(\text{rio}+\text{elev})\text{p}(\cdot)$	4	390.29	1.37	0.17	0.49
	$\Psi(\text{elev}+\text{estação})\text{p}(\cdot)$	4	390.83	1.91	0.13	0.62
	$\Psi(\text{hand}+\text{elev})\text{p}(\cdot)$	4	390.9	1.98	0.12	0.74

320

321

322 **Discussão**

323

324

325

Nós utilizamos a comunidade de mamíferos terrestres monitorados através de armadilhas fotográficas para testar se a variação sazonal exerce efeito na abundância, ocupação e detectabilidade dessas espécies, sugerindo que há alteração no uso do habitat condicionado à disponibilidade de

326 recursos, como alimento e água. Nossos resultados indicaram que independente do esforço amostral
327 e da estação (seca/chuvosa), não houve diferença significativa na composição e abundância total das
328 espécies. A riqueza de espécies encontrada neste estudo foi similar à outros estudos realizados na
329 Amazônia utilizando armadilhas fotográficas [9,12,28,50], registrando desde espécies comuns
330 àquelas consideradas mais raras, assim como as ameaçadas de extinção.

331 Nossa hipótese de que os mamíferos podem modificar sua área de uso de acordo com as
332 estações considerou que a sazonalidade marcante, tanto pela quantidade de chuva quanto pela
333 disponibilidade de frutos e sementes em cada estação [14], é um elemento chave influenciando a
334 dinâmica das espécies na área. Portanto, a similaridade na composição e abundância total das espécies
335 entre as estações pode ser explicado pelo fato das espécies serem residentes na área. De maneira geral,
336 uma variação temporal marcante é mais evidente em espécies migratórias, enquanto que a abundância
337 de espécies residentes pode permanecer constante durante todo o ano [51]. O nosso resultado foi
338 semelhante ao encontrado para outros estudos em áreas de terra firme, o quais também observaram
339 apenas três espécies apresentando diferenças significativas na abundância entre os períodos [16,28].
340 Costa et al [16] observou que as diferenças na abundância foram maiores quando as florestas de terra
341 firme foram comparadas às de várzea. Essa movimentação lateral entre os diferentes tipos florestais
342 é explicada pelo longo período de alagamento das áreas de várzea, o qual restringe o fluxo de espécies
343 estritamente terrestres e de sub-bosque durante a alta no pulso de inundação e, por outro lado, oferece
344 um grande aporte de frutos e sementes no solo quando as águas baixam [17].

345 Mesmo não observando grandes variações na abundância, nossos resultados mostraram
346 algumas evidências de que tanto a detectabilidade quanto a ocupação de mamíferos podem variar
347 sazonalmente na FLONA de Caxiuanã. Entre as espécies analisadas, a sazonalidade foi importante
348 na detectabilidade de *C. paca* e *D. leporina*, apresentando, respectivamente, menor e maior
349 probabilidade de detecção durante a estação chuvosa. Esse efeito contrário que observamos para estes
350 dois roedores provavelmente está associado as estratégias de forrageamento e hábitos de vida de cada
351 espécie. Por exemplo, ambas as espécies podem se alimentar de frutos e sementes, porém apresentam

352 períodos de atividades antagônicos, sendo *C. paca* um animal primariamente noturno e *D. leporina*
353 apresentando seus picos de atividade durante o dia [52–55]. Este fator também explicaria a influência
354 da temperatura na detectabilidade de *C. paca*, mas não de *D. leporina*. Nossos resultados sugerem
355 que uma temperatura mais alta implicaria em uma menor movimentação de *C. paca* e,
356 conseqüentemente, menor detecção. O mesmo foi observado para as espécies de tatu do gênero
357 *Dasypus*, os quais também são notívagos [2].

358 Embora alguns estudos tenham discutido a influência da temperatura no padrão de atividade
359 das espécies [54,56,57], nós devemos ser cautelosos diante do efeito desta variável na detectabilidade.
360 Isso porque nossas estimativas de temperatura correspondem a médias diárias, não contemplando a
361 variação ou amplitude da temperatura ao longo de todo o dia e, portanto do momento específico da
362 detecção. Na FLONA de Caxiuanã observamos que a temperatura pode variar entre 23.4°C e 33.7° ao
363 longo de 24 horas (dados não publicados do monitoramento climático do projeto TEAM Network).

364 Assim como proposto neste estudo, Martin et al [18] estudando a comunidade de mamíferos
365 em uma floresta tropical na Tanzânia, não observaram influência da estação na detectabilidade da
366 maioria das espécies analisadas (exceção apenas para o porco africano [*Potamochoerus larvatus*]),
367 mesmo considerando que o maior volume de chuva implicaria em um padrão diferente na
368 movimentação dos animais e uma potencial diferença na sensibilidade das armadilhas fotográficas.
369 Além da variável categórica utilizada por Martin et al [18], nosso estudo também incluiu os valores
370 de precipitação de cada período e, ainda assim, a variável teve suporte apenas nos modelos de *D.*
371 *leporina*, indicando que o volume de chuva não exerce influência direta na probabilidade de detecção
372 das espécies.

373 A ocupação variou conforme a estação para *D. leporina* e *M. americana*, ou seja, a proporção
374 de sítios ocupados foi maior para estas espécies durante a estação chuvosa, corroborando em parte
375 nossa hipótese, já que era esperado que espécies como *C. paca*, *M. nemorivaga*, *P. tajacu* e *T.*
376 *terrestris*, as quais também se alimentam de frutos e sementes, apresentassem diferenças em sua área
377 de uso em função da sazonalidade. No caso de *C. paca*, a ocorrência esteve associada à proximidade

378 de corpos d'água e áreas de baixa elevação, confirmando um padrão já observado para espécie
379 [27,28]. Assim, a não associação de *C. paca* à variável estação pode estar relacionada ao uso de
380 recursos provenientes da floresta de igapó, a qual apresenta uma composição florística diferenciada
381 e poderia oferecer recursos em períodos diferentes do que a floresta de terra firme [25].

382 A sazonalidade já foi associada como um fator chave na movimentação de *P. tajacu*,
383 observando-se migrações dentro de sua área de vida reguladas por flutuações na disponibilidade de
384 alimentos [13,58]. No entanto, nossos melhores modelos para *P. tajacu* não indicaram associação
385 significativa entre a ocupação e a sazonalidade, ou a qualquer outra variável. Resultados similares
386 foram relatados previamente para variáveis descritoras de habitat, não sendo encontrada relação entre
387 a abundância de *P. tajacu* e a disponibilidade de frutos, altitude ou distância de rios e igarapés [27].
388 Também observamos a ausência de preditores significativos nos modelos de *M. nemorivaga*,
389 sugerindo que a ocorrência desses dois ungulados pode não ser limitada por um determinado
390 gradiente ou mesmo estar associada a outros fatores bióticos ou de interações interespecíficas não
391 mensurados neste estudo.

392 Para *Tapirus terrestris* apenas a elevação apresentou efeito positivo na ocupação, o que difere
393 de outros estudos nos quais a proximidade de corpos d'água aparece como um dos principais
394 preditores para a ocorrência desta espécie [59,60]. Além disso, a ocupação de *T. terrestris* é bastante
395 associada a presença de palmeiras [p.ex., buriti (*Mauritia flexuosa*)] das quais a espécie se alimenta
396 [60,61]. Na FLONA de Caxiuanã, o buriti é mais abundante em áreas de várzea, as quais não foram
397 amostradas neste estudo [25], portanto uma maior investigação é necessária para elucidar a influência
398 da elevação na ocupação desta espécie.

399 Como esperado, os grandes felinos e as espécies do gênero *Dasybus* não foram afetados pela
400 sazonalidade. Predadores de topo, como *Panthera onca*, utilizam o habitat em função da distribuição
401 de suas presas, sendo menos influenciados por variáveis como elevação ou distância de corpos d'água
402 [62]. Ainda assim, *P. onca* + *P. concolor* apresentaram uma relação positiva com a distância vertical
403 à drenagem, o que difere do padrão geral encontrado para estas espécies [63,64]. Já para as espécies

404 de *Dasybus* a maior ocupação esteve associada à proximidade da distância à drenagem e a elevação,
405 confirmando seus hábitos de construir tocas em terrenos íngremes ao longo de encostas de igarapés
406 [2].

407

408 **Conclusões**

409 Este estudo apresenta novos dados para compreensão da dinâmica sazonal de mamíferos
410 terrestres em florestas tropicais, contabilizando a probabilidade de detecção das espécies. Nossos
411 resultados demonstram que a sazonalidade influenciou a ocupação e detecção de espécies como *C.*
412 *paca*, *D. leporina* e *M. americana*, enquanto que a ocorrência de outras espécies analisadas não foi
413 influenciada pela estação mas sim por outras características do habitat, como elevação e distância
414 vertical à drenagem.

415 Nosso resultados mostram que a comunidade de mamíferos terrestres na FLONA de Caxiuanã
416 está bastante íntegra, tendo sido observadas espécies importantes para a manutenção das florestas,
417 como grandes dispersores e predadores de topo. Este estudo contribui para a avaliação do *status* desta
418 comunidade, e também ressalta que o monitoramento contínuo é essencial para avaliar as potenciais
419 mudanças na dinâmica destas espécies diante das atividades extrativistas aprovadas no plano de
420 manejo da unidade [24]. Nós sugerimos que futuros estudos ampliem o número de espécies analisadas
421 e incorporem outros fatores para compreender o que influencia a distribuição e permanência de
422 mamíferos em uma área de grande interesse para preservação.

423

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431

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599 **Lista de Material Suplementar**

600 **Tabela S1 – Modelos utilizados para avaliar os efeitos da estação (seca/chuvosa), precipitação**
601 **(prec) e temperatura (temp) na probabilidade de detecção (p) das oito espécies de mamíferos**
602 **analisadas.**

603 **Tabela S2 – Modelos utilizados para avaliar os efeitos da estação (seca/chuvosa), distância do**
604 **rio principal (rio), distância vertical à drenagem (hand) e elevação (elev) na probabilidade de**
605 **ocupação (Ψ) das oito espécies de mamíferos analisadas.**

FIGURAS

Fig 1

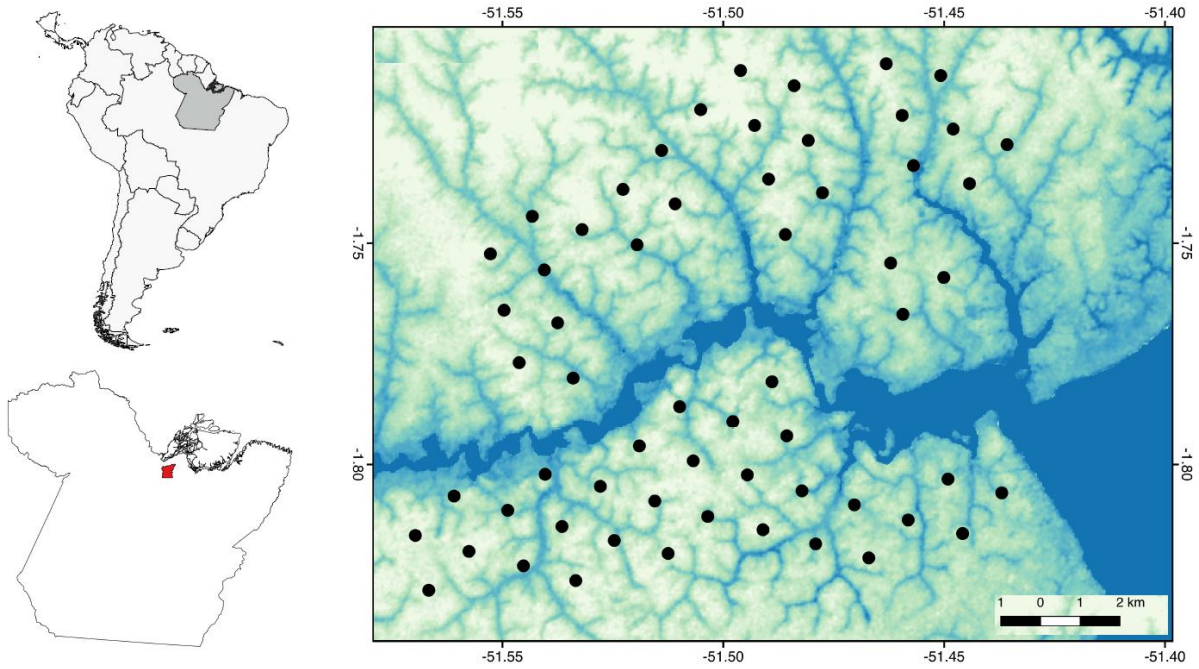


Fig 2

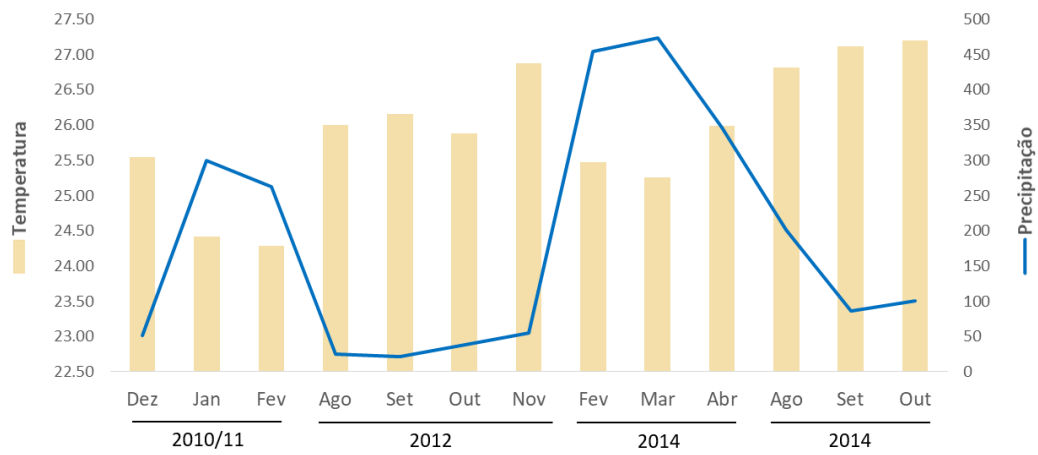


Fig 3

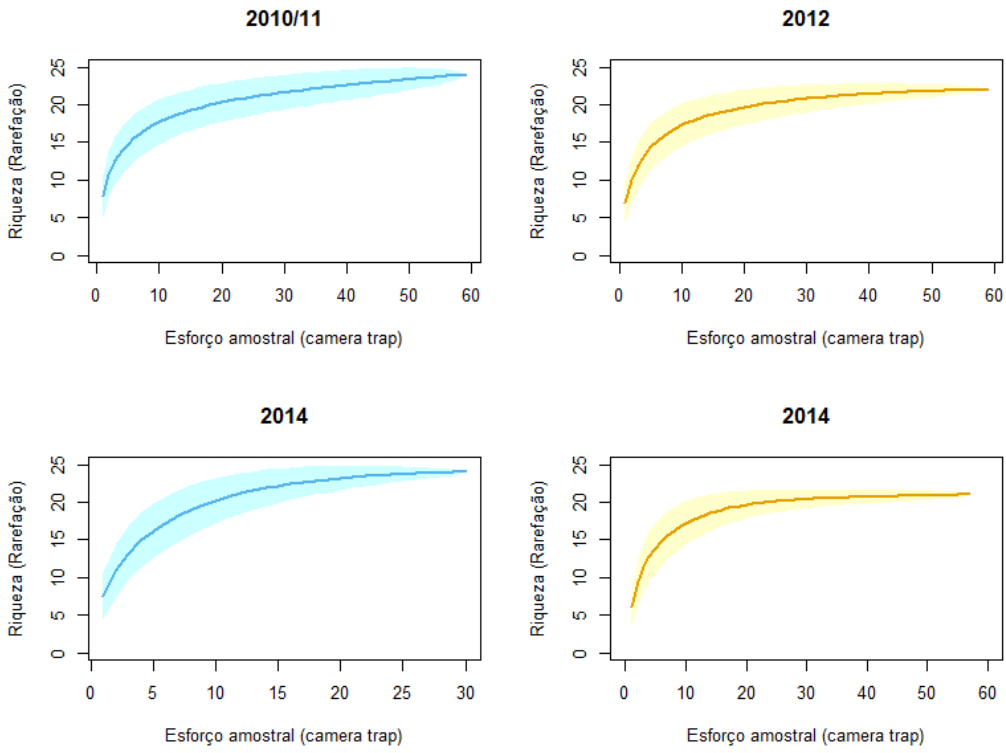


Fig 4

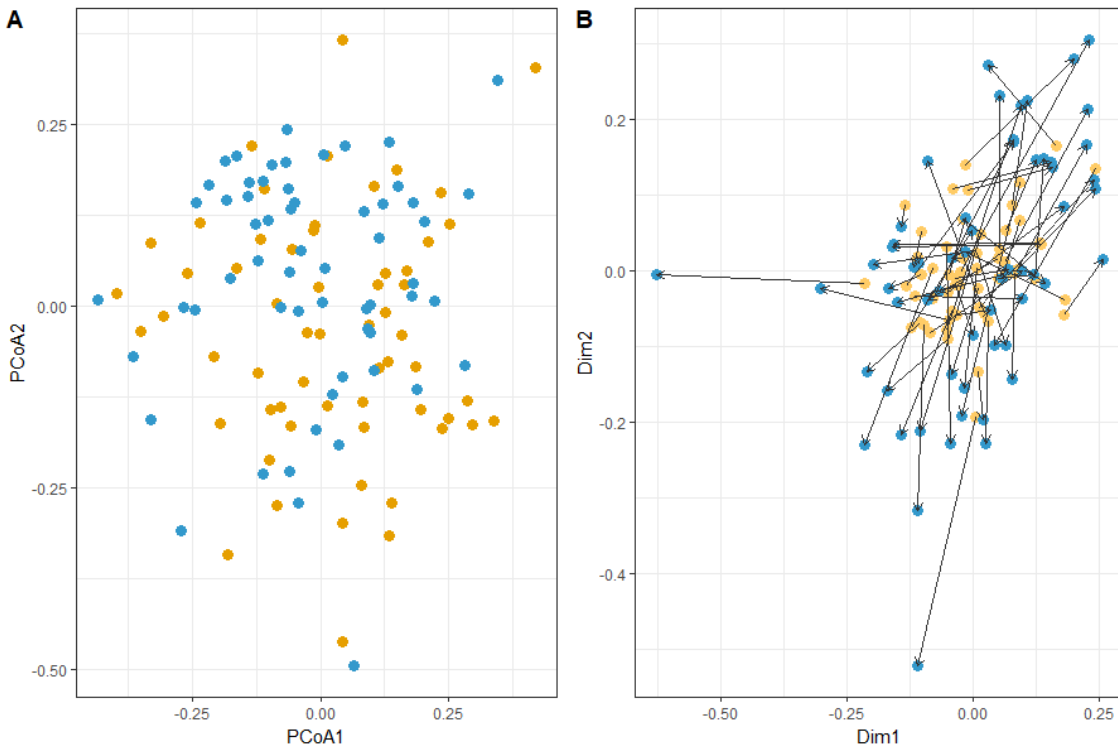


Fig 5

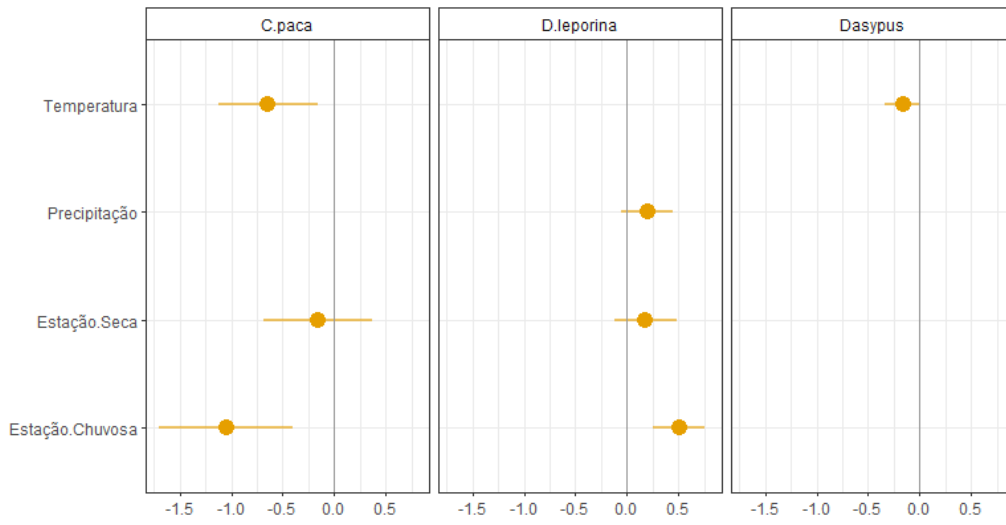
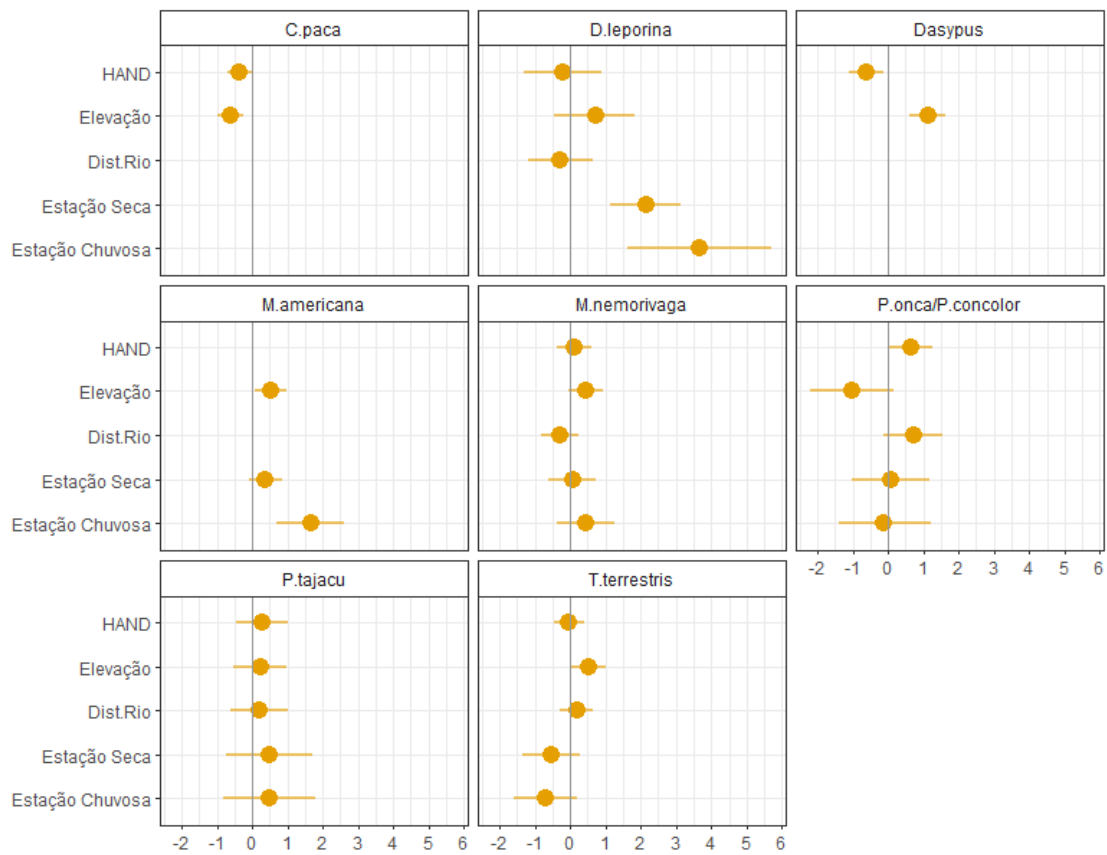


Fig 6



MATERIAL SUPLEMENTAR

Tabela S1 – Modelos utilizados para avaliar os efeitos da estação (seca/chuvosa), precipitação (prec) e temperatura (temp) na probabilidade de detecção (p) das oito espécies de mamíferos analisadas.

Espécies	Modelos	K	QAIC	Δ	QAICWt	Cum.Wt
<i>Cuniculus paca</i>	$\Psi(.)p(\text{estação}+\text{temp})$	5	664.43	0.00	0.40	0.40
	$\Psi(.)p(\text{temp})$	4	665.62	1.19	0.22	0.61
	$\Psi(.)p(\text{global})$	6	665.99	1.56	0.18	0.80
	$\Psi(.)p(\text{prec}+\text{temp})$	5	666.97	2.53	0.11	0.91
	$\Psi(.)p(.)$	3	669.22	4.78	0.04	0.94
	$\Psi(.)p(\text{estação})$	4	669.69	5.25	0.03	0.97
	$\Psi(.)p(\text{prec})$	4	670.96	6.53	0.02	0.99
	$\Psi(.)p(\text{estação}+\text{prec})$	5	671.31	6.88	0.01	1.00
<i>Dasyprocta leporina</i>	$\Psi(.)p(\text{estação})$	4	756.35	0.00	0.23	0.23
	$\Psi(.)p(\text{prec})$	4	756.40	0.05	0.23	0.46
	$\Psi(.)p(\text{estação}+\text{prec})$	5	756.76	0.41	0.19	0.65
	$\Psi(.)p(\text{prec}+\text{temp})$	5	757.30	0.96	0.14	0.79
	$\Psi(.)p(\text{estação}+\text{temp})$	5	757.76	1.42	0.11	0.90
	$\Psi(.)p(\text{global})$	6	758.73	2.39	0.07	0.97
	$\Psi(.)p(\text{temp})$	4	760.88	4.53	0.02	1.00
	$\Psi(.)p(.)$	3	764.68	8.33	0.00	1.00
<i>Dasyopus spp.</i>	$\Psi(.)p(\text{temp})$	4	781.59	0.00	0.28	0.28
	$\Psi(.)p(.)$	3	782.46	0.88	0.18	0.46
	$\Psi(.)p(\text{estação})$	4	783.04	1.46	0.13	0.59
	$\Psi(.)p(\text{estação}+\text{temp})$	5	783.23	1.64	0.12	0.71
	$\Psi(.)p(\text{prec}+\text{temp})$	5	783.50	1.91	0.11	0.82
	$\Psi(.)p(\text{prec})$	4	784.07	2.48	0.08	0.90
	$\Psi(.)p(\text{estação}+\text{prec})$	5	784.85	3.27	0.05	0.95
	$\Psi(.)p(\text{global})$	6	785.19	3.60	0.05	1.00
<i>Mazama americana</i>	$\Psi(.)p(.)$	3	832.00	0.00	0.30	0.30
	$\Psi(.)p(\text{temp})$	4	833.21	1.21	0.16	0.47
	$\Psi(.)p(\text{prec})$	4	833.77	1.78	0.12	0.59
	$\Psi(.)p(\text{estação})$	4	833.88	1.88	0.12	0.71
	$\Psi(.)p(\text{prec}+\text{temp})$	5	834.28	2.29	0.10	0.80
	$\Psi(.)p(\text{estação}+\text{temp})$	5	834.44	2.45	0.09	0.89
	$\Psi(.)p(\text{estação}+\text{prec})$	5	834.91	2.91	0.07	0.96
	$\Psi(.)p(\text{global})$	6	836.20	4.21	0.04	1.00
<i>Mazama nemorivaga</i>	$\Psi(.)p(.)$	3	488.57	0.00	0.37	0.37
	$\Psi(.)p(\text{temp})$	4	490.42	1.85	0.15	0.51

	$\Psi(.)p(\text{prec})$	4	490.45	1.88	0.14	0.65
	$\Psi(.)p(\text{estaç\~{a}o})$	4	490.53	1.96	0.14	0.79
	$\Psi(.)p(\text{estaç\~{a}o}+\text{prec})$	5	492.02	3.45	0.07	0.86
	$\Psi(.)p(\text{prec}+\text{temp})$	5	492.08	3.51	0.06	0.92
	$\Psi(.)p(\text{estaç\~{a}o}+\text{temp})$	5	492.34	3.77	0.06	0.98
	$\Psi(.)p(\text{global})$	6	494.02	5.45	0.02	1.00
<i>P. onca + P. concolor</i>	$\Psi(.)p(.)$	2	419.79	0.00	0.31	0.31
	$\Psi(.)p(\text{temp})$	3	420.80	1.01	0.19	0.50
	$\Psi(.)p(\text{estaç\~{a}o})$	3	421.46	1.66	0.14	0.64
	$\Psi(.)p(\text{prec})$	3	421.62	1.82	0.13	0.76
	$\Psi(.)p(\text{estaç\~{a}o}+\text{temp})$	4	422.48	2.69	0.08	0.85
	$\Psi(.)p(\text{prec}+\text{temp})$	4	422.80	3.01	0.07	0.91
	$\Psi(.)p(\text{estaç\~{a}o}+\text{prec})$	4	423.46	3.66	0.05	0.96
	$\Psi(.)p(\text{global})$	5	424.15	4.36	0.04	1.00
<i>Pecari tajacu</i>	$\Psi(.)p(.)$	3	278.70	0.00	0.35	0.35
	$\Psi(.)p(\text{estaç\~{a}o})$	4	280.27	1.57	0.16	0.51
	$\Psi(.)p(\text{temp})$	4	280.33	1.62	0.16	0.67
	$\Psi(.)p(\text{prec})$	4	280.62	1.92	0.13	0.80
	$\Psi(.)p(\text{estaç\~{a}o}+\text{prec})$	5	282.19	3.49	0.06	0.86
	$\Psi(.)p(\text{estaç\~{a}o}+\text{temp})$	5	282.27	3.57	0.06	0.92
	$\Psi(.)p(\text{prec}+\text{temp})$	5	282.33	3.62	0.06	0.98
	$\Psi(.)p(\text{global})$	6	284.19	5.49	0.02	1.00
<i>Tapirus terrestris</i>	$\Psi(.)p(.)$	2	392.19	0.00	0.32	0.32
	$\Psi(.)p(\text{estaç\~{a}o})$	3	393.49	1.30	0.17	0.48
	$\Psi(.)p(\text{temp})$	3	394.04	1.85	0.13	0.61
	$\Psi(.)p(\text{prec})$	3	394.19	2.00	0.12	0.72
	$\Psi(.)p(\text{estaç\~{a}o}+\text{prec})$	4	394.96	2.77	0.08	0.80
	$\Psi(.)p(\text{estaç\~{a}o}+\text{temp})$	4	394.97	2.77	0.08	0.88
	$\Psi(.)p(\text{global})$	5	395.19	3.00	0.07	0.95
	$\Psi(.)p(\text{prec}+\text{temp})$	4	396.03	3.83	0.05	1.00

Tabela S2 – Modelos utilizados para avaliar os efeitos da estação (seca/chuvosa), distância do rio principal (rio), distância vertical à drenagem (hand) e elevação (elev) na probabilidade de ocupação (Ψ) das oito espécies de mamíferos analisadas.

Espécies	Modelos	K	QAIC	Δ	QAICWt	Cum.Wt
<i>Cuniculus paca</i>	$\Psi(\text{hand}+\text{elev})\text{p}(\text{estação}+\text{temp})$	7	643.77	0.00	0.55	0.55
	$\Psi(\text{elev})\text{p}(\text{estação}+\text{temp})$	6	646.00	2.23	0.18	0.73
	$\Psi(\text{global})\text{p}(\text{estação}+\text{temp})$	9	647.23	3.45	0.10	0.82
	$\Psi(\text{rio}+\text{elev})\text{p}(\text{estação}+\text{temp})$	7	647.51	3.74	0.08	0.91
	$\Psi(\text{elev}+\text{estação})\text{p}(\text{estação}+\text{temp})$	7	647.59	3.82	0.08	0.99
	$\Psi(\text{hand})\text{p}(\text{estação}+\text{temp})$	6	654.13	10.36	0.00	0.99
	$\Psi(.)\text{p}(\text{estação}+\text{temp})$	5	655.46	11.69	0.00	0.99
	$\Psi(\text{rio}+\text{hand})\text{p}(\text{estação}+\text{temp})$	7	655.56	11.79	0.00	1.00
	$\Psi(\text{hand}+\text{estação})\text{p}(\text{estação}+\text{temp})$	7	655.61	11.84	0.00	1.00
	$\Psi(\text{rio})\text{p}(\text{estação}+\text{temp})$	6	655.72	11.95	0.00	1.00
	$\Psi(\text{estação})\text{p}(\text{estação}+\text{temp})$	6	657.07	13.30	0.00	1.00
	$\Psi(\text{rio}+\text{estação})\text{p}(\text{estação}+\text{temp})$	7	657.27	13.50	0.00	1.00
<i>Dasyprocta leporina</i>	$\Psi(\text{elev})\text{p}(\text{estação}+\text{prec})$	6	756.26	0.00	0.16	0.16
	$\Psi(\text{estação})\text{p}(\text{estação}+\text{prec})$	6	756.26	0.00	0.16	0.32
	$\Psi(\text{elev}+\text{estação})\text{p}(\text{estação}+\text{prec})$	7	756.47	0.21	0.14	0.46
	$\Psi(.)\text{p}(\text{estação}+\text{prec})$	5	756.94	0.68	0.11	0.57
	$\Psi(\text{hand}+\text{estação})\text{p}(\text{estação}+\text{prec})$	7	757.60	1.34	0.08	0.66
	$\Psi(\text{rio}+\text{estação})\text{p}(\text{estação}+\text{prec})$	7	757.72	1.46	0.08	0.73
	$\Psi(\text{rio}+\text{elev})\text{p}(\text{estação}+\text{prec})$	7	758.08	1.82	0.06	0.80
	$\Psi(\text{hand}+\text{elev})\text{p}(\text{estação}+\text{prec})$	7	758.26	2.00	0.06	0.86
	$\Psi(\text{hand})\text{p}(\text{estação}+\text{prec})$	6	758.45	2.19	0.05	0.91
	$\Psi(\text{rio})\text{p}(\text{estação}+\text{prec})$	6	758.88	2.62	0.04	0.95
	$\Psi(\text{global})\text{p}(\text{estação}+\text{prec})$	9	759.72	3.46	0.03	0.98
	$\Psi(\text{rio}+\text{hand})\text{p}(\text{estação}+\text{prec})$	7	760.45	4.19	0.02	1.00
<i>Dasyopus spp.</i>	$\Psi(\text{hand}+\text{elev})\text{p}(\text{temp})$	6	798.44	0.00	0.66	0.66
	$\Psi(\text{global})\text{p}(\text{temp})$	8	801.06	2.62	0.18	0.84
	$\Psi(\text{elev})\text{p}(\text{temp})$	5	802.44	4.00	0.09	0.93
	$\Psi(\text{elev}+\text{estação})\text{p}(\text{temp})$	6	804.34	5.90	0.03	0.97
	$\Psi(\text{rio}+\text{elev})\text{p}(\text{temp})$	6	804.44	5.99	0.03	1.00
	$\Psi(\text{rio}+\text{hand})\text{p}(\text{temp})$	6	817.48	19.04	0	1
	$\Psi(\text{hand})\text{p}(\text{temp})$	5	819.65	21.21	0	1
	$\Psi(\text{hand}+\text{estação})\text{p}(\text{temp})$	6	821.52	23.08	0	1
	$\Psi(.)\text{p}(\text{temp})$	4	823.51	25.07	0	1
	$\Psi(\text{rio})\text{p}(\text{temp})$	5	824.08	25.64	0	1
	$\Psi(\text{estação})\text{p}(\text{temp})$	5	825.49	27.05	0	1
	$\Psi(\text{rio}+\text{estação})\text{p}(\text{temp})$	6	826.08	27.64	0	1
<i>Mazama americana</i>	$\Psi(\text{elev}+\text{estação})\text{p}(\cdot)$	5	779.74	0.00	0.59	0.59

	$\Psi(\text{estação})p(.)$	4	783.24	3.50	0.10	0.69
	$\Psi(\text{global})p(.)$	7	783.57	3.83	0.09	0.78
	$\Psi(\text{elev})p(.)$	4	784.63	4.88	0.05	0.83
	$\Psi(\text{rio+estação})p(.)$	5	784.64	4.89	0.05	0.88
	$\Psi(\text{hand+estação})p(.)$	5	785.19	5.45	0.04	0.92
	$\Psi(\text{rio+elev})p(.)$	5	786.27	6.53	0.02	0.95
	$\Psi(\text{hand+elev})p(.)$	5	786.36	6.62	0.02	0.97
	$\Psi(.)p(.)$	3	787.09	7.34	0.02	0.98
	$\Psi(\text{rio})p(.)$	4	788.22	8.48	0.01	0.99
	$\Psi(\text{hand})p(.)$	4	788.93	9.19	0.01	1.00
	$\Psi(\text{rio+hand})p(.)$	5	790.21	10.47	0.00	1.00
<i>Mazama nemorivaga</i>	$\Psi(\text{elev})p(.)$	4	481.20	0.00	0.23	0.23
	$\Psi(\text{rio+elev})p(.)$	5	481.94	0.74	0.16	0.38
	$\Psi(.)p(.)$	3	482.32	1.12	0.13	0.51
	$\Psi(\text{elev+estação})p(.)$	5	482.62	1.42	0.11	0.62
	$\Psi(\text{hand+elev})p(.)$	5	483.01	1.81	0.09	0.72
	$\Psi(\text{estação})p(.)$	4	483.72	2.51	0.06	0.78
	$\Psi(\text{rio})p(.)$	4	483.91	2.71	0.06	0.84
	$\Psi(\text{hand})p(.)$	4	484.31	3.11	0.05	0.89
	$\Psi(\text{global})p(.)$	7	484.74	3.53	0.04	0.92
	$\Psi(\text{rio+estação})p(.)$	5	485.27	4.07	0.03	0.95
	$\Psi(\text{hand+estação})p(.)$	5	485.70	4.50	0.02	0.98
	$\Psi(\text{rio+hand})p(.)$	5	485.85	4.65	0.02	1.00
<i>P. onca + P. concolor</i>	$\Psi(\text{hand+elev})p(.)$	4	411.59	0	0.39	0.39
	$\Psi(\text{rio+elev})p(.)$	4	412.4	0.81	0.26	0.65
	$\Psi(\text{global})p(.)$	6	412.96	1.38	0.19	0.84
	$\Psi(\text{hand})p(.)$	3	415.49	3.9	0.06	0.89
	$\Psi(\text{elev})p(.)$	3	416.61	5.03	0.03	0.93
	$\Psi(\text{hand+estação})p(.)$	4	417.13	5.55	0.02	0.95
	$\Psi(\text{rio+hand})p(.)$	4	417.35	5.76	0.02	0.97
	$\Psi(\text{elev+estação})p(.)$	4	418.57	6.99	0.01	0.98
	$\Psi(.)p(.)$	2	419.79	8.21	0.01	0.99
	$\Psi(\text{rio})p(.)$	3	420.26	8.68	0.01	1
	$\Psi(\text{estação})p(.)$	3	421.58	10	0.00	1
	$\Psi(\text{rio+estação})p(.)$	4	422	10.42	0.00	1
<i>Pecari tajacu</i>	$\Psi(.)p(.)$	3	275.76	0.00	0.26	0.26
	$\Psi(\text{hand})p(.)$	4	277.15	1.39	0.13	0.40
	$\Psi(\text{elev})p(.)$	4	277.40	1.63	0.12	0.51
	$\Psi(\text{rio})p(.)$	4	277.51	1.75	0.11	0.62
	$\Psi(\text{estação})p(.)$	4	277.76	2.00	0.10	0.72
	$\Psi(\text{hand+elev})p(.)$	5	278.66	2.90	0.06	0.78

	$\Psi(\text{rio+hand})p(.)$	5	279.08	3.32	0.05	0.83
	$\Psi(\text{hand+estação})p(.)$	5	279.15	3.39	0.05	0.88
	$\Psi(\text{rio+elev})p(.)$	5	279.22	3.46	0.05	0.93
	$\Psi(\text{rio+estação})p(.)$	5	279.50	3.74	0.04	0.97
	$\Psi(\text{elev+estação})p(.)$	5	280.72	4.96	0.02	0.99
	$\Psi(\text{global})p(.)$	7	282.61	6.85	0.01	1.00
<i>Tapirus terrestris</i>	$\Psi(\text{elev})p(.)$	3	388.92	0	0.33	0.33
	$\Psi(\text{rio+elev})p(.)$	4	390.29	1.37	0.17	0.49
	$\Psi(\text{elev+estação})p(.)$	4	390.83	1.91	0.13	0.62
	$\Psi(\text{hand+elev})p(.)$	4	390.9	1.98	0.12	0.74
	$\Psi(.)p(.)$	2	392.19	3.27	0.06	0.81
	$\Psi(\text{rio})p(.)$	3	392.5	3.58	0.05	0.86
	$\Psi(\text{rio+hand})p(.)$	4	393.83	4.91	0.03	0.89
	$\Psi(\text{global})p(.)$	6	393.91	4.99	0.03	0.92
	$\Psi(\text{hand})p(.)$	3	394.05	5.13	0.03	0.94
	$\Psi(\text{estação})p(.)$	3	394.05	5.13	0.03	0.97
	$\Psi(\text{rio+estação})p(.)$	4	394.22	5.3	0.02	0.99
	$\Psi(\text{hand+estação})p(.)$	4	395.94	7.02	0.01	1.00

5. CONCLUSÃO GERAL

Do ponto de vista da conservação da diversidade, o presente estudo avaliou a singularidade ecológica em termos de composição de espécies em cada área de estudo, e mais especificamente, em cada ponto amostral (i.e., *camera trap*), permitindo identificar os processos que explicam uma maior ou menor diversidade β entre as comunidades de mamíferos terrestres em oito florestas neotropicais. O estudo mostra que áreas de floresta contínua foram mais similares entre si e diferiram significativamente das áreas fragmentadas, resultando em maiores estimativas de diversidade β para as áreas menores ($>$ LCBD). Tanto a substituição quanto a diferença na riqueza de espécies atuam entre estas comunidades, mas foi a diferença na riqueza de espécies o principal fator para a variação encontrada entre as áreas.

A diversidade β esteve associada à distância espacial e também à fatores da paisagem, como o tamanho da área e aspectos da vegetação (NDVI e área basal). Outro ponto relevante foi a identificação de quais as espécies que mais contribuem para a diversidade β (SCBD). As espécies com maior SCBD apresentaram maior abundância, ocupação naïve e são em sua maioria herbívoras, enquanto que espécies carnívoras obtiveram os menores índices. Os resultados indicam que as comunidades de mamíferos em áreas de floresta contínua são mais complexas do que as áreas fragmentadas, nas quais os herbívoros são abundantes e carnívoros de grande porte, como onça pintada (*P. onca*) e onça parda (*P. concolor*), estão localmente extintos ou apresentam menor abundância relativa. Através desta abordagem proposta por LEGENDRE & DE CÁCERES (2013), a qual considera a contribuição local (LCBD) e das espécies (SCBD) para a diversidade β , é possível identificar e focar esforços de conservação em sítios ou espécies específicos, sendo uma ferramenta fundamental para o desenvolvimento de planos de manejo e restauração nestas áreas a fim de manter a diversidade regional (γ).

A variação na riqueza e abundância de espécies são características que podem influenciar nos mecanismos de seleção de recursos, atividades circadianas e uso do espaço das espécies, principalmente àquelas que são ecologicamente similares, como os felinos. Este estudo ampliou o conhecimento sobre os mecanismos de coexistência, avaliando os padrões de uso de espaço e sobreposição nos padrões de atividade de cinco espécies felinos [onça pintada (*P. onca*), onça parda (*P. concolor*), jaguatirica (*L. pardalis*), jaguarundi (*H. yagouaroundi*) e gato maracajá (*Leopardus wiedii*)] ao longo de oito áreas florestais que apresentam diferentes contextos de paisagem.

Os resultados mostram que onça pintada, onça parda e jaguatirica exibiram padrões claros de diferenciação no uso do habitat, havendo maior influência da disponibilidade de presas do que das variáveis ambientais e da interação entre as espécies. Os menores coeficientes de sobreposição nos padrões de atividade foram observados entre as espécies menores (jaguarundi-jaguarundi e

jaguarundi-gato-maracajá), sugerindo que a competição interespecífica desempenha um papel importante entre jaguatirica e as espécies menores de felinos. O estudo revela que há algum nível de sobreposição espacial e temporal, principalmente entre as três espécies de maior porte, mas vai além ao avaliar numa escala fina a disponibilidade local de recursos e os padrões de atividade, detectando o particionamento de nicho e as diferenças no comportamento dos felinos entre os locais de estudo.

Por fim, discutiu-se a influência da sazonalidade nos padrões de movimentação das espécies em função da variação da disponibilidade de água e recursos alimentares (considerando que a disponibilidade de flores e frutos é maior na estação seca). O estudo vêm preencher uma lacuna no conhecimento sobre a dinâmica sazonal de espécies em florestas tropicais, pois a grande maioria dos estudos é de curto prazo ou a amostragem é realizada apenas durante os períodos de menor precipitação. Os resultados demonstram que a composição de espécies e a abundância total não variaram significativamente entre as estações, porém que a sazonalidade influenciou a ocupação e detecção de espécies como paca (*C. paca*), cotia (*D. leporina*) e veado vermelho (*M. americana*). A ocorrência de outras espécies analisadas não foi influenciada pela estação ou variáveis climáticas, mas sim por características do habitat, como elevação e a distância vertical à drenagem.

Do ponto de vista metodológico, não houve diferença significativa na riqueza e abundância total das espécies entre os períodos de amostragem e estações, mesmo considerando diferenças no esforço amostral em cada um (apenas 30 armadilhas fotográficas foram instaladas durante a estação chuvosa em 2014, enquanto que 60 foram instaladas nos demais períodos). Isso indica que o monitoramento através de armadilhas fotográficas é bastante eficiente para registrar a mastofauna terrestre e seus padrões gerais de riqueza e abundância quando utiliza-se um esforço concentrado e um desenho amostral que contemple uma extensão de área suficiente para englobar diferentes características do habitat. Nosso estudo demonstrou que o efeito da sazonalidade pode ser limitado para mamíferos considerados residentes na área (i.e., não migratórios), mas ressalta a importância de considerar mudanças ao longo do ano para o melhor entendimento da dinâmica destas espécies em florestas tropicais.

Este estudo destaca a importância do uso de diferentes abordagens para descrever os padrões de diversidade de mamíferos terrestres de uma das regiões mais ricas do planeta. Compreender como essa diversidade está distribuída em diferentes escalas, seja em um ponto de armadilha fotográfica, um sítio ou uma região, permite uma melhor avaliação de como as características bióticas, fatores espaciais, bem como os desencadeados por ações antrópicas, podem influenciar os mamíferos terrestres e suas interações. Estas informações são fundamentais no delineamento de estratégias para a conservação tanto das espécies quanto das próprias florestas.

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