

UNIVERSIDADE DE SÃO PAULO  
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO  
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

**“Drivers of game species depletion in sustainable-use protected areas of the  
Brazilian Amazon”**

**“Vetores da depleção de espécies cinegéticas em áreas protegidas de uso  
sustentável na Amazônia Brasileira”**

Ricardo Sampaio

Tese apresentada à Faculdade de Filosofia,  
Ciências e Letras de Ribeirão Preto da  
Universidade de São Paulo, como parte das  
exigências para obtenção do título de Doutor em  
Ciências, obtido no Programa de Pós-Graduação  
em Biologia Comparada

Ribeirão Preto - SP

(2021)



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Orientador: Prof. Dr. Adriano Garcia Chiarello

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1. Efetividade de áreas protegidas 2. Caça de subsistência  
3. Defaunação 5. Carne de caça 6. Manejo de base comunitária 7. Conhecimento ecológico tradicional 8. Riqueza de espécies 9. Modelagem da ocupação 10. Manejo de fauna.

*In memory of **Peter Crawshaw Jr**, who unfortunately was one of the thousands of victims of COVID in Brazil in 2021.*

*Peter was one of the pioneers in the study and conservation of the jaguar in Brazil, in addition to being the founder of the National Center for Research and Conservation of Carnivorous Mammals (CENAP/ICMBio), where I am currently working.*

*Unfortunately, I did not have the honor of working with him, as he had already retired when I joined CENAP.*

*Back in 2012, when I was still the head of the Purus National Forest (Boca do Acre/AM), in a workshop organized by CENAP I could know him personally. I will never forget his words, that were something like this:*

*“Ricardo, I just worked and visited disturbed places in the Amazon. I really want to visit an intact spot there; I really wish to see a lot of animals! Do you know any place like that and easy to get in Boca do Acre?”*

*The brightness in his eyes during these works is alive in my memory until today, and I found there the same passion for the “wild nature” that literally threw me in this career and in this doctoral thesis.*

*A few years later I met him quickly at CENAP, he was going to the Roosevelt river with George Shaller, and the brightness in those eyes was stronger than ever...*

*This thesis is certainly one of his countless legacies and is dedicated in his memory, for all his pioneering spirit, courage, passion, and dedication to the protection and management of Brazilian biodiversity.*

I dedicate this thesis to my family, especially to my mother, **Rosa Maria Piccolo Sampaio**, for all her encouragement and support during all stages of my life!

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## **Resumo**

Grande parte das áreas protegidas localizadas em florestas tropicais são de uso sustentável (SURs), onde assentamentos humanos e a extração sustentável de recursos naturais são permitidos. A caça sobre vertebrados terrestres é amplamente distribuída em florestas tropicais, o que pode causar a depleção de espécies cinegéticas no interior de SURs e prejudicar sua efetividade na proteção da biodiversidade. Nesta tese de doutorado, baseado em dados coletados em nove SURs da porção central e do sudoeste da Amazônia brasileira, avaliei se a percepção local de caçadores (Capítulo I), as ocorrências locais e regionais de espécies de caçadas (Capítulo II) e suas abundâncias relativas (Capítulo III) são afetadas pelas pressões de caça exercidas por comunidades locais e áreas urbanas, pelo nível de proteção local e por variáveis de qualidade ambiental. Os impactos negativos da caça foram reduzidos em comunidades humanas com maior acesso a proteína aquática, com menor demanda urbana (mais distantes das cidades) e com menor perda de habitat em seus arredores. O nível de proteção mostrou efeito positivo sobre a percepção dos caçadores em relação a alterações nas abundâncias agregadas das espécies caçadas, porém as abundâncias relativas de duas espécies, estimadas por armadilhas fotográficas, foram reduzidas no interior das SURs. Estes resultados indicam que estratégias de conservação em florestas tropicais devem priorizar (1) a redução da demanda urbana de carne de caça; (2) o manejo da proteína animal aquática em áreas alagáveis para aliviar a pressão sobre as espécies terrestres, e; (3) o incentivo a planos de manejo de base comunitária da caça de subsistência. Tais estratégias devem ser priorizadas em comunidades localizadas (i) no interior de áreas protegidas; (ii) mais próximas às áreas urbanas; (iii) com maior dependência sobre a carne de caça, e; (iv) com níveis mais elevados de perda de habitat em seus arredores.

**Palavras-chave**

Efetividade de áreas protegidas; caça de subsistência; Defaunação; Carne de caça;  
Manejo de base comunitária; Conhecimento ecológico tradicional; Riqueza de espécies;  
Modelagem da ocupação; Manejo de fauna.

## **Abstract**

A considerable portion of tropical protected areas are Sustainable-Use Reserves (SURs), where human settlements and sustainable natural resource extraction are legally permitted. Hunting on game species is widespread in tropical forests, that can deplete game populations within SURs and to reduce their effectiveness on biodiversity conservation. In this doctoral thesis, based on data from nine SURs located in the central and southwestern portion of Brazilian Amazon, I evaluated if the local hunter's perception about local game abundance change (chapter I), the local and regional occurrences of terrestrial game species (chapter II) and their relative abundances (chapter III) are affected by hunting pressures exerted by local communities and urban areas, the local level of protection and variables considering local environmental quality. The negative impacts of hunting on game species were reduced in human communities having more access to aquatic protein, with reduced wildmeat urban demand (farther from the cities) and with lower habitat loss in their vicinities. The local level of protection showed a positive effect in the local game abundance change perceived by local hunters, however the relative abundances of two hunt-sensitive species, estimated by camera traps, were reduced inside SURs. The results provide valuable information to support evidence-based conservation strategies in tropical forests that should prioritize: (1) the reduction of wild meat urban demand; (2) the management of local aquatic animal protein in floodplain areas to relieve pressure on terrestrial game species; (3) the implementation of community-based management plans for subsistence hunting in human communities (i) inside protected areas; (ii) closer to urban areas; (iii) with higher dependency of terrestrial protein, and; (iv) with higher levels of habitat loss in the catchment areas around them.

**Keywords**

Protected area effectiveness; Subsistence hunting; Defaunation; Bushmeat; Community-based management; Traditional ecological knowledge; Species richness; Occupancy modelling; Wildlife management.

## **General introduction**

### **Protected areas are effective in safeguarding biodiversity**

The tropical forests shelter the greatest portion of global terrestrial vertebrate biodiversity (Jenkins et al., 2013) and they are responsible for about 30% of the terrestrial global carbon stock (Dixon et al., 1994). However, all tropical forests today are threatened and somehow affected by anthropogenic impacts, which include hunting, climate change, agriculture, and timber extraction (Wright, 2010).

One of the most efficient conservation strategies to reduce the human pressure on tropical biodiversity was the conception and establishment of Protected Areas (hereafter PAs; Andam et al., 2008). PAs aim, in variable degrees, to restrict human impacts on biodiversity, reducing the conversion of natural habitat into “human landscapes”. At the global level, more than 250,000 PAs have been established, covering around 16% of the world’s terrestrial landscape (UNEP-WCMC, 2021). However, in tropical forests, the area of PAs is proportionally reduced, covering only around 7% of all tropical forests landscapes (Wright, 2010).

The International Union for Conservation of Nature (IUCN) proposed six different kinds of PAs with distinct levels of human activities permission (see Dudley et al., 2010). The categories I to IV are typically more restrictive of human extraction of natural resources and land-use changes, while the categories V and VI are designated to serve as sustainable-use management reserves (hereafter, SURs), which ensures human-wildlife coexistence and natural resource extraction (Dudley et al., 2010).

Several studies showed the positive effects of all kinds of PAs on the conservation of species and landscapes (Blanco et al., 2020). Protected areas are efficient not only to reduce the extinction of species (Butchart et al., 2012) and the loss

of habitats (Jusys, 2016; Shah et al., 2021), being also efficient at increasing carbon storage (Walker et al., 2020). However, not all PAs can successfully reduce human pressure on biodiversity (Geldmann et al., 2019). Several factors including PA design and management, habitat specificities, and sociopolitical context affect their effectiveness (Barnes et al., 2017; Shah et al., 2021). For instance, in tropical PAs, management is considered crucial to achieving biodiversity conservation, but only 50% of them are managed effectively (Laurance et al., 2012).

### **The disputed effectiveness of sustainable-use reserves**

The human extraction of natural resources without the proper management inside sustainable-use reserves has led researchers to call into question the long-term effectiveness of this kind of tropical PA in serving the interests of biodiversity conservation (Terborgh and Peres, 2017). In fact, SURs prevented less habitat loss than the strictly protected areas (Shah et al., 2021). There is little scientific evidence supporting the sustainability of human extractivism of natural resources and land-use changes inside SURs, which generally suffer from several limitations to implement clear management guidelines and actions to guarantee the livelihood of local people and protect tropical biodiversity (see Laurance et al., 2012). Besides, SURs are of low priority for governments, and the absence of enforcement and stimulus to more economically sustainable activities encourage local people to convert forest to profitable but unsustainable land-use practices.

The aggregated area of SURs in tropical forests, however, covers a huge portion of the protected territory, covering around 40% of the total PA land according to Schmitt et al., (2009). Sustainable-use reserves are crucially important to prevent deforestation, forest fires, and loss of carbon storage (Nelson and Chomitz, 2011; Nolte

et al., 2013; Pfaff et al., 2015; Soares-Filho et al., 2010), being considered fundamental to protect tropical biodiversity conservation (Peres, 2011). However, these assessments based on forest-covered areas generally fail to capture the more cryptic sub-canopy impacts on biodiversity induced by human extractive activities for either subsistence or trade (Peres et al., 2006).

These sub-canopy impacts typically precede more predatory forms of human land use and can impact tropical forests even in otherwise pristine sites (Peres and Lake, 2003). For instance, the populations of Brazil nut tree (*Bertholletia excelsa*), a non-timber extractive resource that promotes a considerable income contribution to the local dweller of Brazilian Amazon SURs, have been affected by the extraction of the seeds and posterior trade. Without proper management, the populations of Brazil nut trees tend to succumb due to senescence (Peres, 2003).

### **Does hunting convert sustainable-use reserves into “Paper parks”?**

One of the most widespread sub-canopy anthropogenic disturbances occurring in tropical forests is the hunting of terrestrial and arboreal vertebrates (Fa et al., 2002; Ripple et al., 2016). Those vertebrates are an essential form of protein acquisition, contributing to the food security of people living inside tropical forests (Ingram et al., 2021; Nasi et al., 2011; Nielsen et al., 2018; Nunes et al., 2019b). Presumably, the extraction of forest vertebrates deeply affects the populations of hunted species and the forest dynamics. Species most impacted by hunting are large and slow-breeding vertebrates (Benítez-López et al., 2019; Bogoni et al., 2020a; Osuri et al., 2020; Peres, 2000; Robinson and Redford, 1991) since according to the optimal foraging theory, they are preferred prey and are targeted first by hunters (Alvard, 1993). These effects lead to a deterministic process of defaunation that can empty extensive areas of pristine tropical

forests of large game species (Benítez-López et al., 2019; Redford, 1992; Wilkie et al., 2011), including significant portions of tropical SUR.

The defaunation induced by overhunting in tropical forests can drive several cascading ecological processes (Crooks and Soulé, 1999; Fa and Brown, 2009; Peres and Dolman, 2000; Ripple et al., 2016; Scabin and Peres, 2021). Many of those processes compromise ecosystem services provided by the hunted species (Bogoni et al., 2020b; Rodrigues et al., 2020), such as seed dispersal (Terborgh et al., 2008; Wright et al., 2007), carbon stocking (Bello et al., 2015; Chanthorn et al., 2019; Osuri et al., 2016; Peres et al., 2016; Sobral et al., 2017) and the supply of animal protein for the livelihood of rural poor people in the tropics (Nasi et al., 2011; Nunes et al., 2019b; Redford and Robinson, 1987).

Despite the increasing interest regarding hunting pressure as a driver of defaunation, the mechanisms of defaunation of tropical forests at local and regional scales are still understudied (Fa and Brown, 2009). Furthermore, our understanding of how wide gradients of hunting pressure depleting game vertebrate populations remains unclear. That is especially true for those areas with distinct levels of protection, including the tropical SURs and their surroundings. For instance, a few decades ago the international trade in furs and skins in the Amazon led to local depletion of sensitive game species in sites more accessible to humans, located in the proximities of the main rivers (Antunes et al., 2016). However, this practice was banned by the Brazilian government in 1966 (Antunes et al., 2019) and the current patterns of local depletion of exploited species can be regulated by local and regional features beyond human accessibility, with the domestic consumption of wildmeat likely assuming a key role of game depletion currently.

Several studies have pointed out that hunting pressure resulting from human population density, is the main reason for the current reduction of the population of game species populations in tropical forests (Benítez-López et al., 2017; Bennett and Robinson, 2000; Fa and Brown, 2009; Peres, 2000; Peres and Palacios, 2007), where bushmeat trade severely increases defaunation in tropical forests (Morton et al., 2021). At local scale, the depletion of species irradiates from rural human settlements into the interior of pristine forests (Constantino, 2015; Levi et al., 2011, 2009; Parry and Peres, 2015), as local hunters acted as central place foragers (Sirén et al., 2004) around their houses. However, the accessibility to cities increases the regional demand for bushmeat protein expanding the impacts on exploited species (Abrahams et al., 2017; Benítez-López et al., 2017; Parry and Peres, 2015). Lastly, the sustainability of subsistence hunting in tropical forests can only be achieved under low human density (Benchimol et al., 2017; Hallett et al., 2019; Kirkland et al., 2020; Kümpel et al., 2009), which generally does not exceed 1 person by km<sup>2</sup> (Robinson and Bennett, 2000).

The combination of poor comprehension of hunting pressure impacts over game species in tropical forest SURs with the absence of clear policies to regulate the consumption of game species is a cause of concern. The main concern is that sustainable-use reserves of tropical forest may be inefficient to promote the sustainability of natural resources uses by local people, which could fail to avoid depletion of game species in long term. These reserves might be operating as “paper parks” (Hockings et al., 2001), since forest areas are gradually depleted of important game species (Harrison, 2011).

## **Sustainable-use reserves of the Brazilian Amazon**

The largest remaining portion of tropical forests on the planet is in the Amazon basin, which is also considered one of the most pristine and less defaunated remaining tropical forests of the world (Benítez-López et al., 2019). Approximately 60% of the Amazon forest territory is inside the Brazilian territory where several PAs were established in the last decades (Jenkins and Joppa, 2009).

Excluding officially recognized Indigenous Lands, the Brazilian government established 339 PAs that altogether cover around 28% of the Amazon biome (Brasil, 2020). There is also a total of 257 SURs in the Brazilian Amazon, and their aggregated territory accounts for more than 60% of the total protected territory (excluding the officially recognized Indigenous Lands), covering a total area of 775,680 km<sup>2</sup> (Brasil, 2020). If this territory was a country, it would be among the 40 largest countries in the world (List of countries and dependencies by area, 2021). This huge territory represents an excellent opportunity to understand how hunting pressure affects game species populations, and to assess the mitigatory effects of the local level of protection.

Almost 75% of the Brazilian Amazon SURs territory is composed of three PA types: (1) Extractive and (2) Sustainable Development Reserves, and (3) Public Forests (totaling 570,430 km<sup>2</sup>; Brasil, 2020). Extractive and Sustainable Development Reserves were generally created by social and political demand to provide official territories to the livelihoods of *caboclos* or *ribeirinhos*, which exhibit traditional lifestyles (Fearnside, 1989). In contrast, Public Forests were created by the Brazilian government to regulate and to stimulate timber production in some areas. However, because a great part of these territories was occupied by *caboclos* or *ribeirinhos*, the Brazilian National Protected Area System (SNUC; Brasil, 2000) recognized the rights of these populations to sustainable extraction of natural resources for their livelihoods.

These Amazonian *caboclos* or *ribeirinhos* are communities of mixed-descent residents including rubber-tappers descendants living in semi-subsistence. Currently, these communities subsist on small slash-and-burn agriculture, extraction of non-timber products, and hunting and fishing provide a major part of their protein demand. Typically, these communities of *caboclos* or *ribeirinhos* in the Amazon basin are distributed along the rivers (Fig. 1).



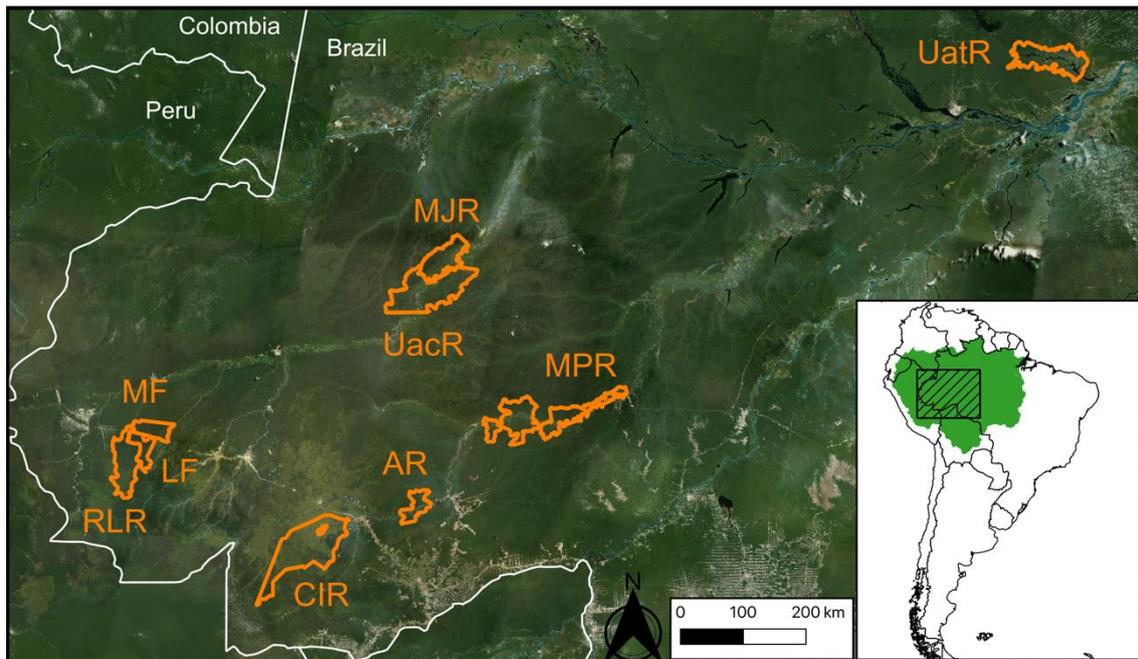
**Figure 1** – Aerial photography showing the Jurucuá community, located at the margin of Purus river, inside the Médio-Purus Extractive Reserve, located in Amazonas State, Brazil. Photo: Henrique Gonçalves.

Apart from poorly understanding how hunting pressure impacts on hunted species in the Brazilian SURs, management practices of terrestrial game species still have not been implemented yet (Campos-Silva et al., 2017). Also, conservation strategies for sustainable hunting management have been neglected by the Brazilian government (Antunes et al., 2019) despite positive results from isolated community-based initiatives of game management at the local level (Oliveira and Calouro, 2019; Vieira et al., 2015).

**The purpose of this thesis**

My main objective with this thesis is improving the knowledge about the impacts of hunting pressure on neotropical forest terrestrial and arboreal vertebrates. More precisely I aimed to identify the main drivers of the game species depletion induced by this form of human extractive activity and to evaluate if sustainable-use reserves are in fact reducing game depletion compared to areas outside the borders of these reserves. With this in mind, I used data collected in nine SURs and their surroundings, which correspond to a large geographical scale of around 1,750 km of distance among sites and covering a range of 450,000 km<sup>2</sup> located at the central and southwestern portions of the Brazilian Amazon in the states of Acre and Amazonas.

To reach those goals, I aggregated two distinct datasets (see Fig. 2): the first one was provided by Dr. Mark I. Abrahams, who collected data in three SURs located at Uatumã and Juruá rivers, inside and the vicinities of the Uatumã (UatR) and Uacari (UacR) Sustainable Development Reserves and the Médio Juruá Extractive Reserve (MJR), during the years of 2013 and 2015, during his PhD at the East Anglia University (UK). The second dataset was collected by myself between the years of 2018 and 2019, in six SURs located at Caeté, Liberdade and Purus rivers, encompassing the interior and surroundings of the Cazumbá-Iracema Extractive Reserve (CIR; Caeté); the Riozinho da Liberdade Extractive Reserve (RLR) and Liberdade (LF) and Mogno (MF) State Forests at Liberdade river; the Arapixi (AR) and Médio Purus (MPR) Extractive Reserves in the Purus river.



**Figure 2** – The enclosed panel shows the map of South America and the limits of the Amazon biome in green and the limits of countries in black. The main panel is a zoom over Brazilian Amazon map and the locations of the nine Sustainable-Use Reserves studied (orange polygons): Cazumbá-Iracema Extractive Reserve (CIR); Arapixi Extractive Reserve (AR); Riozinho da Liberdade Extractive Reserve (RLR), Liberdade State Forest (LF) and Mogno State Forest (MF); Médio Juruá Extractive Reserve (MJR); Uacari Sustainable-Use Reserve (UacR); Médio Purus Extractive Reserve (MPR), and; Uatumã Sustainable-Use Reserve (UatR).

In order to investigate the main drivers of game species depletion at local and regional scales in SURs and their surroundings, I integrated these two datasets and used three different approaches aimed at assessing: (1) local perception of a hunter on game species stocks; (2) local occurrences of game species, and (3) local abundances of game species. These approaches are addressed in three chapters of this thesis, detailed below.

In the first chapter, I analyzed data on the Traditional Ecological Knowledge (hereafter, TEK) of 211 subsistence hunters inhabiting 93 local communities within and immediately outside of those nine SURs. I evaluated if the five features of local human communities: (1) size; (2) age, (3) distance to SURs boundaries; (4) travel distance to

urban areas, and (5) the extent of neighboring floodplain area, influenced local hunter's perception about (i) game species local abundances changes; (ii) species composition of the most consumed species, and; (iii) their perceived levels of local depletion.

In the second chapter, I assessed local occurrences of forest terrestrial vertebrate species through 720 automatic cameras triggered by motion or heat (camera-traps), deployed in the catchment areas around 100 human communities inside and outside those nine SURs. I analyzed the drivers affecting the local and regional species assemblies, according to their propensity to be locally hunted. I specifically evaluated the effects afforded by a wide range of (1) local and (2) city hunting pressures; (3) the local level of protection; (4) habitat loss; (5) stream length, and; (6) floodplain extension on (i) local species richness; (ii) local assembly integrity, and; (iii) dissimilarities in assembly composition among sites.

In the third chapter, I used the incidence data from 18 game or non-game species recorded by the 720 camera traps to estimate their site-level relative abundances, using Bayesian Royle-Nichols N-mixture model (Kéry and Royle, 2015; Royle and Nichols, 2003). I specifically evaluated if variation on the (1) local and (2) city hunting pressures; (3) the local level of protection; (4) habitat loss; (5) stream length, and; (6) floodplain extension can affect the relative abundance of the focal species.

Finally, at the end of this thesis (Annex I), I present my personal experience in one of the human communities that I studied, the "Periquito" community located inside the Riozinho da Liberdade Extractive Reserve in Acre State. This experience exemplifies how, without any previous expectation and preparation, my data could be used as evidence influencing the community local decisions considering their rudimentary game vertebrate hunting management.

I hope that the results of this thesis improve our understanding of the hunted-based defaunation process in tropical forests. More specifically, I hope to identify the relative importance of both urban (city) and rural (settlements) demands for wildmeat on game species depletion and to assess how or if the level of protection afforded by the establishment of sustainable-use protected areas is mitigating this source of defaunation. I also expect that these results support tropical SURs stakeholders with the scientific evidence needed for the establishment of local and regional conservation wildlife management plans. Such evidence is important to improve the biodiversity conservation value of SURs and its role in providing livelihood for local people living inside these reserves, contributing, therefore, to reduce their stigma of being “Paper Parks”.

**Chapter I: Floodplain extent and distance to urban centers drive the perceived sustainability of game hunting by inhabitants of Amazonian sustainable-use protected areas**

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## **Introduction**

Tropical forests are the most biodiverse terrestrial ecosystems, shelter two-third of all species globally, and are facing unprecedented anthropogenic pressures (Gardner et al., 2010). The most successful strategy to protect this biodiversity is to avoid deforestation through the establishment of Protected Areas (hereafter PAs; Andam et al., 2008).

Sustainable-Use Reserves (hereafter, SURs; IUCN Category VI) comprise a considerable proportion of the aggregate protected acreage across the tropics (or 40% of the territory, Schmitt et al., 2009) and Amazon (Peres, 2011) but, often controversially, they attempt to reconcile human-wildlife coexistence with sustainable natural resource extraction (Dudley et al., 2010).

Forest cover assessments often fail to capture the most cryptic sub-canopy impacts on biodiversity induced by the extraction of a wide spectrum of nontimber forest products for either subsistence or commerce (Peres et al., 2006). These activities typically precede more predatory forms of land use and can impact tropical forests even in otherwise apparently pristine sites (Peres and Lake, 2003; Ingram et al. in press). However, the frequently escalating demographic impacts of nontimber resource harvesting calls into question the effectiveness of SURs in serving the long-term interests of biodiversity conservation (Terborgh and Peres, 2017).

Hunting of terrestrial and arboreal vertebrates is widely considered the most widespread pattern of anthropogenic disturbance in tropical forests (Fa et al., 2002). Hunting alters the populations of game species (Benítez-López et al., 2019; Harrison, 2011; Milner-Gulland et al., 2003), and disrupts effective seed dispersal and forest carbon storage (Bello et al., 2015; Muller-Landau, 2007; Peres et al., 2016). The acquisition of animal protein through hunting is, however, an essential component of the subsistence economy of tropical forest dwellers, and a growing concern in the food

security of indigenous and traditional communities (Nasi et al., 2011; Nunes et al., 2019b).

Lowland Amazon hosts the largest contiguous tracts of tropical forest on Earth, including many PAs established over the last 35 years (Jenkins and Joppa, 2009). Brazil accounts for three-quarters of this territory, but >60% of the total PA area (excluding officially recognized Indigenous Lands) consists of SURs that are legally human-occupied (Brasil, 2020). The total area of SURs covers 775,600 km<sup>2</sup>, approximately 77% of which entirely lack a management plan and a clear mandate to implement natural resource management regulations (Brasil, 2020).

Despite incipient but positive cases of community-based game management initiatives within some SURs (Oliveira and Calouro, 2019; Vieira et al., 2015), conservation strategies to promote their sustainable management have been entirely neglected by the Brazilian government (Antunes et al., 2019). This reinforces concerns that multiple-use tropical forest reserves will become “paper parks” that fail to protect biodiversity, while forest areas gradually hemorrhage populations of key game species (Harrison, 2011). However, our understanding of how and the extent to which hunting intensity truly depletes game vertebrate populations under different landscape and human geography contexts remains unclear.

Compared to formally unprotected areas, it is widely recognized that tropical PAs inhibit the worse impacts of overhunting (Benítez-López et al., 2017). The magnitude of these effects depends on several local to regional scale factors, including human settlement size and settlement age (Beirne et al., 2019; Jerozolinski and Peres, 2003; Stafford et al., 2017), distance to urban centers and physical accessibility to catchment areas (Abrahams et al., 2017; Benítez-López et al., 2017; Peres and Lake,

2003), and the availability of alternative animal protein for local human populations (Endo et al., 2016).

Here, we examine the Traditional Ecological Knowledge (hereafter, TEK) of 211 long-term subsistence hunters inhabiting 93 local communities within and immediately outside nine sustainable-use reserves of the central-western Brazilian Amazon. Specifically, we assess the perceived impacts of hunting on exploited forest vertebrate species. TEK represents the cumulative experience acquired over thousands of years of direct human contact with the environment (Berkes, 1993) and has been successfully used to assess human impacts on biodiversity (Boissière et al., 2013; Parry and Peres, 2015; Thompson et al., 2020).

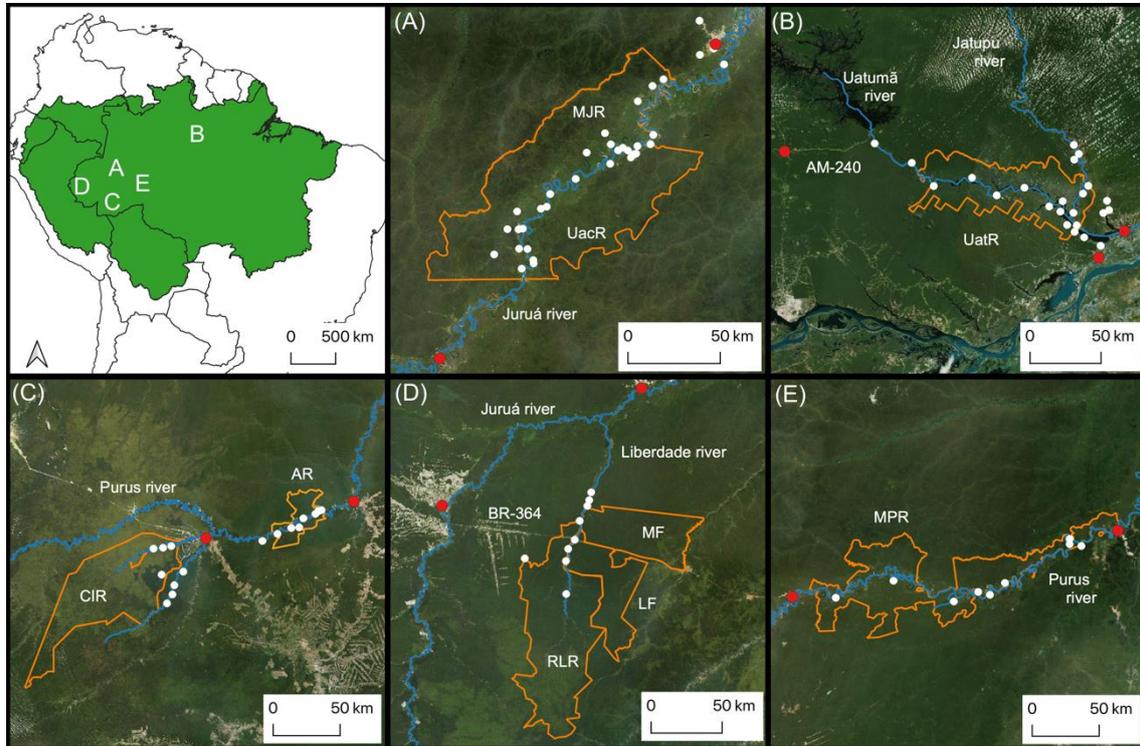
We tested the general hypothesis that larger and older semi-subsistence settlements located far from protected areas and near urban centers exert higher pressure on forest game vertebrates. Conversely, we expected lower overall hunting pressure within village catchment areas if they are surrounded by greater extents of seasonally-flooded forests and water bodies, which are good proxies of aquatic animal protein availability. Specifically, we examined how local perceptions of hunting pressure and game stocks relate to (1) settlement size and age, (2) distance to reserve boundaries; (3) distance to urban areas, and (4) the extent of neighbouring floodplain areas. To do so, we quantified reported perceptions of prey availability, the species composition of the most consumed terrestrial vertebrate prey, and their perceived levels of local depletion.

## **Methods**

### *Study area*

We collected TEK data in the central-western portion of the Brazilian Amazon during two stages. In the first stage, between 2013 and 2015, we collected data in the regions of

the middle Juruá and Uatumã rivers (Fig. 1A and B), as described by Abrahams et al., (2017). In the second stage, during 2018 and 2019, we implemented new data acquisition in the regions of upper Juruá and upper Purus rivers basins (Fig. 1C, D, E).



**Fig. 1** – Maps of the locations of the five study regions (panels A-E) within lowland Amazon (green portion of the upper left panel), South America. (A) Médio Juruá Extractive Reserve (MJR) and Uacari Sustainable-Use Reserve (UacR); (B) Uatumã Sustainable-Use Reserve region; (C) Cazumbá-Iracema Extractive Reserve (CIR) and Arapixi Extractive Reserve (AR); (D) Riozinho da Liberdade Extractive Reserve (RLR), Liberdade State Forest (LF) and Mogno State Forest (MF); and (E) Médio Purus Extractive Reserve. The 93 local communities surveyed here, their nearest urban centers, the Protected Area boundaries, and main rivers are shown as white dots, red dots, orange polygons and blue lines, respectively.

In the middle Juruá region, we obtained data at both local communities and urban neighbourhoods (hereafter, *communities*) located within and immediately outside two adjacent SURs, the Uacari Sustainable Development Reserve (UacR) and the Médio Juruá Extractive Reserve (MJR), located near the towns of Carauari and

Itamarati in the state of Amazonas (hereafter, Médio Juruá Reserves; JR). This landscape is comprised of a mix of unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests, as well as permanent water bodies. In the Uatumã region, we collected data within and immediately outside the Uatumã Sustainable Development Reserve (UatR), located near the towns of São Sebastião do Uatumã and Itapiranga in the state of Amazonas. The landscape is comprised mainly of *terra firme* and a small portion of seasonally-flooded forests, locally referred to as *igapó*, and permanent water bodies. We deliberately boosted the generalization power to this study by including regions drained by both nutrient-rich white-water (Juruá-Purus) and nutrient-poor black-waters (Uatumã), thereby capturing nearly the full gradient of soil fertility of central-western Amazonia.

In the upper Juruá and Purus regions, we interviewed local inhabitants living both within and immediately outside SURs in three subregions: (1) Cazumbá-Iracema (CIR; Caeté and Macauã rivers) and Arapixi (AR; Purus river) Extractive Reserves (Fig. 1C); (2) Riozinho da Liberdade Extractive Reserve (RLR; Liberdade river), Liberdade State Forest (LF; Liberdade river), Mogno State Forest (MF; Liberdade river), hereafter Liberdade Reserves (LR; Fig. 1D); and the (3) Médio Purus Extractive Reserve (MPR; Purus river; Fig. 3E). All communities at Cazumbá-Iracema and some communities at Arapixi are located near the town of Sena Madureira (state of Acre), while the other Arapixi communities are located near the city of Boca do Acre (state of Amazonas). The two cities nearest the communities of LR are Cruzeiro do Sul (Acre) and Ipixuna (Amazonas). Local communities at MPR are nearest the cities of Pauini and Lábrea (Amazonas). The landscapes of CIR and LR are predominantly comprised of *terra firme* forests and to a minor extent, flooded forest, while the landscape at AR and MPR

consist primarily of *terra firme* forests, although *várzea* forests are important elements of the landscape.

Regions encompassing all of these reserves are inhabited by *ribeirinhos*, former rubber-tappers living in semi-subsistence communities of mixed-descent. These local dwellers practice terrestrial subsistence hunting using firearms, mainly 24- and 36-gauge shotguns, with no reported use of snares and gun-traps. Sites in western Amazon encompass highly productive white-water floodplain ecosystems (Fig. 1A, C, D, E), while those in Central Amazon (Fig. 1B) encompasses much lower productivity black-water rivers (Junk et al., 2015), potentially resulting in lower faunal biomass density (Emmons, 1984).

#### *Local interviews*

This study was conducted under ethical approval from the University of East Anglia Ethical Review Board and the University of São Paulo Ethics Committee. We obtained explicit permission to conduct interviews from all participating local communities and informants. We interviewed subsistence hunters, who were willing informants and had been indicated to us using a snow-balling approach (Newing, 2010) within these communities.

We applied semi-structured questionnaires to 211 subsistence hunters, 69% and 31% of whom were carried out with local people living inside and outside the nine SURs examined here, respectively. Most of these interviews were conducted in the region of CIR and AR (34%), with the remaining interviews as following: LR (23%), JR (24%), MPR (12%) and UatR (8%). We interviewed between 1 and 12 resident hunters per community ( $2.23 \pm 2.30$  informants, mean  $\pm$  SD), amounting to 93 local communities.

We used a semi-structured questionnaire to obtain data on (1) hunters' perceptions of change in game abundance within the catchment areas near their communities over the previous 10 years (i.e. "worse now"; "no change"; and "better now"); (2) their currently available prey profile, i.e. the three most-hunted and most-consumed prey species, ranked by the hunter's own perception of the number of individuals of each species that had been consumed; (3) the perception of local depletion for each of 16 game species hunted in central-western Amazon (Table 1), expressed by the distance they would be required to travel on foot from their households to detect direct or indirect signs of each species, and (4) the age of each community, defined as the number of years since the community had been officially established. Hunters were also asked about their age and how frequently they accessed the forests around their communities as part of their regular year-round activities.

**Table 1** – A checklist of species that were the subject of semi-structured interviews, ordered by the reportedly most to least hunted and consumed prey species (expressed as a percentage of the aggregated prey rankings of all respondents (P %), their body mass (kg) and finite rate of natural population increase ( $\lambda_{\max}$ ). Species codes are given for the subset of species for which perceived depletion was analyzed (expressed as the reported travel distance to the nearest locality where they had been detected).

English name	Species name	Species code	P (%)	kg <sup>1</sup>	$\lambda_{\max}$ <sup>1</sup>
Lowland paca*	<i>Cuniculus paca</i>	Cuni.pa	17.8	9.5	1.95
Collared peccary*	<i>Pecari tajacu</i>	Peca.ta	16.6	25.0	2.01
Red brocket deer*	<i>Mazama americana</i>	Maza.am	11.5	30.0	1.42
Agouti	<i>Dasyprocta</i> spp.	-	9.5	4.5	3.00
White lipped peccary*	<i>Tayassu pecari</i>	Taya.pe	7.6	32.0	1.58
Large tinamou*	<i>Tinamus</i> spp.	Tina.sp	6.6	1.2	1.50
Small armadillo	Nonspecific small cingulata	-	6.4	6.0	1.91
Grey brocket deer*	<i>Mazama nemorivaga</i>	Maza.ne	6.2	18.0	1.61

Curassow*	<i>Mitu sp. or Crax sp.</i>	Mitu.Crax	4.9	3.0	1.47
Brazilian tapir*	<i>Tapirus terrestris</i>	Tapi.te	4.1	160.0	1.22
Spix's guan	<i>Penelope jacquacu</i>	-	2.3	1.3	1.49
Howler monkey*	<i>Alouatta spp.</i>	Alou.sp	1.9	6.5	1.17
South American red squirrel	<i>Hadroskiurus spadiceus</i>	-	1.2	1.2	3.50
Woolly monkey*	<i>Lagothrix spp.</i>	Lago.sp	0.7	8.7	1.12
Trumpeter	<i>Psophia spp.</i>	-	0.5	1.2	1.30
Capybara	<i>Hydrochoerus hydrochaeris</i>	-	0.5	31.5	1.99
Red/yellow footed tortoise*	<i>Chelonoidis spp.</i>	Chel.sp	0.5	4.6	2.50
Large-headed capuchin	<i>Sapajus macrocephalus</i>	-	0.4	3.4	1.15
South American coati	<i>Nasua nasua</i>	-	0.1	5.1	1.26
Spider monkey*	<i>Ateles spp.</i>	Atel.sp	0	9.0	1.08
Jaguar	<i>Panthera onca</i>	Pant.on	0	80.0	1.60
Puma	<i>Puma concolor</i>	Puma.co	0	45.0	1.36
Giant armadillo*	<i>Priodontes maximus</i>	Prio.ma	0	30.0	1.80
Giant anteater	<i>Myrmecophaga tridactyla</i>	Myrm.tr	0	30.5	1.70

1 - Abrahams et al., (2017). \* Species included in the two metrics of local game depletion (kg/km; All.spp; see Methods section).

We used the biological traits of all reported prey species (see Table 1) to create two prey profile indices as perceived by each hunter. We calculated the (1) mean body size (body mass, kg) and (2) reproductive rate of each reported prey profile, using the mean finite intrinsic rate of natural increase ( $\lambda_{\max}$ ) of the three most consumed prey species reported by each hunter. These traits have been widely used to determine the demographic consequences of hunting in tropical forests (e.g. Fa et al., 2002).

Based on the assumption that the gradient of depletion of hunted species radiates from individual households into inland forests (as in all central-place foragers; Sirén et al., 2004), a proxy of species depletion can be obtained by the perceptions of local

residents about the minimum distance (km) travelled to detect any signs of each game species, including sightings, tracks, scats, bark scratches, vocalizations and carcasses. We derived these travel distances from the known georeferenced household of each interviewee to the nearest locality where signs of each of the 16 focal species could be detected.

We calculated this as the amount of time that each interviewee estimated would be required to travel from their household to reach the nearest site at which any given species (or signs thereof) could normally be encountered, and then multiplied this time estimate by the mean hunter travel velocity, considering the mode of transport they reportedly used (see details in Abrahams et al., 2017). We excluded from this analysis travel distance data for grey brocket deer (*Mazama nemorivaga*) at CIR and woolly monkeys (*Lagothrix* spp.) at CIR, LR and UatR, since most interviewees in these regions reported long-term natural absences of these species in the vicinities of their communities. We then truncated outlier values of the detection travel distance data to 30 km, given that the mean radial day range of Amazonian central-place hunters is 5-6 km (Sirén et al., 2004). Moreover, several of our interviewees reported they seasonally used temporary hunting camps located up to 24 km from their communities and could hunt as far as 6 km from these camps.

We then used these travel distances as a proxy of perceived degree of local prey depletion, except for travel distances for three rarely or not consumed species (puma [*Puma concolor*], jaguar [*Panthera onca*] and giant anteater [*Myrmecophaga tridactyla*]). We divided the mean body mass of the remaining 13 species by their respective local detection distances to calculate the mean body mass detected per km per hunter (kg/km). In addition, we calculated the mean detection travel distance for all prey species as estimated by each hunter (All.spp).

### *Explanatory spatial variables*

We derived all spatial variables using QGIS 3.14 (QGIS, 2021). We defined the size of each community studied as the total number of households inside a 1-km buffer of the community centroid. We digitized every household within 1 km of the central-point of each community, through visual inspection of Bing Maps aerial photographs using the Open-layers plugin (1:2000) (see Table 2). We performed this mapping using 2019 aerial photographs for the middle Juruá and Uatumã datasets. We assumed that no major positional change in human settlements had taken place since our field sampling (2013-2015). For the upper Juruá-Purus dataset we performed supervised mapping using 2018 aerial photographs.

1 **Table 2** – Description of the selected independent variables used in mixed-effects models, applied to data collected at 93 local communities. For each explanatory variable we  
 2 report the predicted impact on the perceived local game abundance (GA), the mean body size and reproductive rate of the reported prey profile (PP) and the reported travel  
 3 distance to the nearest location where each prey species could be detected (TDD).

Independent variables	Code	Unit of measure	GA and PP	TDD
Population size of community	SIZE	Number of households ( $\log_{10}$ )	Negative	Positive
Age of community	AGE	Years	Negative	Positive
Travel distance to urban centers	CITY	Sqrt (km)	Positive	Negative
Distance to Protected Area boundaries	PROTE	km	Positive	Negative
Extent of surrounding flooded areas	FLOOD	Proportion	Positive	Negative

4

To represent the effect of protection level afforded by PAs on local communities, we calculated the Euclidean distance (km) between each community and the nearest boundary of the SUR in each region. Reserves within either the Juruá river (Fig. 1A) or the Liberdade river regions (Fig. 1D) are adjacent to each other and therefore we merged their perimeters into a single polygon. In order to capture the reserve protection effect, we assumed positive or negative values for distances to communities located either inside or outside each SUR polygon, respectively.

We estimated the access distance from each human settlement to the nearest urban center by digitizing rivers and roads (paved and unpaved) that residents reportedly used. These access distances can vary seasonally since some unpaved roads are only usable during the dry season while some river channels become navigable only during the wet season, reducing travel time and distance to the nearest city. Given this seasonal variation, we calculated the mean access distance to the nearest city for each human settlement by averaging estimates from both the dry and wet seasons.

We assumed that the available aquatic protein is comprised mostly of fish and to a lesser degree aquatic reptile species (caiman and aquatic turtles and their eggs). We also assumed that the availability of aquatic animal protein to local people is directly related to the local amount of suitable habitat for exploited aquatic and semi-aquatic species. Thus, we created a proxy of local aquatic animal protein availability using the proportional area around each community comprised of seasonally and permanently flooded areas (hereafter, *flooded area*). We calculated this metric by aggregating, within 5-km of the centroid of any given community, the total area of permanent water bodies (e.g. river channels, oxbow lakes), plus all forests that become seasonally flooded, divided by the total 5-km buffer area. We extracted these data from a raster file described in Hess et al. (2015).

### *Statistical analysis*

Our five explanatory variables are summarized in Table 2. We performed all statistical analyses using R 4.0.4. software (R.Core.Team, 2021). Prior to analyses we checked data distributions and relationships among response and predictor variables using dispersion plots and we log- or sqrt-transformed data whenever necessary, following Zuur et al., (2010). We also explored correlations (Pearson value > |0.7|) and collinearity (Variance Inflation Factor > 3) among explanatory variables (R base and USDM package; Naimi et al., 2014). We rescaled variables (mean = 0 and SD = 1) to enable model convergence and variable effect size comparisons (Harrison et al., 2018).

We used mixed-effects models (see Bolker et al., 2009) to evaluate the effects of (1) settlement size and (2) age, (3) distance to reserve boundaries, (4) distance to urban areas, and (5) the extent of neighbouring floodplain areas had on (a) the perceived local game abundance, (b) the species composition of the three most consumed terrestrial vertebrate prey (in reported prey profiles); and (c) their perceived levels of local depletion, expressed by the detection travel distance to different game species (Table 2). We accounted for spatial dependence among informants by specifying “community” as a random effect, since we interviewed more than one informant in each community. We opted to show only the effects of the global models (equation #1), since minimal adequate models can overestimate the effect size of significant predictors (Harrison et al., 2018) and global models better indicate the direction and intensity of the effects of explanatory variables.

$$Y_i = \beta_0 + \beta_1 * Size_i + \beta_2 * Age_i + \beta_3 * PA\ distance_i + \beta_4 * City\ distance_i + \beta_5 * Flooded\ area_i + \gamma * Community_i \quad (1)$$

Since local perceptions of game stocks in forest areas near settlements are ordinal (“declining”; “no change”; “increasing”), we examined these using cumulative link mixed models (CLMM function; Ordinal package; Christensen, 2018). Prey profile metrics and local depletion data were analyzed using either Gamma (GLMM) or Gaussian (LMM) Generalized Linear Mixed Models (glmer and lmer functions of the lme4 package; Bates et al., 2015). GLMMs were more parsimonious (lower AIC value) than LMMs, but since all our GLMMs were overdispersed (Harrison et al., 2018), we decided to retain the use of LMMs.

In order to increase the credibility of the inferential power of the effect sizes of all of our models, we used the function *bootstrap\_parameters* of the *parameters* R package (Lüdtke et al., 2020), with 5,000 model iterations based on resamples (with replacements) to create a distribution of coefficients for each variable, as well as their respective confidence intervals.

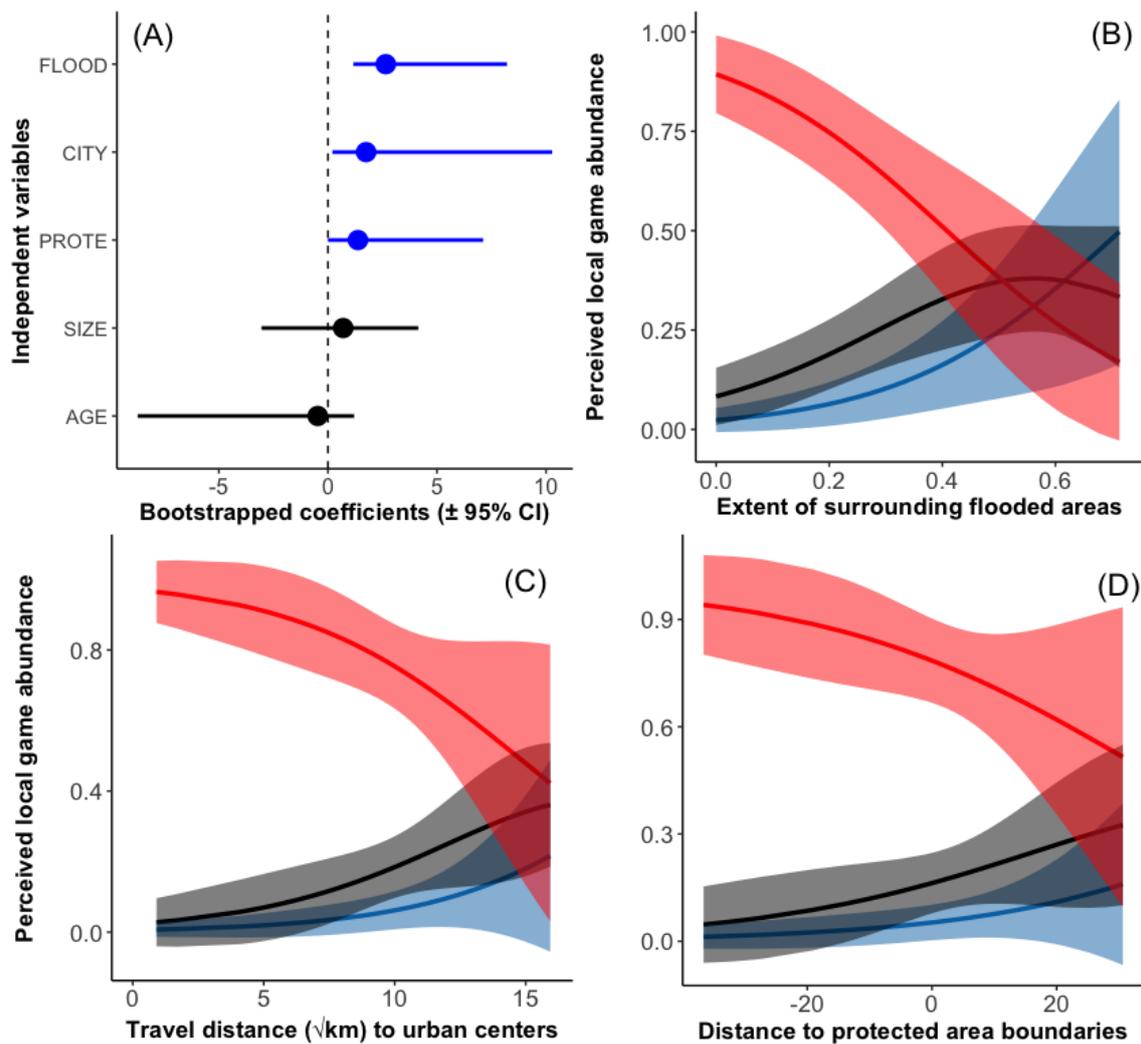
## **Results**

The mean age of local hunters interviewed was 45.03 ( $\pm 14.80$ ) years, 64% of all respondents entered into the forest at least once weekly, 26% at least once monthly and 8% once annually.

Nineteen taxa of terrestrial bird and mammals were described as regularly consumed by our interviewees (Table 1) with lowland paca (*Cuniculus paca*), collared peccary (*Pecari tajacu*), red brocket deer (*Mazama americana*) and agouti (*Dasyprocta* spp.) encompassing over 55% of all species reported.

Local perceptions on local game abundance showed that most of the interviewed hunters (69%) perceived an overall ‘worsening’ situation, whereas 16% stated that no change had occurred, and 15% perceived that the overall game availability situation had

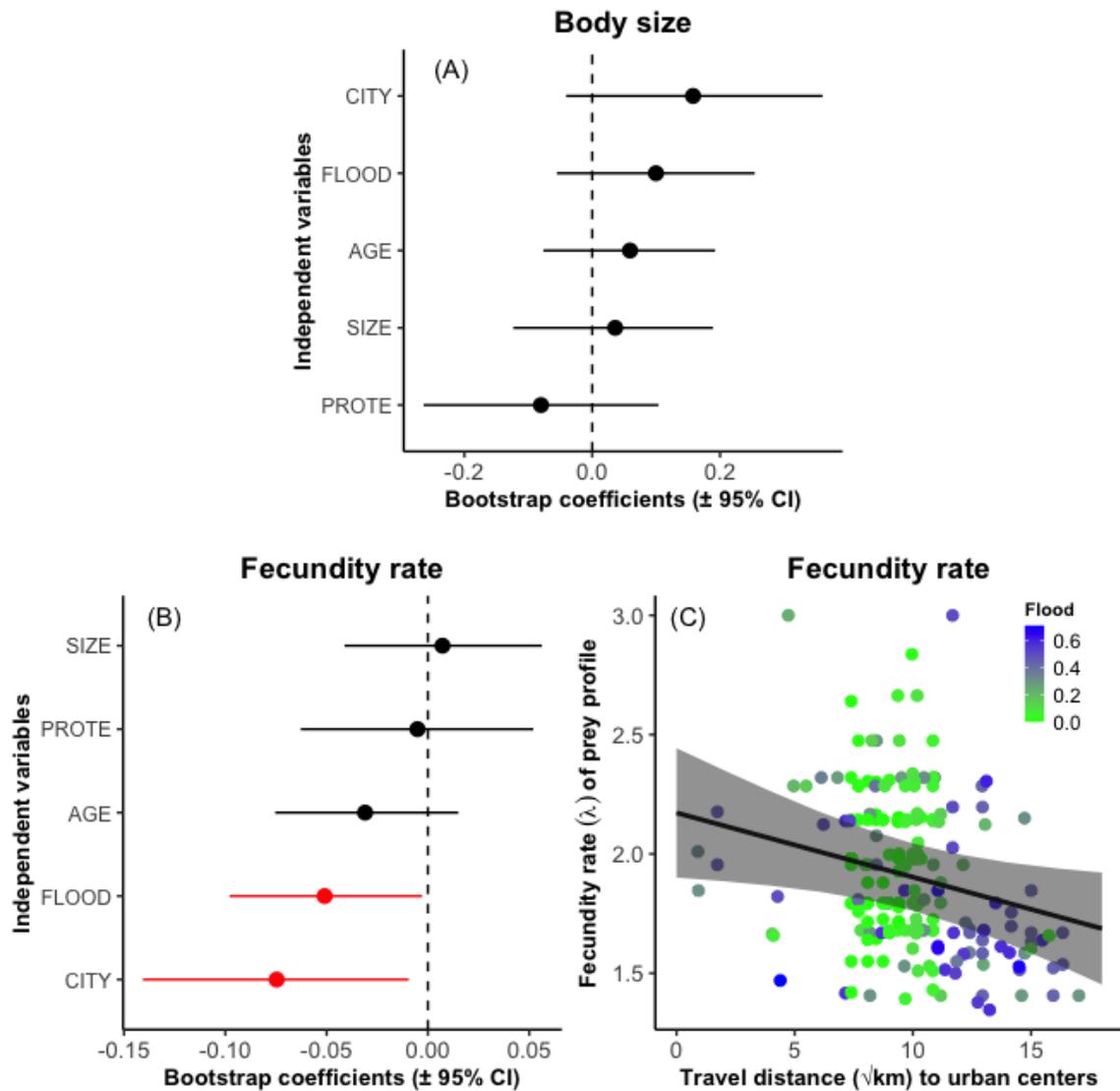
‘improved’. Hunters living in communities surrounded by a higher fraction of seasonally-flooded area were more likely to perceive an overall improvement in local game abundance (Fig. 2A and B). In contrast, local informants living in communities farther from urban centers and inside the boundaries of Protected Areas experienced a significant perceived positive temporal change in overall game abundance (Fig. 2A, C and D).



**Fig. 2** – Panels synthesizing results of Cumulative Link Mixed Models of perceived game abundance. Panel A shows the magnitude and direction of the effects (bootstrapped coefficients ± 95% confidence intervals) of independent variables. (FLOOD = Extent of adjacent flooded area; PROTE = Distance to protected area boundaries; CITY = Travel distance to urban centers, SIZE = Population size of the community; AGE = Age of the community) on the perception of local game abundance, ordered from the most positive to the most negative effect. Panels B, C and D show the estimated probability (± 95%

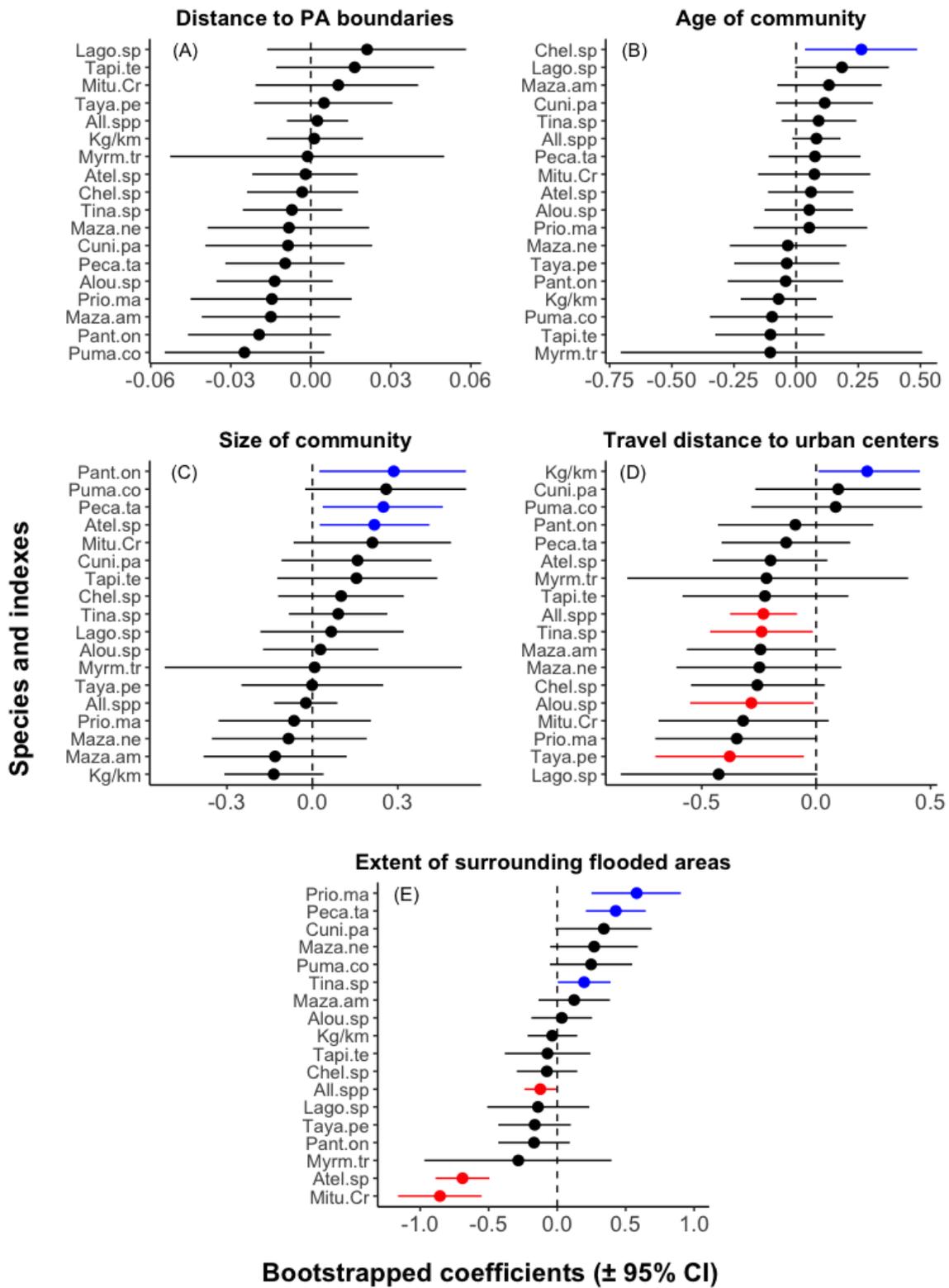
confidence interval) of the proportions of responses over the perceived local game abundance (“declining” in red, “no change” in black; and “increasing” in blue) according to the extent of adjacent flooded area, travel distance to urban centers and distance to protected area boundaries, respectively.

The mean body mass (per hunter) of the three most hunted game species ranged from 1.23 to 74.0 kg ( $22.63 \pm 19.5$  kg, mean  $\pm$  SD) and none of our explanatory variables significantly affected the body mass distribution of reported prey profiles (Fig. 3A). The mean species reproductive rate ( $\lambda_{\max}$ ) within reported prey profiles (per hunter) ranged from 1.35 to 3.0 ( $1.90 \pm 0.32$ , mean  $\pm$  SD), and hunters farther from urban areas and residents of communities adjacent to larger areas of seasonally-flooded habitat harvested low-fecundity prey species more frequently (Fig. 3B and C).



**Fig. 3** – Panels synthesizing results of Generalized Linear Mixed Models showing the magnitude and direction of effects (standardized coefficients  $\pm$  95% confidence intervals) of independent variables (FLOOD = Extent of adjacent flooded area; PROTE = Distance to protected area boundaries; CITY = Travel distance to urban centers, SIZE = Population size of the community; AGE = Age of the community) on the prey profile indices of average body size (A) and fecundity rate (B) for the three reportedly most hunted species. Panel C shows the relationships between prey profile metrics of fecundity rate, travel distance to urban centers and extent of adjacent flooded area (Flood). The estimated fecundity rate of prey profiles and 95% confidence interval are represented by a black line with a grey border, while the extent of adjacent flooded area is represented by the green to blue colour gradient of the data points.

Detection travel distances per hunter for any of the 16 game species considered here (Table 2) ranged from 0.15 to 30 km ( $6.98 \pm 9.86$  km, mean  $\pm$  SD). Hunters living farther into core areas of SURs reported shorter detection distances to signs of nine species, but these effects were not significant (Fig. 4A). Hunters living in older communities reported longer detection travel distances to yellow- or red-footed tortoises (*Chelonoidis* spp.) and marginally to woolly monkeys (Fig. 4B). Hunters in larger communities reported longer detection distances for jaguar, collared peccary and spider monkey (*Ateles* spp.), and marginally for puma. Although hunters in these large communities reported an overall smaller size structure of desirable prey detected per distance travelled (kg/km), this effect was only marginally significant (Fig. 4C).



**Fig. 4** – Panels synthesizing results of Generalized Linear Mixed Models showing the magnitude and direction of effects (bootstrapped coefficients  $\pm$  95% confidence intervals) of five independent predictors on reported travel distances exercised by hunters to detect 16 forest vertebrate taxa, prey biomass per distance travelled (kg/km) and mean distance to detect an aggregate pool of 13 hunted species (All.spp).

Hunters living farther from urban centers experienced shorter detection travel distances for all species in aggregate (All spp.) and higher overall prey biomass per distance travelled (kg/km; Fig. 4D). Under this landscape context, 14 species could also be encountered nearer local communities. Three species showed significant effects (namely, large tinamou [*Tinamus* spp.], howler monkey [*Alouatta* spp.], white lipped peccary [*Tayassu pecari*]), and distances to five harvest-sensitive taxa were also marginally affected by the distance to the nearest city (spider monkey, footed tortoise, curassow [*Mitu* or *Crax* spp.], giant armadillo [*Priodontes maximus*] and woolly monkey; Fig. 4D).

Hunters living in communities surrounded by larger areas of adjacent floodplains reported significantly longer detection travel distances for giant armadillo, collared peccary and large tinamous, and marginally farther distances for lowland paca, grey brocket deer and puma (Fig. 4E). Conversely, these hunters reported significantly shorter detection distances for all species when these were pooled together (All spp.), as well as for spider monkey and curassow, and marginally for white lipped peccary and jaguars (Fig. 4E).

## **Discussion**

Most of the hunters we interviewed reported a decline in local game abundance in the forests surrounding their communities. However, our study demonstrates that Amazonian rural communities enjoying greater access to extensive floodplain areas and located farther from urban centers, were more likely to perceive that local game hunting was sustainable over time. Our data suggest that at the landscape scale, hunting as currently practiced is perceived to detrimentally impact local game assemblages and local livelihoods within and around the nine SURs examined here. Additionally, high-

fecundity species, such as agouti, lowland paca, collared peccary, and red brocket deer, were the most locally consumed species overall. Low-lambda species, on the other hand, were only consumed farther from cities and within communities surrounded by extensive available floodplains where most of the wild animal protein requirements was met by local fisheries. Contrary to our expectations, however, the positive effects of legal protection status of PAs per se were seen only in the perceived local game abundance. Likewise, community demographic configuration (settlement age and size), only impacted the depletion of few game species.

*Sustainability of game hunting is modulated by settlement geography*

Physical accessibility to floodplains, and hence accessibility to more abundant sources of aquatic animal protein, was associated with a generally higher perception that local game hunting was sustainable, which is reinforced by higher offtakes of low-lambda prey species in these catchments. We infer that aquatic resources, wherever they are available, largely meet local animal protein needs, reducing local dependency on terrestrial animal protein via compensatory effects at different timescales, thereby alleviating hunting pressure on alternative terrestrial game stocks. A similar aquatic-terrestrial protein relationship has been observed at much larger scales in West Africa, where the reduction of marine fish stocks resulted in higher rates of game depletion in inland protected areas (Brashares et al., 2004). This compensatory effect can also be seen in western Amazonia. For example, rural Amazonians in general, and riverine communities in particular, tend to consume more fish than game meat, but game meat consumption increases when fish stocks become less seasonally available (Endo et al., 2016).

Moreover, local communities at RDA and RMJ (Juruá River) and RMP (Purus River) have been conducting community-based management of arapaima fish (*Arapaima gigas*) within floodplain oxbow lakes, which further increases the local availability of aquatic protein (Campos-Silva and Peres, 2016; Campos-Silva et al., 2018). It is reasonable to surmise that wise resource management of the local availability on aquatic protein has promoted a reduction in local pressure on terrestrial game species and, consequently, a favourable perception of higher hunting sustainability.

The reduced depletion of harvest-sensitive taxa in community catchment areas embedded in a larger proportion of floodplain areas can be interpreted as a consequence of reduced game meat dependence by the hunters in these communities. This pattern was seen on the perceived depletion of spider monkey, curassow and, marginally so, white-lipped peccary. Shorter travel distances to signs of all game species (All.spp) may also be seen as further indication that, in general, the high availability of aquatic animal protein reduces the size of the spatial depletion envelope induced by central-place terrestrial hunting.

Nevertheless, for some species, the counterintuitive relationship we found between the extent of seasonally-flooded habitats near communities and their perceived wildlife depletion could be better explained by habitat associations. Species such as giant armadillo, collared peccary, lowland paca, grey brocket deer, puma and tinamou, show higher habitat preference for unflooded than flooded forests (Alvarenga et al., 2018; Hugaasen and Peres, 2007). Accordingly, these species were typically detected farther from riverine and lacustrine communities near river channels, which were therefore farther removed from upland forest areas, particularly considering that

floodplain areas in some of our study areas could be as extensive as 25-30 km wide on both banks of the river (middle Juruá and Purus rivers).

Travel distance to the nearest town or city was the most important predictor of the mean fecundity rate of the most consumed game species across the 93 communities examined here. Hunters in more remote communities clearly perceived hunting to be generally more sustainable. Moreover, only two game species failed to show a signal of travel distance to urban centers in terms of detection distances away from hunters' households. Hunters living farther from urban areas also reported higher biomass (kg/km) of prey species detected in the vicinities of their communities and shorter detection distances for all species. This pattern was statistically significant for four exploited species (large tinamou, howler monkey, white-lipped peccary and woolly monkeys), and marginally so for four other harvest-sensitive species (spider monkey, footed tortoise, curassow and giant armadillo).

Overall, these results are consistent with previous studies in that many tropical cities can drain wild meat for both local consumption and trade, and low-fecundity species are typically depleted in peri-urban areas (Peres, 2010). Urban proximity is the most important negative driver of population abundance in tropical forest game species (Benítez-López et al., 2017) and, although wild meat trade is illegal in Brazil (see Antunes et al., 2019), urban consumption of wild meat is both prevalent and widespread throughout the Amazon (Chaves et al., 2017; Parry et al., 2014). This is especially the case of small market towns, such as those spatially related to our communities, where local people still enjoy eating wild terrestrial vertebrates and do rely on a steady supply of domestic protein (El Bizri et al., 2019).

### *Household geography and hunting sustainability*

Local hunters living in communities located in core reserve areas were more likely to perceive hunting to be sustainable. Within these reserves, human pressure on biodiversity is expected to be lower due to restrictions in land use and management actions (Gray et al., 2016). Amazonian reserves are also less physically accessible via their river and road networks than unprotected forests elsewhere (Peres and Lake, 2003), and illegal hunting is less likely to occur in more inaccessible sites, including remote Amazonian protected areas (Kauano et al., 2017).

Only some game species were meaningfully affected by the demographic profile of the communities we studied. Older communities significantly perceived local depletion only for yellow- and red-footed tortoises, whereas this effect was uninformative for woolly monkeys. These illustrate cases of highly harvest-sensitive and preferred game species that have been depleted in many overhunted portions of Amazon (Peres and Palacios, 2007). Community size (numbers of consumers) significantly impacted only jaguars, collared peccaries and spider monkeys. Although the age and size of local communities may strongly influence local depletion of Amazonian game vertebrates (Jerozolimski and Peres, 2003), this is not substantiated by at least some studies (Abrahams et al., 2017; Stafford et al., 2017). Given the spatial configuration of our study settlements, it is possible that the landscape scale effect size of urban centers and local availability of aquatic protein override the additional impacts of local community demographics.

The mean body mass of prey species is generally lower in overhunted catchment areas in the Amazon (Jerozolimski and Peres, 2003), not least because large-bodied vertebrates are often both preferred target species and more sensitive to hunting (Bodmer et al., 1994; Bogoni et al., 2020a). Our measure of body size of the most

consumed species was, however, not influenced by any of our predictors. In previously depleted Amazonian forests, subsistence hunters can respond by simply travelling farther to pursue larger-bodied prey wherever these are still available (Alvard, 1993; Levi et al., 2011), and this is likely occurring well beyond the most depleted areas around our study communities. In our study reserves in Acre (LR and CIR), for example, local hunters frequently erected and maintained temporary hunting camps farther than 10 km away from their villages, where they seasonally pursued the most preferred game species. These camps effectively overcome even large species-specific depletion envelopes to ensure ready access to under-harvested populations of even the most desirable species, but this option can only work under contexts of relatively low village densities and vast tracts of undisturbed forests.

#### *Conclusion and conservation implications*

In summary, our interviews revealed clear signs of negative impacts of subsistence hunting within and around human-occupied protected areas of the Brazilian Amazon. Yet, local availability of alternative aquatic protein near community settlements and greater travel distances to urban centers contributed to an overall pattern of more sustainable game hunting. This study aims to contribute to the design of evidence-based conservation strategies that can enhance natural resource management in sustainable-use tropical forest reserves.

Regional resource management policies should include strategies that can reduce the urban-centric depletion of game species, especially low-lambda species. This should include more efficient surveillance and deterrence of commercial hunting and urban bushmeat trade, as well as provide alternative inexpensive sources of animal protein for urban consumption, including wild fisheries and small domestic livestock.

Community-based management of natural resources has been considered the best available option for the local protection and/or recovery of native biodiversity, in addition to socioeconomic gains in enhancing the living standards of rural populations (Campos-Silva and Peres, 2016; Constantino et al., 2012). Community-based management of aquatic resources can potentially reduce excessive reliance on terrestrial game species and should be prioritized and subsidized in communities located on extensive floodplain areas of the Amazon and elsewhere in the tropics. However, for local communities that lack access to sources of aquatic protein, the best alternative to mitigate the inherent impact of overhunting on terrestrial game species should be the management of subsistence offtakes, with a focus on stringent quotas protecting the most vulnerable low-fecundity species. Given the importance of wild meat to the rural poor (Nunes et al., 2019b), these can be seen as ‘win-win’ management strategies in protecting both local livelihoods and wild game stocks.

## **Chapter II: Assessing the effects of hunting pressure and the level of protection on local and regional occurrences of terrestrial vertebrate species in Amazonia**

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### **Keywords**

Bushmeat; Defaunation; Community-based management; species richness, assembly  
dissimilarities.

## **Introduction**

Hunting on forested vertebrate species is an important human activity impacting the biodiversity of the remaining tropical habitats around the world (Benítez-López et al., 2017; Ripple et al., 2016), being considered the most widespread subcanopy disturbance of tropical forests (Fa et al., 2002). Larger and slow-breeding vertebrate species are affected the most (Osuri et al., 2020; Peres, 2000), and even apparently extensive pristine tropical forests can be depleted of large vertebrates populations (Benítez-López et al., 2019; Redford, 1992; Wilkie et al., 2011).

Hunting is a tropical forest defaunation process that can promote several cascading ecological effects (Fa and Brown, 2009; Peres and Dolman, 2000; Ripple et al., 2016), compromising ecosystem services provided by game species (Bogoni et al., 2020b; Rodrigues et al., 2020), such as seed dispersal (Terborgh et al., 2008; Wright et al., 2007), carbon stock (Bello et al., 2015; Peres et al., 2016; Sobral et al., 2017) and the supply of animal protein for the livelihood of rural poor people in the tropics (Nasi et al., 2011; Nunes et al., 2019b; Redford and Robinson, 1987).

While high human population density results in unsustainable hunting in the tropics, reducing the local diversity of game species (Benítez-López et al., 2017; Fa and Brown, 2009), at low levels of local human population density, sustainability of subsistence hunting can be reached (Benchimol et al., 2017; Hallett et al., 2019; Kirkland et al., 2020). Besides, the local level of territory protection, afforded by the establishment of Protected Areas (PA), generally reduces the effects of hunting pressure on the exploited species (Benítez-López et al., 2017). It is reasonable to infer, therefore, that sites with low human population inside tropical PAs can sustain more game species and more integral assemblies. However, the knowledge on how a wide gradient of hunting pressure, expressed by variations in size and distance of local communities and

cities, structuring the defaunation in tropical forests is still scarce (Fa and Brown, 2009). Besides, there are few evidences of how distinct local level of protection can mitigate the hunting pressure on local game populations.

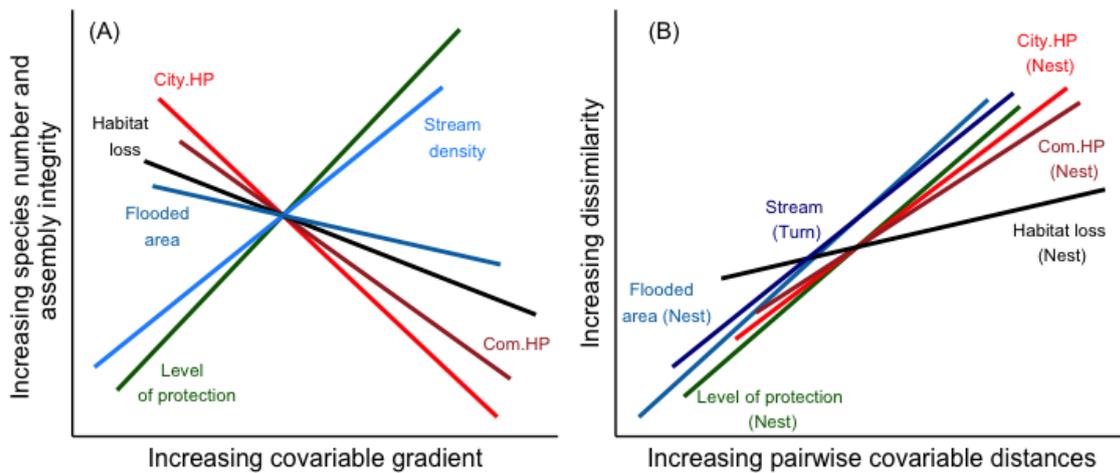
Similarly, our understanding on how hunting pressure promotes dissimilarities among local assemblies ( $\beta$ -diversity; *sensu* Whittaker [1960]) is still incipient, although knowledge on this topic is fundamental for conservation strategies promoting the maintenance of diversity over regional scales (Socolar et al., 2016). Although hunting pressure is expected to increase dissimilarities among sites, no empirical data supporting this pattern has been published to date (Socolar et al., 2016). Only indirect effects are available, such as, for example, forests defaunated of game species and without seed dispersers creating a hyperdominance of tree species able to recruit near to conspecific adults (Terborgh, 2012; Terborgh et al., 2008).

The  $\beta$ -diversity can be divided in two dissimilarity components: turnover and nestedness. The turnover component measures replacement or substitution of species between local assemblages, whereas nestedness refers to a non-random process of species loss between them (Baselga, 2010). Since hunting pressure generally promotes defaunation of larger species, we can assume this species loss as a deterministic process, creating a nestedness pattern where residual assemblages on overhunted sites constituted mainly by a subset of smaller species compared with the less hunted sites.

To better understand how the hunting pressures at local (human communities' density) and regional scales (urban population density) and the level of local protection affect local and regional diversity, we established a sampling design with 720 camera traps deployed in the catchment areas of 100 human communities inside nine Sustainable-Use Protected Areas (SURs) and its surroundings in central-western of Brazilian Amazon.

We accessed local occurrences of terrestrial camera-trappable vertebrate species and grouped them in two local assemblies, game and non-game species, according to their propensity to be hunted locally. Using generalized linear mixed models, we evaluated how the (1) local diversity, and (2) assembly integrity are affected by: (i) community and (ii) city hunting pressure and (iii) level of local protection, including in these models proxies of local habitat quality and environmental variation ([iii] habitat loss and [iv] seasonally flooded area extensions, and; [v] stream length). We also evaluated if the (a) total, (b) turnover, and; (c) nestedness dissimilarities among pairwise assemblies can be associated with the contrast of those five variables and the latitude value using multivariate mixed linear distance matrix.

We hypothesized that the local species diversity will be reduced by both sources of hunting pressures, deforestation and floodplain extension, but will increase with stream length and towards the interior of protected area. Regarding  $\beta$ -diversity, we predict that total and turnover dissimilarities will increase with increasing pairwise contrast of all variables, except for the hunting pressures, habitat loss and floodplain extension, for which increasing pairwise contrast should increase the nestedness dissimilarity among sites (Fig.1). The persistent assemblies in the most disturbed sites should be subsets of the more pristine sites, and all these effects should be more pronounced in the game than non-game local assemblies.

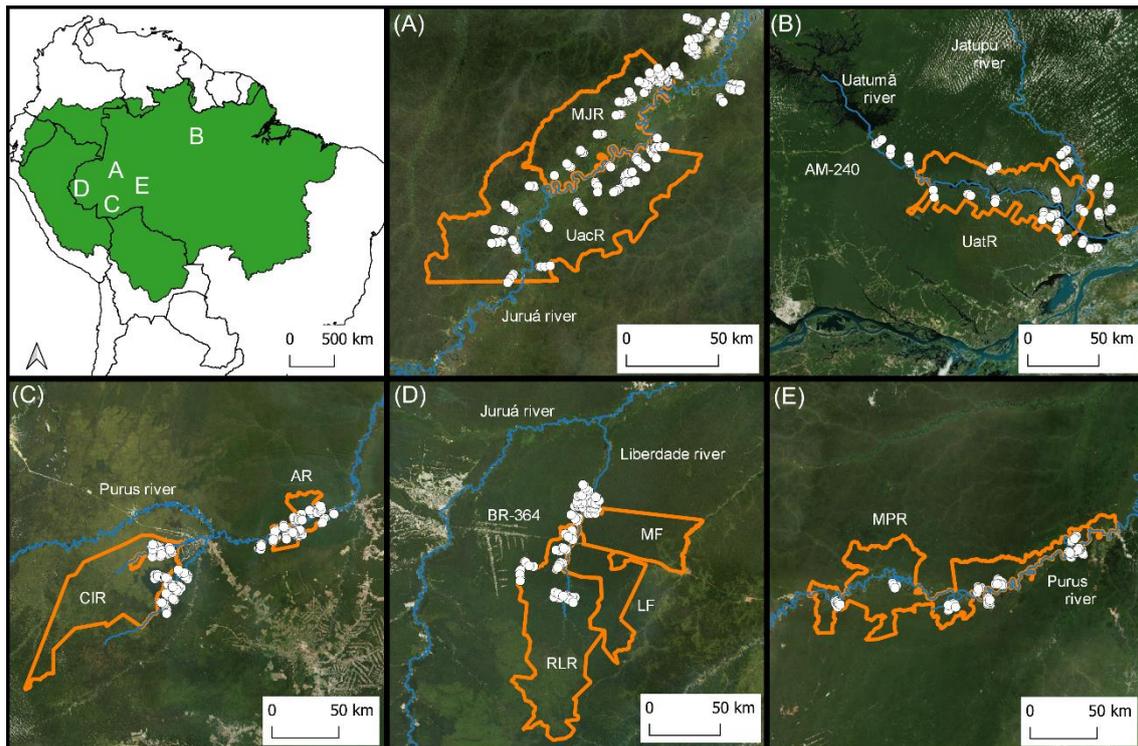


**Figure 1** – Panel (A) shows the expected relationships between the species number and the game assembly integrity and the increasing value of our six predictive covariates. Panel B shows the expected relationships between the two beta-diversity components (turnover [Turn]; nestedness [Nest]) of local game assemblies and the increasing of the pairwise distances of the six variables.

## Methods

### *Study area*

We accessed the local occurrences of terrestrial camera trappable species in the central-western portion of Brazilian Amazon during two field-effort stages. In the first stage, carried out between 2013 and 2015, we collected data in the regions of the middle Juruá and Uatumã rivers (Fig. 2A and B; see Abrahams et al., 2017). In the second stage, during 2018 and 2019, we implemented new data acquisition in the regions of upper Juruá and upper Purus rivers basins (Fig. 2C, D, E).



**Figure 2** – Maps of the locations of the five study regions (panels A-E) within lowland Amazon (green portion of the upper left panel), South America. (A) Médio Juruá Extractive Reserve (MJR) and Uacari Sustainable-Use Reserve (UacR); (B) Uatumã Sustainable-Use Reserve region; (C) Cazumbá-Iracema Extractive Reserve (CIR) and Arapixi Extractive Reserve (AR); (D) Riozinho da Liberdade Extractive Reserve (RLR), Liberdade State Forest (LF) and Mogno State Forest (MF); and (E) Médio Purus Extractive Reserve. The 720 camera traps deployed, their nearest urban centers, the Protected Area boundaries, and main rivers are shown as white dots, red dots, orange polygons and blue lines, respectively.

In the middle Juruá region, we collected local occurrences of species in the catchment areas of local communities and urban neighbourhoods (hereafter, *communities*) located within and immediately outside two adjacent SURs, the Uacari Sustainable Development Reserve (UacR) and the Médio Juruá Extractive Reserve (MJR), located near the towns of Carauari and Itamarati in the state of Amazonas (hereafter, Médio Juruá Reserves; JR). This landscape is comprised of a mix of unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests, as well as permanent

water bodies. In the Uatumã region, we installed camera traps near human communities within and immediately outside the Uatumã Sustainable Development Reserve (UatR), located near the towns of São Sebastião do Uatumã and Itapiranga in the state of Amazonas. The landscape is comprised mainly of *terra firme* and a small portion of seasonally-flooded forests, locally referred to as *igapó*, and permanent water bodies.

In the upper Juruá and Purus regions, we collected data near local communities within and immediately outside SURs in three subregions: (1) Cazumbá-Iracema (CIR; Caeté and Macauã rivers) and Arapixi (AR; Purus river) Extractive Reserves (Fig. 2C); (2) Riozinho da Liberdade Extractive Reserve (RLR; Liberdade river), Liberdade State Forest (LF; Liberdade river), Mogno State Forest (MF; Liberdade river), hereafter Liberdade Reserves (LR; Fig. 2D); and the (3) Médio Purus Extractive Reserve (MPR; Purus river; Fig. 2E). All communities at Cazumbá-Iracema and some communities at Arapixi are located near the town of Sena Madureira (state of Acre), while the other Arapixi communities are located near the city of Boca do Acre (state of Amazonas). The two nearest cities to the communities of LR are Cruzeiro do Sul (Acre) and Ipixuna (Amazonas). Local communities at MPR are nearest to the cities of Pauini and Lábrea (Amazonas). The landscapes of CIR and LR are predominantly comprised of *terra firme* forests and to a minor extent, flooded forest, while the landscape at AR and MPR consist primarily of *terra firme* forests, although *várzea* forests are important elements of the landscape.

Sites in western Amazon encompass highly productive white-water floodplain ecosystems (Fig. 2A, C, D, E), while those in Central Amazon (Fig. 2B) encompasses much lower productivity black-water rivers (Junk et al., 2015), potentially resulting in lower faunal biomass density (Emmons, 1984).

### *Local occurrences of focal species*

The local occurrences of species were obtained by camera traps (hereafter CT; remotely activated digital cameras triggered by motion or temperature change). A total of 720 CTs were deployed in the catchment areas in the vicinities of 100 human communities in contiguous primary *terra firme* forest. The total sampling effort reached 30,445.15 traps.days and the number of days each CT operated ranged from 0.5 to 62.08 days ( $42.28 \pm 12.44$  days; mean  $\pm$  SD; see Table 1).

**Table 1** – Total number and effort of Camera Traps (CT) deployed, and the total of human communities accessed. MJR - Médio Juruá Extractive Reserve and Uacari Sustainable-Use Reserve; UatR - Uatumã Sustainable-Use Reserve CIR - Cazumbá-Iracema Extractive Reserve; AR - Arapixi Extractive Reserve; RL - Riozinho da Liberdade Reserves and; MPR - Médio Purus Extractive Reserve.

Dataset	Region	Total of CT	Effort in trap.days	Total of communities
#1	MJR	193	6423	32
#1	UatR	95	2708.1	21
#2	CIR	119	6075.5	10
#2	AR	96	4751.5	14
#2	RL	115	5458	14
#2	MPR	102	5029	9
	Total	720	30445.1	100

In the first stage, a total of 288 CTs were deployed (Bushnell Trophy-Cam and Reconyx HC500 Hyperfire), during the dry season, in the continuous unflooded forests located in the catchment areas of local communities. Most of these CTs were deployed at 350m, 1000m, 3000m and 6000m from the human communities towards interior of forests (see Abrahams *et al.* [2017] for details). In the second stage, the majority of the 432 CTs (Bushnell Trophy-Cam) were deployed following the Abrahams *et al.* (2017)

protocol during the dry season. Due to local difficulties and access restrictions to unflooded forests near some human communities in the second stage, 26 CT were installed in seasonally flooded forests in MPR. All the 720 CT were unbaited and installed approximately 30 cm above the forest floor and at least 20 m away from human trails. The distances from each CT to the nearest human community centroid (COM.Dist) ranged from 75m to 15 km ( $3.5 \pm 2.4$  km, mean  $\pm$  SD; see Table 2).

**Table 2** – Description of the explanatory variables used in all analyses. Each variable is classified according to their features. Codes, description, type and range of each are presented.

Category	Covariable	Code	Description	Type	range (mean $\pm$ SD)
Camera	Effort	EFF	Total of operating days	Camera site	0.5 to 62.08 (42.3 $\pm$ 12.4)
Habitat	Stream density	STREAM	Stream total length (m)	GIS 500 m	0 to 2365.9 (426.8 $\pm$ 549.4)
Habitat	Flooded extension	FLOOD	Extension around camera (m <sup>2</sup> )	GIS 500 m	0 to 0.72 (0.04 $\pm$ 0.11)
Habitat	Habitat loss extension	HABITAT	Extension around camera (m <sup>2</sup> )	GIS 500 m	0 to 0.86 (0.07 $\pm$ 0.15)
Nuisance	Latitude value	LAT	Latitude value (decimal degree)	Camera site	-72.23 to - 57.94 (67.03 $\pm$ 3.85)
Anthropogenic	Protected area distance	PROTE	Euclidean distance to PA limit (km)	Camera site	-44.48 to 31.46 (76.8 $\pm$ 12.75)
Anthropogenic	Community size	COM	Total of household	Community	1 to 497 (12.97 $\pm$ 23.9)
Anthropogenic	Community distance	COM.Dist	Euclidean distance to community (km)	Camera site	0.075 to 15 (3.5 $\pm$ 2.4)
Anthropogenic	Local hunting pressure	COM.HP	Total of household / $\sqrt{}$ km	Camera site	0.14 to 120.9 (4.18 $\pm$ 6.9)
Anthropogenic	City size	CITY	Total of urban population	City	4472 to 55326 (20801 $\pm$ 13169)
Anthropogenic	City distance	CITY.Dist	Access distance to nearest city (km)	Camera site	9.49 to 278.8 (113.47 $\pm$ 67)
Anthropogenic	City hunting pressure	CITY.HP	Urban population / $\sqrt{}$ km	Camera site	272 to 10804 (2288 $\pm$ 1657)

### Studied taxa

We restricted our focal species to 32 terrestrial and semi-terrestrial camera-trappable forested vertebrate species (27 mammals and 5 birds taxa, see Table 3), which could be identified at least to genus level on CT's images. We grouped congeneric species from different study regions such as acouchis (*Myoprocta pratti* and *Myoprocta acouchy*) and treated them as single ecospecies (hereafter, *species*). Similarly, closely related species that could not be consistently identified to species level, such as *Dasyopus kappleri* and *Dasyopus novemcinctus*, were also grouped into single species. Images of domestic animals, humans, small passerines, primates, bats, small lizards, non-game bird species and insects were excluded from further analysis.

**Table 3** – List of the 32 target taxa ordered by order classification and their preference to be locally hunted (Game), followed by their scientific and English names. Taxa were described if they were recorded (R), not recorded (NR) or no confirmed occurrence (NO) in each region studied. MJR - Médio Juruá Extractive Reserve and Uacari Sustainable-Use Reserve; UatR - Uatumã Sustainable-Use Reserve; CIR - Cazumbá-Iracema Extractive Reserve; AR - Arapixi Extractive Reserve; RL - Riozinho da Liberdade Reserves and; MPR - Médio Purus Extractive Reserve.

Scientific name	English name	Game	MJR	UatR	CIR	LR	AR	MPR
<u>Mammals</u>								
<i>Tapirus terrestris</i>	Lowland tapir	Yes	R	R	R	R	R	R
<i>Panthera onca</i>	Jaguar	Yes	R	R	R	R	R	R
<i>Puma concolor</i>	Puma	Yes	R	R	R	R	R	R
<i>Tayassu pecari</i>	White lipped peccary	Yes	R	NR	R	R	R	R
<i>Mazama americana</i>	Red brocket deer	Yes	R	R	R	R	R	R
<i>Priodontes maximus</i>	Giant armadillo	Yes	R	R	R	R	R	R
<i>Pecari tajacu</i>	Collared peccary	Yes	R	R	R	R	R	R
<i>Mazama nemorivaga</i>	Grey brocket deer	Yes	R	R	NO	R	R	R
<i>Leopardus pardalis</i>	Ocelot	Yes	R	R	R	R	R	R

<i>Cuniculus paca</i>	Paca	Yes	R	R	R	R	R	R
<i>Puma yagouaroundi</i>	Jaguarundi	Yes	R	R	R	R	R	R
<i>Leopardus wiedii</i>	Margay	Yes	R	R	R	R	R	R
<i>Nasua nasua</i>	South American coati	Yes	R	R	R	R	R	R
<i>Dasyprocta</i> spp.	Agouti	Yes	R	R	R	R	R	R
Nonspecific cingulata small	Small cingulata	Yes	R	R	R	R	R	R
<i>Hadroskiurus spadiceus</i>	Southern Amazon red squirrel	Yes	R	NO	R	R	R	R
<i>Myrmecophaga tridactyla</i>	Giant anteater	No	R	R	R	R	R	R
<i>Dinomys branickii</i>	Pacarana	No	NO	NO	R	R	NO	NO
<i>Atelocynus microtis</i>	Short-eared dog	No	R	NO	R	R	R	R
<i>Speothos venaticus</i>	Bush dog	No	NR	NR	R	R	R	R
<i>Procyon cancrivorus</i>	Crab-eating raccoon	No	R	NR	R	R	R	R
<i>Eira barbara</i>	Tayara	No	R	R	R	R	R	R
<i>Tamandua tetradactyla</i>	Southern Tamandua	No	R	R	R	R	R	R
<i>Galictis vittata</i>	Greater Grison	No	NR	NR	R	R	NR	NR
<i>Sylvilagus brasiliensis</i>	Tapiti	No	NO	NO	R	R	NO	NO
<i>Didelphis marsupialis</i>	Common opossum	No	R	R	R	R	R	R
<i>Myoprocta</i> spp.	Acouchi	No	R	R	R	R	R	R
<u>Birds</u>								
<i>Mitu</i> or <i>Crax</i> spp.	Curassow	Yes	R	R	NR	NR	R	R
<i>Penelope jacquacu</i>	Spix's guan	Yes	R	NO	R	R	R	R
<i>Psophia</i> spp.	Trumpeters	Yes	R	R	R	R	R	R
<i>Tinamus</i> spp.	Large tinamou	Yes	R	R	R	R	R	R
<i>Crypturellus</i> spp.	Small tinamou	Yes	R	R	R	R	R	R

Based on our interviewed data (Sampaio *et al.* in review., Abrahams *et al.* 2017), we grouped the taxa in two distinct assemblies composed by: (1) non-game species and (2) game taxa (Table 3). Species were included in the game category if they were

locally consumed or slaughtered when considered livestock predators by at least one of our interviewed.

We assumed the local diversity of species as the aggregated number of species recorded in each CT. We assessed the local assembly integrity in each CT through the Sorensen similarity index, similarly to Banks-Leite *et al.* (2014). Sorensen similarities were calculated between the local and regional assemblies by each CT, using the function *vegdist* of *vegan* R package (Oksanen *et al.* 2019; [1 - Sorensen dissimilarity]). Regional assemblies were defined by the poll of species recorded in all CTs of each region, summed to the unrecorded species that potentially can occur in each region (recorded and not recorded species presented in Table 3). The potential occurrences of each species were examined by their geographic distribution maps accessed at IUCN Red list of threatened species website (<https://www.iucnredlist.org>).

#### *Spatial explanatory variables*

We derived all spatial variables using QGIS 3.14 (QGIS, 2021). In order to quantify the local hunting pressure exerted by local communities (COM.HP; see Table 2). We used a 1:2000 scale to count the number of all households inside no-overlapping 1-km buffers around the centroid of the two nearest human community of each CT, through a visual inspection in aerial photographs of Bing Maps from Open-layer (QGIS, 2021). These visual inspections were performed on 2019 aerial photographs in the regions of the middle Juruá and Uatumã rivers, assuming that no major changes have occurred in the human communities since the period of sampling (2013-2015). For the regions of upper Juruá and upper Purus rivers basins, we used aerial photographs of 2018 and 2019. We assumed exponential effects of the communities distances, then we divided their sizes by the square root of the Euclidean distance of communities to each CT (COM.Distance), and finally we calculated the mean of these two terms, as expressed in equation #1.

$$\text{COM. HP} = \frac{(\text{COM1 size} \div \sqrt{\text{COM1.Dist}}) + (\text{COM2 size} \div \sqrt{\text{COM2.Dist}})}{2} \quad (1)$$

We quantified the hunting pressure exerted by the nearest urban center of CTs (CITY.HP) accessing the size of urban population of each city (CITY; see Table 2; IBGE 2010) divided by the squared root of the access distance travelled by local people residing in the nearest community of each CT and summed the Euclidean distance from from CT to community (CITY.Dist; Table 2). We digitized rivers and roads (paved and unpaved) that residents of communities reportedly used to travel to the nearest city during the dry season, as described in equation #2.

$$\text{CITY. HP} = \frac{\text{CITY}}{\sqrt{\text{CITY. Dist}}} \quad (2)$$

To represent the effect of protection level afforded by PAs on CT, we calculated the Euclidean distance (km) between each CT and the nearest boundary of the SUR. Reserves within either the Juruá river (Fig. 1A) or the Liberdade river regions (Fig. 2D) are adjacent to each other and therefore we merged their perimeters into a single polygon. In order to capture the reserve protection effect, we assumed positive or negative values for CT distances to communities located either inside or outside each SUR polygon, respectively.

The remaining environmental metrics (see Table 2) were calculated in a buffer of 500 meters around each CT, being: (1) proportion of habitat loss extension around CT, expressed by the deforested area (km<sup>2</sup>), using the accumulated deforestation up to the year 2015 to the regions of the middle Juruá and Uatumã rivers and up to 2018 to

the regions of upper Juruá and upper Purus rivers basins (“Projeto de Monitoramento do Desmatamento na Amazônia Legal”; INPE 2019); (2) stream length around CT, which corresponds to the total length of all perennial streams (data from Venticinque *et al.* [2016]); (3) proportion of seasonally floodplain area around CT, which corresponds to the sum of all area classified as seasonally floodplain from the raster file presented in Hess *et al.*, (2015).

### *Statistical analyses*

Our eight explanatory variables, besides the sizes and distances of communities and cities are summarized in Table 2. We performed all statistical analyses using R 4.0.4. software (R.Core.Team, 2021). Prior to analyses we checked data distributions and relationships among response and predictor variables using dispersion plots and we log- or sqrt-transformed data whenever necessary, following Zuur *et al.*, (2010). We used *R base* package to explore correlations (Pearson value  $> |0.7|$ ) and *USDM* package (Naimi *et al.*, 2014) to explore collinearity (Variance Inflation Factor  $> 3$ ) among predictors (Table S1). We rescaled variables (mean = 0 and SD = 1) to enable model convergence and variable effect size comparisons (Harrison *et al.*, 2018).

We used mixed-effects models (see Bolker *et al.*, 2009) to evaluate the effects of (1) community hunting pressure (2) city hunting pressure, (3) distance to reserve boundaries, (4) stream length, the extent of neighboring (5) floodplain areas and (6) habitat loss had on (a) the species richness and (b) assembly integrity of non-game and game assemblies. We accounted for spatial dependence among CTs by specifying “community” as a random effect, since we deployed several CT in each community. We control for sampling effort heterogeneity using the logarithm of the number of days of each CT remained in operation as a model offset variable.

We fitted Poisson linear mixed models for count data (species richness) using the function *glmer* of the R package *lme4* (Bates et al., 2015) and evaluated for overdispersion (see Harrison *et al.*, 2018) using the function *testDispersion* of the R package *DHARMA* (Hartig, 2020). We fitted beta linear mixed models for proportional data (assembly integrity) using the function *mixed\_model* of the R package *GLMMadaptive* (Rizopoulos, 2021).

In order to analyze the variations in assemblies dissimilarities among sites, we previously removed the major sampling effort size effect on the composition of local assemblies recorded by us (see Plotkin & Muller-Landau 2002), once our two datasets presented distinct sampling effort goals: 30-day and 45-day for the first and second stages, respectively. We filtered both datasets, excluding those camera traps with less than 24 days of sampling and limited the recorded data up to 36 days of samplings, resulting in a balanced sampling effort of 24-36 days for 648 CTs.

Based on presence-absence data of non-game and game species in the 648 CTs, we calculated the Sorensen ( $\beta_{sor}$ ), Turnover (Simpson dissimilarity;  $\beta_{sim}$ ) and Nestedness ( $\beta_{sor} - \beta_{sim} = \beta_{nes}$ ) dissimilarities among CTs, using the function *beta.pair* of the *beta-part* R package (Baselga et al., 2020).

We created pairwise matrices of Euclidean distances for each predictor, using the function *dist* of the *vegan* R package (Oksanen et al., 2019). We used only the latitude value as nuisance variable, since we previously identified correlation (see Table S2) among the (1) the geographic distance among CTs, the pairwise Euclidean distances of (2) Latitude, (3) Longitude and (4) the endemism. To calculate the endemism pairwise distance, we followed the endemism as described in Ribas *et al.* (2012), where “0” distance was set to CTs in the same endemism center and “1” to CTs at distinct endemism centers.

We finally used the multivariate mixed linear distance matrix, specifying “community” as a random effect, to test the pairwise associations among (1) Sorensen; (2) Turnover and (3) Nestedness dissimilarities of the non-game and games local assemblies with the distance matrices of our predictive variables: (1) community hunting pressure (2) city hunting pressure, (3) distance to reserve boundaries, (4) stream length, the extent of neighbouring (5) floodplain areas and (6) habitat loss, and; (6) latitude value, using the function *mixed.mdmr* of the *MDMR* R package (McArtor, 2018).

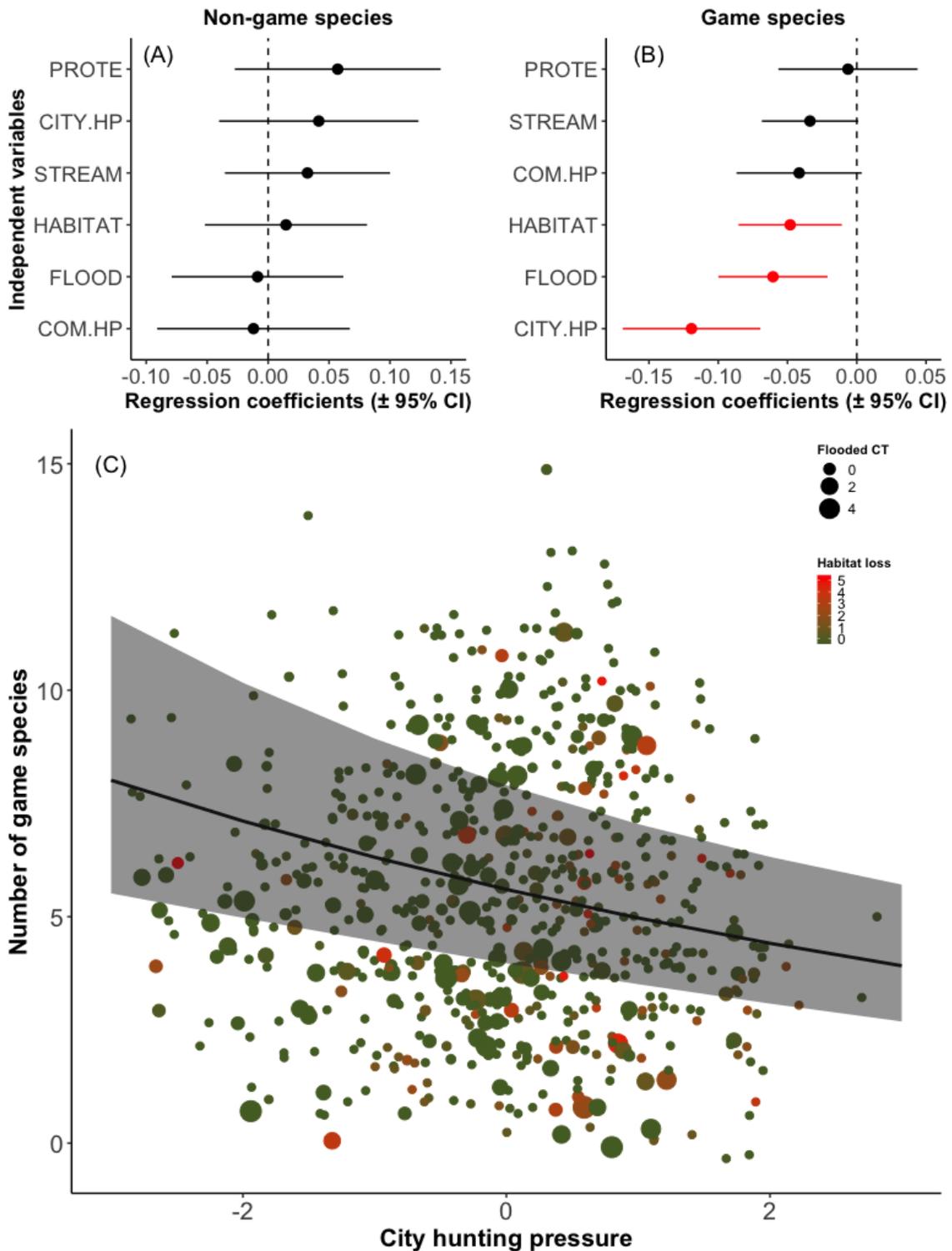
We opted to assess the effects of our predictor variables using only global models of our mixed models, since minimal adequate models (i.e., more parsimonious models) can overestimate the effect size of significant predictors (Forstmeier and Schielzeth, 2011; Harrison et al., 2018) and global models better indicate the direction and intensity of the explanatory variables effects.

## **Results**

Our study evaluated local game depletion on a wide range of hunting pressure and wide geographic area inside and outside sustainable-use reserves in tropical forests. More specifically, this included eight urban areas ranging from around 4,000 to 55,000 residents and 100 local human communities ranging from 1 to 497 households (see Table 2).

Considering our list of 32 focal terrestrial camera-trappable species, the regions with higher species number were located at Acre state. In the LR and CIR regions 31 and 30 species were recorded, respectively. In AR and MPR 29 species were recorded, 28 were recorded in MJR and 23 species were recorded in UatR (see Table 3).

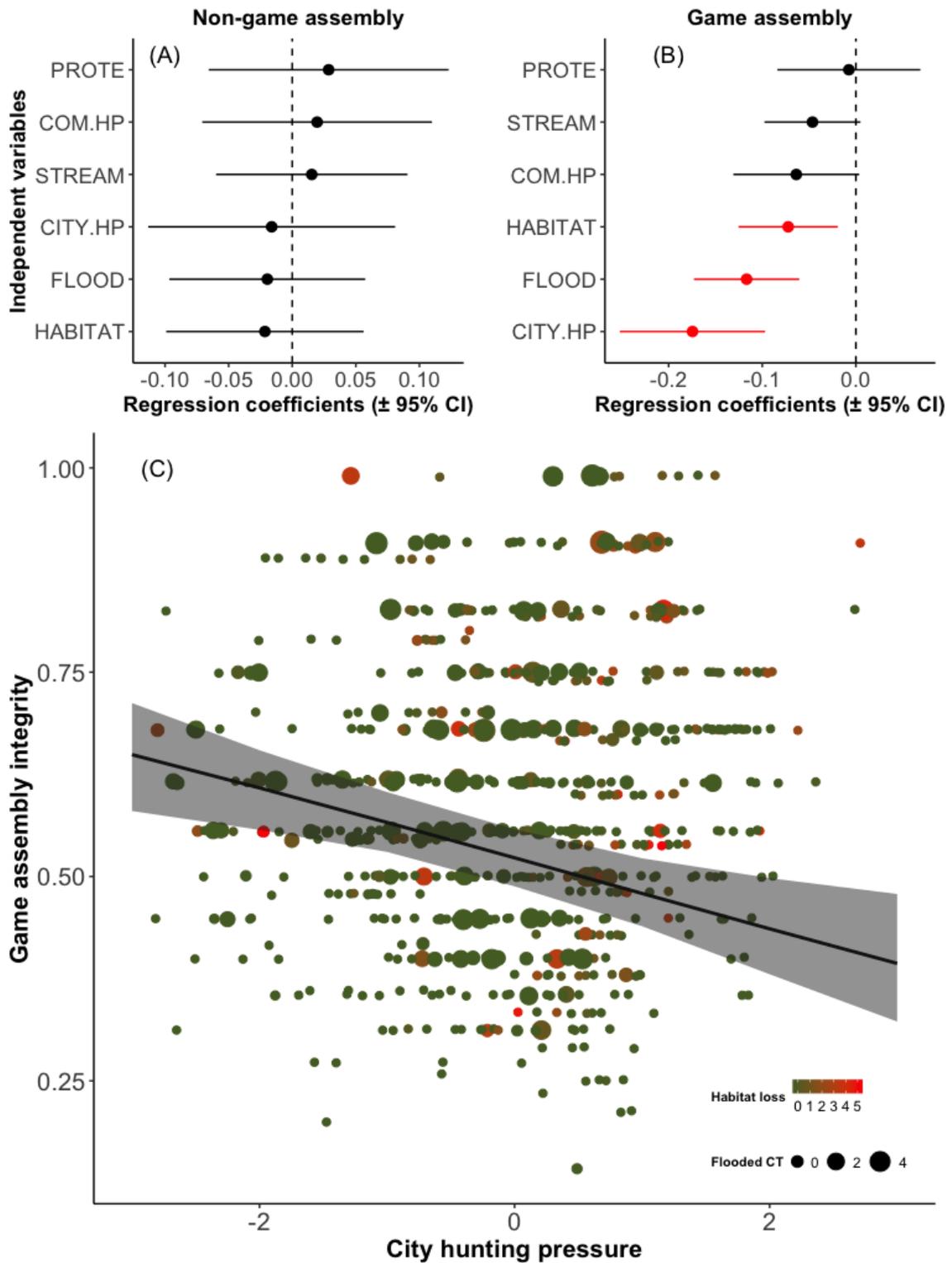
The total number of non-game species richness ranged from 0 to 7 (mean  $\pm$  SD;  $1.32 \pm 1.18$ ) and it was not significantly affected by any of our set variables (Fig. 3A). In turn, the total number of game species richness ranged from 0 to 15 (mean  $\pm$  SD;  $5.5 \pm 2.8$ ) and was negatively affected by the extensions of habitat loss, floodplain extension and the city hunting pressure; stream length and community hunting pressure showed marginal negative effects (Fig. 3B and C).



**Figure 3** – Panels synthesizing results of Generalized Linear Mixed Models showing the magnitude and direction of effects (standardized betas  $\pm 95\%$  confidence intervals) of independent variables (FLOOD – Flooded area extension around camera trap; STREAM – Stream density; HABITAT – Habitat loss extension; PROTE – Protected Area limit distance; COM.HP – Community hunting pressure; CITY.HP – City hunting pressure) on non-game species numbers (A) and game species number (B). Panel C shows

the relationships between the local game species number and the city hunting pressure and the extent of flooded area around camera trap (Flooded CT) and the adjacent habitat loss around camera trap (Habitat loss). The estimated game species number values and 95% confidence interval are represented by a black line with a grey border, while the extent of habitat loss is represented by the green to red color gradient and the flooded area around camera trap by the size of the dots.

The proportion of non-game assembly integrity ranged from 0.22 to 1 (mean  $\pm$  SD;  $0.78 \pm 0.17$ ) and it was not significantly affected by any of our set variables (Fig. 4A). The proportion of game assembly integrity ranged from 0.14 to 1 (mean  $\pm$  SD;  $0.59 \pm 0.17$ ), which reduced with habitat loss and floodplain extension and city hunting pressure; stream length and community hunting marginally reduced it (Fig. 4B and C).



**Figure 4** – Panels synthesizing results of Generalized Linear Mixed Models showing the magnitude and direction of effects (standardized betas  $\pm$ 95% confidence intervals) of independent variables (FLOOD – Flooded area extension around camera trap; STREAM – Stream density; HABITAT – Habitat loss extension; PROTE – Protected Area limit distance; COM.HP – Community hunting pressure; CITY.HP – City hunting pressure) on the integrity of non-game assembly (A) and game assembly (B). Panel C shows

the relationships between the integrity of game assembly and the city hunting pressure and the extent of flooded area around camera trap (Flooded CT) and the adjacent habitat loss around camera trap (Habitat loss). The estimated game species number values and 95% confidence interval are represented by a black line with a grey border, while the extent of habitat loss is represented by the green to red color gradient and the flooded area around camera trap by the size of the dots.

Our site pairwise comparisons showed that total dissimilarity of both non-game and game assemblies were mainly driven by the Turnover component of dissimilarity (73% and 74% of all dissimilarity, respectively; Table 4). The higher the pairwise contrast in floodplain extension and latitude were correlated with the reducing and increasing, respectively, of the Sorensen and Turnover dissimilarities of the non-game assemblies (Table 4; Fig. S1). The contrast of floodplain extension, stream length, latitude and city hunting pressure were associated with the increasing the Sorensen dissimilarity of game assemblies (Table 4; Fig. S2), and excepting the city hunting pressure, all these variables were associated with the increasing of the Turnover dissimilarity among game assemblies (Table 4; Fig. S2).

**Table 4** – Percentage (%) of contribution of Turnover and Nestedness on Sorensen dissimilarity in the composition of game and non-game assembly in our study. Distance-based multivariate mixed regression omnibus statistic in the relation to the Sorensen dissimilarity and the two  $\beta$ -diversity components (Turnover and Nestedness) according to the distance matrices of seven independent variables. Values in bold correspond to those with p-value < 0.05 and the signals in parentheses (+/-) indicate the direction of the effect.

Independent variable	Non-game assembly			Game assembly		
	Omnibus (Sorensen)	Omnibus (Turnover)	Omnibus (Nestedness)	Omnibus (Sorensen)	Omnibus (Turnover)	Omnibus (Nestedness)
% of contribution on dissimilarity		74% ± 43%	26% ± 43%		73% ± 32%	27% ± 32%
Omnibus	<b>15.80</b>	<b>16.77</b>	3.57	<b>40.92</b>	<b>51.15</b>	-7.30
Intercept	0.73	0.79	0.24	0.11	0.12	0.16
Flooded area extension	<b>4.45 (-)</b>	<b>5.00 (-)</b>	-4.73	<b>7.62 (+)</b>	<b>11.6 (+)</b>	-8.90
Stream density	1.91	2.00	1.11	<b>6.25 (+)</b>	<b>8.21 (+)</b>	-5.71
Latitude	<b>2.91 (+)</b>	<b>3.04 (+)</b>	1.73	<b>7.02 (+)</b>	<b>9.14 (+)</b>	-4.96
Habitat loss extension	0.54	0.37	4.01	<b>6.81 (+)</b>	<b>8.64 (+)</b>	-1.35
Protected area distance	-0.03	-0.20	3.30	1.09	1.47	1.22
City hunting pressure	1.69	1.77	-1.05	<b>2.53 (+)</b>	2.15	5.27
Community hunting pressure	2.25	2.22	1.40	1.62	0.67	9.10

## Discussion

Our results provide valuable information how hunting pressure and local level of protection can affect local occurrences of camera-trappable terrestrial and semi-terrestrial game and non-game species. We clearly show that city hunting pressure, together with habitat loss and floodplain extension, significantly reduce local species diversity and assembly integrity of game species occurring around human communities located inside and surroundings of SURs of Brazilian Amazon. On the other hand, local species diversity and assembly integrity of non-game species were not affected by our set of predictors. We also found species replacement (turnover dissimilarity) as the principal component of pairwise site species composition. Non-game species assemblies' total and turnover dissimilarities were related with environmental variables contrast only; floodplain extension and latitude contrasts were associated with the reduction and increase, respectively, with both dissimilarities. In turn, total dissimilarity among assemblies of game species was positively related with the contrasts of all environmental predictors plus city hunting pressure, and except the city hunting pressure, all of them were related with the increasing of replacement of species.

### *Hunting pressure effects on camera-trappable game species diversity*

Both sources of hunting pressure negatively affected local game richness species and assembly integrity, but only city hunting showed a significant effect. These results agree with our predictions derived from several past studies about the hunting on tropical forests game species (Abrahams et al., 2017; Benítez-López et al., 2019; Osuri et al., 2020; Peres and Palacios, 2007). The bushmeat trade in Brazil is illegal, however the subsistence consumption by local traditional communities is not (see Antunes et al., 2019). The local consumption of wildmeat usually impact the populations of game

species near the vicinities of rural human communities in tropical forests (Abrahams et al., 2017; Beirne et al., 2019), nevertheless, in our settings the demand for local wildmeat consumption does not seem to be strong enough to significantly structure local game assemblies.

Rather, the major effects on game species resulted from the higher demand of urban centers, with the reduction of game diversity and assembly integrity being a product of the understory bushmeat trade with urban centers, that is usually high in tropical forests (Fa and Brown, 2009; Morton et al., 2021; Rija et al., 2020), including the Brazilian Amazon (Chaves et al., 2017; El Bizri et al., 2019; Parry et al., 2014). In accordance with El Bizri *et al.* (2020), approximately two-thirds of rural hunters interviewed in their study reported selling bushmeat in central Amazon, mainly to urban areas where it can reach the highest prices. It is reasonable to assume, therefore, that local communities closer to larger urban center are under higher demand for bushmeat trade, resulting in the current local depletion pattern of game species in the communal catchment areas sampled in our study. Furthermore, this local communities are more accessible to city hunters (Benítez-López et al., 2017; Peres and Lake, 2003), that certainly increased the local erosion of game species.

In disagreement with our previous hypothesis, however, our data showed that both sources of hunting pressures were not mitigated by the local level of protection, since the distance to the SURs border didn't show the expected positive effects on local species richness and assembly integrity. This suggests that the urban demand on bushmeat is affecting the long-term conservation even further inside these kind of PAs, even though illegal hunting activities has been found to decrease with increasing inaccessibility inside Amazon PAs (Kauano et al., 2017). Brazilian Amazon SURs suffer from an absence of a clear and effective national policy of community-based subsistence hunting management

plans (Antunes et al., 2019; Sampaio et al., in press). The lack of bottom-up conservation strategies like that could be the main factor explaining the absence of potential positive protection level effect on game biodiversity in our study. These results suggest that tropical SURs, lacking appropriate local hunting management, have reduced potential value for biodiversity conservation.

The effect we found for stream length was also unexpected (see Paredes *et al.* 2017). Its marginally negative rather than positive effects on local richness and assembly integrity of game species might, nevertheless, result from the increased local hunter accessibility provided by small perennial streams, as previously reported in Amazon forests (Abrahams et al., 2017; Michalski et al., 2015). This possibility is backed by the observation that local hunt trails and camps were generally found nearby streams around human communities in our study area (R. Sampaio pers. obs).

Considering pairwise dissimilarities among local assemblies, the city hunting pressure contrast increased with only the Sorensen dissimilarity, as the result of local game species number reduction. In disagreement to our previous predictions, however, this loss of species wasn't a determinist process since the nestedness component didn't was associated with the pairwise contrast of hunting pressure. We suspect that this unexpected result might derive from the relatively low forest loss and fragmentation in our study landscapes. While hunting pressure combined with habitat loss resulted in nestedness assemblies in central Amazon (Sampaio et al., 2010), our sampling sites are surrounded by vast tracts of continuous primary forests with reduced accessibility and lower hunting pressure, where the dispersal rates of individuals and species from pristine to hunted sites are still possibly high. This landscape configuration might facilitate the underlying mechanisms maintaining regional metacommunities, such as "source-sink", "mass effect" and "rescue effect" (see Leibold *et al.* 2004), all of which

contribute to the random component of game species loss induced by hunting. This system could only operate, nevertheless, where large tracts of pristine forest are still present, like in our study areas.

#### *Environmental features structuring local game diversity*

The Amazonian inundation pulse can operate such as an environmental filter selecting arboreal and semi-arboreal species able to inhabit seasonally flooded forests but only a reduced number of terrestrial species are able to migrate to these habitats in the dry season (Alvarenga et al., 2018; Costa et al., 2018; Haugaasen and Peres, 2005).

According with our expectations, the floodplain area extension reduced the local diversity and assembly integrity, however, only for game species. The seasonal pulse of inundation has been shown to be more effective in game terrestrial species, since several of them, such as Brazilian tapir (*Tapirus terrestris*), giant armadillo (*Priodontes maximus*), collared peccary (*Pecari tajacu*), agouti (*Dasyprocta* spp.), lowland paca (*Cuniculus paca*), white lipped peccary (*Tayassu pecari*) and brocket deer species (*Mazama* spp.) were not recorded in central Amazon flooded forests (Alvarenga et al., 2018).

The local level of habitat loss impacted the detection rates (Abrahams et al., 2017) and the occupancy (Whitworth et al., 2019) of terrestrial vertebrates in Amazon. In our study, however, the habitat loss around CT only affected game species. It's reasonable to think that the small-scale habitat modification as a result of clear-cut of primary forest by local people around communities, can reduce the local availability of resources for game species, especially the richness and availability of important fruit resources. Habitat loss was determinant to the persistence of frugivorous mammal species in tropical fragmented forests (Magioli et al., 2021). The majority of our focal

game species are frugivorous (14 from 21 species) and less than the half of total number the non-game species are frugivorous (5 from 11 species), it's reasonable to suppose that the reduction of this important fruit resources induced by habitat loss was detrimental to game local diversity.

### *The replacement of species*

The pairwise dissimilarities comparisons were mainly governed, in both assemblies, by the replacement component. Environmental heterogeneity among sites has been shown to increase the dissimilarity of species assemblies, increasing the replacement of species in tropical forests (Dambros et al., 2020; Melo et al., 2009; Morlon et al., 2008). In agreement with this pattern, our results indicated that latitude variation, that express contrast in environmental, geographical and endemism features, acted as environmental filter of species occurrences, since we found a positive association among species replacement and latitudinal contrast. Similarly, the pairwise contrast in stream density also was associated with species turnover.

The mammal assemblies in seasonally flooded forests (*várzea*) generally form a subset of those inhabiting unflooded forests (*terra firme*) in central Amazon (Alvarenga et al., 2018), however, we did not find evidence supporting this pattern. Our study included a wider gradient of seasonally flooded area proportion, including areas with lower inundation pulse (our southwestern sites) than those of central Amazonian sites of Alvarenga et al., (2018). The seasonall migration of terrestrial species from unflooded to flooded forests could be facilitated in areas with lower regional inundation (Costa et al., 2018), reducing the potentio nested dissimilarities among sites, a pattern captured in our study. Besides, our gradient of flodplain extension contrast revealed their effect of environmental filter in species occurrence and habitat preferences, it was associated

with the increasing and reducing the replacement dissimilarities of game and non-game species, respectively, and further research is needed in order to clarify and understand this process.

Our metric of habitat loss extension didn't promote habitat isolation such as in more intensive human occupied landscapes and in disagreement with our predictions, however it was associated with the replacement of game species. It was shown that anthropogenic disturbance can increase the replacement of native species by exotics and/or by non-forested neotropical mammal species (Beca et al., 2017; Sales et al., 2020). This, however, is not the case of our study since we didn't record any exotic or non-forest specialized species in CTs. In our study, the habitat loss extension acted as ecological filter, since only a reduced number of game species were able to persist in sites with more proportion of habitat loss, as described for neotropical small mammals (Püttker et al., 2015). The human land use (secondary forests, agricultural fields and cattle pastures) on the deforested patches in our study were dependent on social and economic regional contexts (Sampaio, R. unpublished data), which may result in idiosyncratic patterns of filtering the persistent species.

#### *Concluding remarks and conservation considerations*

This study aims to contribute to the design of evidence-based conservation strategies that can mitigate the effects of hunting pressure on game species and provided insights to contribute to natural resource management mainly in sustainable-use tropical forest reserves.

In summary, the city hunting pressure, together with habitat loss and floodplain area extension, reduce the local diversity and assembly integrity of game taxa near human communities located in the interior and surroundings of SURs of the Brazilian

Amazon. Species replacement was the dominant component among site dissimilarities; excepting the hunting pressures and local level of protection, most environmental variables were associated with the increasing in the replacement of all species.

These findings reinforce that the tropical conservation stakeholders should prioritize regional resource management policies aiming the reduction of urban demand on bushmeat, including more efficient surveillance and deterrence of commercial hunting and urban bushmeat trade, to provide alternative inexpensive sources of animal protein for urban consumption (fisheries and small domestic livestock) or even the regulation of wild meat surplus sales by traditional communities (van Vliet et al., 2019). Wildlife community-base management mainly inside SURs can reduced the local scales game diversity collapse, where communities with great accessibility to urban areas and with great proportion of habitat loss should be prioritized, besides the human use of this deforested patches should increase the local availability of resources for game species. The conservation of regional diversity of game species will only be effective if wide portions of intact forests can be protected in order to guaranty the individual dispersion dynamics from no hunted sites to the communal catchment areas around human communities.

### **Chapter III: Drivers of reduction on game forested vertebrate abundance in sustainable-use Amazonian protected areas**

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#### **Keywords**

Occupancy modelling; subsistence hunting; defaunation; game depletion; wildlife  
management.

## **Introduction**

The most effective conservation strategy to avoid tropical biodiversity losses is admittedly the establishment of Protected Areas (hereafter PAs; Andam et al., 2008). In the last few decades a great number of PAs were established in the tropical forests, covering around 7% of all landscape (Wright, 2010). Almost 40% of these protected territory is composed by Sustainable-Use Reserves (Schmitt et al., 2009), which are PAs that seek to preserve nature while allowing exploitation of natural resources by local communities (hereafter, SURs; IUCN Categories V and VI; Dudley et al., 2010).

The long-term sustainability of the human livelihoods and extraction of natural resources inside SUR, however, will succeed only if based on scientific planning for the controlled and sustainable-use of the nature resources (Woodley et al., 2019). Their extremely low budget, lack of infrastructure and specialized personnel limit the achievements of their conservation goals (Watson et al., 2014). Most SURs can be considered “paper parks” (Dudley and Stolton, 1999), lacking effective management plans (Laurance et al., 2012) or questioned conservation effectiveness (Terborgh and Peres, 2017).

Vertebrate species hunting is the most widespread form of human livelihood and extractivism in tropical forests (Fa et al., 2002), occurring even in the most isolated and apparently pristine sites, which is the case of most SURs in tropical forests (Peres and Lake, 2003). This anthropogenic pressure might compromise the stock of game species or empty tropical forests of large and slow breeding vertebrate species (Benítez-López et al., 2019; Bogoni et al., 2020a; Harrison, 2011; Redford, 1992; Wilkie et al., 2011). Consequently, vertebrate hunting triggers several cascading ecological effects (Ripple et al., 2016) and compromises ecosystem services provided by game species (Bogoni et al., 2020b; Rodrigues et al., 2020).

Several studies have assumed that higher human density population increases hunting pressure. The depletion of game species generally occurs in areas near human settlements, roads and cities (Abrahams et al., 2017; Beirne et al., 2019; Benítez-López et al., 2017; Harrison, 2011; Lhoest et al., 2020). The negative effects of hunting on exploited species have been reported to be higher outside PAs (Benítez-López et al., 2017) and hunter's perceptions about the improvement of local abundance of game species inside SURs were higher than those living outside (R. Sampaio et al., n.d.). Despite advances in the knowledge of the drivers of game depletion induced by hunting in tropical forests, the effects of wide gradients of hunting pressure on local population of game species is still reduced (Fa and Brown, 2009).

We lack information, for instance, on how strong are the population's declines of exploited species caused by the hunting pressures exerted at local scales, oriented by the bushmeat consumption at the rural human settlement level, and those caused by urban demand and consumption. We also lack information about how the local level of protection can mitigate the effects of wildmeat consumption at local and regional levels.

In this study, we took the advantage of cameras automatically triggered by heat and motion (camera traps) that are recognized as effective to access local occurrences of terrestrial game species (Wearn and Glover-Kapfer, 2019). We deployed 720 camera traps over a wide range of hunting pressure that includes the communal catchment areas around 100 rural human settlement, located at varied distances from eight urban areas inside and in the vicinity of nine SURs in central and western portion of the Brazilian Amazon.

We assumed that hunting pressure promotes variation on local abundance of game species and used mixture models that accounts for detection heterogeneity induced by site-level variation in species abundance (Royle and Nichols, 2003). Using

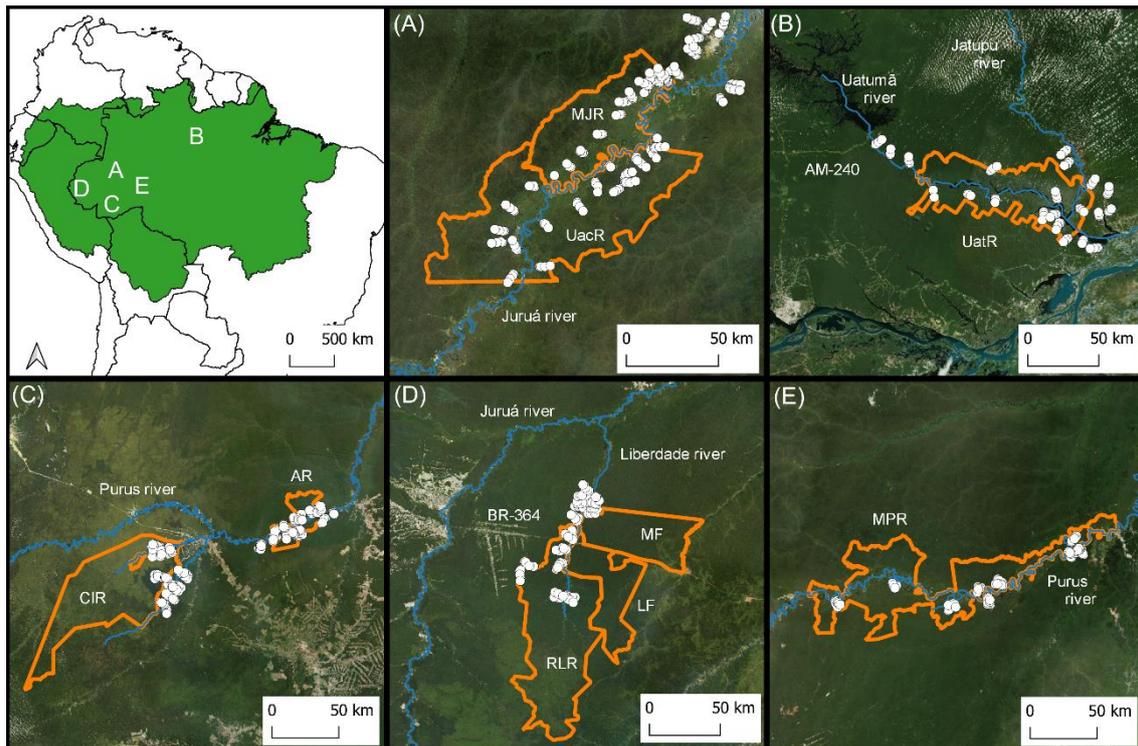
this modelling, we were able to estimate the number of individuals available for detection around the camera trap, such as a proxy of species local abundance ( $\lambda$ ) from unmarked individuals of 15 game terrestrial vertebrate species, two large felid species (*Panthera onca* and *Puma concolor*) and the largest mirmecophagous, the giant anteater (*Myrmecophaga tridactyla*).

Specifically, we evaluated the effects of hunting pressure caused by local (i) communities and (ii) city hunting pressures, (iii) local level of protection (distance from the perimeter of protected areas) and three local environmental features: (iv) stream length, (v) extension of seasonally flood areas and (vi) habitat loss extension around each camera trap, on the local relative abundances of 18 terrestrial vertebrate species. We expected that both sources of hunting pressure will reduce the abundance of larger and more sensitive species and increasing levels of protection (towards the interior of protected area) will mitigate the hunting pressure effect and, consequently, will increase the local abundances, mainly for more sensitive game species. We also expected that our three environmental quality local predictors will show species-specific effects on local relative abundance of species.

## **Methods**

### *Study area*

Our camera trap data came from two field-effort stages in the central and southwestern portion of Brazilian Amazon. In the first stage, during 2013 and 2015, we collected data in the regions of middle Juruá and Uatumã rivers (Fig. 1A-B). In the second stage, during 2018 and 2019, we implemented new data acquisition in the regions of upper Juruá and upper Purus rivers basins (Fig. 1C, D, E).



**Figure 1** – Maps of the locations of the five study regions (panels A-E) within lowland Amazon (green portion of the upper left panel), South America. (A) Médio Juruá Extractive Reserve (MJR) and Uacari Sustainable-Use Reserve (UacR); (B) Uatumã Sustainable-Use Reserve region; (C) Cazumbá-Iracema Extractive Reserve (CIR) and Arapixi Extractive Reserve (AR); (D) Riozinho da Liberdade Extractive Reserve (RLR), Liberdade State Forest (LF) and Mogno State Forest (MF); and (E) Médio Purus Extractive Reserve. The 697 camera traps deployed, their nearest urban centers, the Protected Area boundaries, and main rivers are shown as white dots, red dots, orange polygons and blue lines, respectively.

In the middle Juruá region, we collected local occurrences of species around local communities and urban neighbourhoods (hereafter, *communities*) located within and immediately outside two adjacent SURs, the Uacari Sustainable Development Reserve (UacR) and the Médio Juruá Extractive Reserve (MJR), located near the towns of Carauari and Itamarati in the state of Amazonas (hereafter, Médio Juruá Reserves; JR). This landscape is comprised of a mix of unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests, as well as permanent water bodies. In the Uatumã region, we

installed camera traps near human communities within and immediately outside the Uatumã Sustainable Development Reserve (UatR), located near the towns of São Sebastião do Uatumã and Itapiranga in the state of Amazonas. The landscape is comprised mainly of *terra firme* and a small portion of seasonally-flooded forests, locally referred to as *igapó*, and permanent water bodies.

In the upper Juruá and Purus regions, we collected data near local communities within and immediately outside SURs in three subregions: (1) Cazumbá-Iracema (CIR; Caeté and Macauã rivers) and Arapixi (AR; Purus river) Extractive Reserves (Fig. 1C); (2) Riozinho da Liberdade Extractive Reserve (RLR; Liberdade river), Liberdade State Forest (LF; Liberdade river), Mogno State Forest (MF; Liberdade river), hereafter Liberdade Reserves (LR; Fig. 1D); and the (3) Médio Purus Extractive Reserve (MPR; Purus river; Fig. 1E). All communities at Cazumbá-Iracema and some communities at Arapixi are located near the town of Sena Madureira (state of Acre), while the other Arapixi communities are located near the city of Boca do Acre (state of Amazonas). The two nearest cities to the communities of LR are Cruzeiro do Sul (Acre) and Ipixuna (Amazonas). Local communities at MPR are nearest to the cities of Pauini and Lábrea (Amazonas). The landscapes of CIR and LR are predominantly comprised of *terra firme* forests and to a minor extent, flooded forest, while the landscape at AR and MPR consist primarily of *terra firme* forests, although *várzea* forests are important elements of the landscape.

Sites in western Amazon encompass highly productive white-water floodplain ecosystems (Fig. 1A, C, D, E), while those in Central Amazon (Fig. 1B) encompasses much lower productivity black-water rivers (Junk et al., 2015), potentially resulting in lower faunal abundance (Emmons, 1984).

### *Camera trap sampling and studied taxa*

Local occurrences of forested vertebrate species were obtained by camera traps (hereafter CT; remotely activated digital cameras triggered by motion or temperature change). A total of 720 CTs were deployed in the communal catchment areas in the vicinity of 100 human communities mainly in contiguous primary *terra firme* forest. The total sampling effort reached 30,445.15 traps.days and the total effort by CT ranged from 0.5 to 62.08 days ( $42.28 \pm 12.44$  days; mean  $\pm$  SD; see Table 1).

**Table 1** - List of the 18 focal species ordered by mean body mass (Kg) and taxonomic order, followed by their scientific, English names, codes used in the following analyses.

<b>Scientific name</b>	<b>English name</b>	<b>Code</b>	<b>Kg<sup>1</sup></b>
<u>Mammals</u>			
<i>Tapirus terrestris</i>	Brazilian tapir	Tapi.te	160.0
<i>Panthera onca</i>	Jaguar	Pant.on	80.0
<i>Puma concolor</i>	Puma	Puma.co	45.0
<i>Tayassu pecari</i>	White lipped peccary	Taya.pe	32.0
<i>Myrmecophaga tridactyla</i>	Giant anteater	Myrm.tr	30.5
<i>Priodontes maximus</i>	Giant armadillo	Prio.ma	30.0
<i>Mazama americana</i>	Red brocket deer	Maza.am	30.0
<i>Pecari tajacu</i>	Collared peccary	Peca.ta	25.0
<i>Mazama nemorivaga</i>	Grey brocket deer	Maza.ne	18.0
<i>Cuniculus paca</i>	Lowland paca	Cuni.pa	9.5
Nonspecific cingulata small	Small armadillo	Nons.ci	6.0
<i>Nasua nasua</i>	South American coati	Nasu.na	5.1
<i>Dasyprocta</i> spp.	Agouti	Dasy.sp	4.5
<i>Hadroskiurus spadiceus</i>	Southern Amazon red squirrel	Hadr.sp	1.2
<u>Birds</u>			

<i>Mitu</i> or <i>Crax</i> spp.	Curassow	Mitu.Cr	3.0
<i>Penelope jacquacu</i>	Spix's guan	Pene.ja	1.3
<i>Psophia</i> spp.	Trumpeter	Psop.sp	1.2
<i>Tinamus</i> spp.	Large tinamou	Tina.sp	1.2

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1 - Abrahams et al., (2017)

In the first stage, a total of 288 CTs were deployed (Bushnell Trophy-Cam and Reconyx HC500 Hyperfire), during the dry season, in the continuous unflooded forests located in the catchment areas of local communities. Most of these CTs were deployed at 350m, 1000m, 3000m and 6000m from the human communities towards interior of forests (see Abrahams et al., [2017] for details). In the second stage, the majority of the 432 CTs (Bushnell Trophy-Cam) were deployed following the Abrahams et al., (2017) protocol during the dry season. Due to local difficulties and access restrictions to unflooded forests near some human communities, 26 CT were installed in seasonally flooded forests in MPR. All the 720 CT were unbaited and installed approximately 30 cm above the forest floor and at least 20 m away from human trails. The distances from each CT to the nearest human community centroid ranging from 75m to 15 km ( $3.5 \pm 2.4$  km, mean  $\pm$  SD).

In this paper we restricted our focal species to 18 terrestrial and semi-terrestrial vertebrate species (or species groups), which could be detected by CT (Table 1). A total of 17 species were described as locally consumed or slaughtered (Ricardo Sampaio et al., n.d.) and were classified as game species, and only the giant anteater (*Myrmecophaga tridactyla*) was not classified as local game species. We grouped congeners species from different study regions (trumpeters [*Psophia* spp.]); agoutis [*Dasyprocta* spp.]), sympatric congeners (large tinamous [*Tinamus* spp.]); small armadillos [*Dasyopus* spp.]) and treated them as a single ecospecies. We also treated as a single ecospecies the two-curassow genus (*Mitu* sp. and *Crax* sp.) inhabiting our study regions. The southern Amazon red squirrel (*Hadroskiurus spadiceus*) and Spix's guan (*Penelope jacquacu*) didn't occur in the Uatumã region, and the grey brocket deer (*Mazama nemorivaga*) didn't occur in the CIR (see Ricardo Sampaio et al., n.d.), the camera traps of this region were excluded of the modelling of each species.

### *Explanatory variables*

Excepting the effort of operating days by CTs, all the explanatory variables were calculated by Geographic Information System (GIS) using the free software *QGIS* 3.14 (QGIS, 2021), described in Table 2. In order to represent the local level of protection status in the site of each camera trap, we accessed the Euclidean distance (km) among the geographic coordinate of each CT to the perimeter limit of the nearest border of SUR. The SURs in the Liberdade and Juruá rivers are adjacent and, consequently, their limits were merged in a single SUR polygon in each region. We assumed positive values for distances inside and negative for distances outside the Protected Areas.

**Table 2** – Description of the explanatory variables used in the Royle-Nichols occupancy models. Each variable is categorized according to our main hypotheses. Description, type and range of each are presented.

<b>Category</b>	<b>Covariate</b>	<b>Description</b>	<b>Code</b>	<b>Type</b>	<b>Range (mean ± SD)</b>
Camera	Effort (r)	Total of operating days	Eff	Camera site	20 - 39 (35.6 ± 4.6)
Camera	Community ( $\lambda$ )	Cameras by community; total of communities	Com	Camera site	1 - 20 (6.9 ± 3.9); 100
Habitat	Stream lenght (r, $\lambda$ )	Stream total length (m)	Stream	GIS 500 m	0 - 2365.9 (430.6 ± 551.9)
Habitat	Floodplain extension (r, $\lambda$ )	Extension around camera (m <sup>2</sup> )	Flood	GIS 500 m	0 - 0.72 (0.04 ± 0.11)
Habitat	Habitat loss extension (r, $\lambda$ )	Extension around camera (m <sup>2</sup> )	Habitat	GIS 500 m	0 - 0.86 (0.07 ± 0.15)
Anthropogenic	Protected area distance (r, $\lambda$ )	Euclidean distance to PA limit (km)	PA	Camera site	-44.48 - 31.46 (79.8 ± 12.8)
Anthropogenic	Local hunting pressure (r, $\lambda$ )	Total of household / $\sqrt{\text{km}}$	Com.HP	Camera site	0.14 - 120.9 (4.1 ± 6.8)
Anthropogenic	City hunting pressure (r, $\lambda$ )	Urban population / $\sqrt{\text{km}}$	City.HP	Camera site	273 - 10804 (2291 ± 1674)

r - covariable affecting only the individual detection probability.

$\lambda$  - covariable affecting only the relative abundance.

In order to quantify the local hunting pressure by local communities, we established the size of the two closest communities of each CT through a supervised mapping in aerial photographs of Bing Maps from Open-layer (QGIS, 2021). We used a 1:2000 scale to count all households around 10 km of each CT. These supervised mappings were performed on 2019 aerial photographs in the regions of the middle Juruá and Uatumã rivers, we assumed that no major changes had occurred in the human communities since the period of sampling (2013-2015). For the regions of upper Juruá and upper Purus rivers basins, we used aerial photographs of 2018 and 2019. Based on this mapping, we defined the size of communities (COM size) as the summed the household number inside no-overlapping 1-km buffers around the two nearest communities centroids of each CT. We assumed exponential effects of human communities distances, then we divided their sizes by the square root of the Euclidean distance of COM.Dist, and finally we calculated the community hunting pressure (COM.HP) by the mean of these two terms, as expressed in equation #1.

$$\text{COM.HP} = \frac{(\text{COM1 size} \div \sqrt{\text{COM1.Dist}}) + (\text{COM2 size} \div \sqrt{\text{COM2.Dist}})}{2} \quad (1)$$

We quantified the hunting pressure exerted by the nearest urban centre of CTs (CITY.HP) accessing the size of urban population of each city (CITY; IBGE, 2010) divided by the squared root of the access distance travelled by local people (CITY.Dist). We digitized rivers and roads (paved and unpaved) that residents of the nearest community reportedly used to travel to the nearest city during the dry season, as described in equation #2.

$$\text{CITY. HP} = \frac{\text{CITY}}{\sqrt{\text{CITY. Dist}}} \quad (2)$$

In order to control for environmental influence in the local abundances, we calculated around 500 meters of each CT the: (1) stream length, which correspond to the total length of all perennial streams (data from Venticinque et al., 2016); (2) proportion of seasonally flooded area (km<sup>2</sup>), which corresponds to the sum of total area of seasonally flooded area from the raster file presented in Hess et al., (2015), and; (3) proportion of habitat loss extension, expressed by the deforested area (km<sup>2</sup>), using the accumulated deforestation up to the year 2015 to the regions of the middle Juruá and Uatumã rivers and up to 2018 to the regions of upper Juruá and upper Purus rivers basins (“Projeto de Monitoramento do Desmatamento na Amazônia Legal”; INPE, 2019).

### *Statistical analyses*

All statistical analyses were performed in R 4.0.4. software (R.Core.Team, 2021) Previously to the modelling we checked data distribution and relationships among explanatory variables using graphics, and we log and squared-root transformed data when it was necessary, following the protocols described by Zuur et al., (2010). Besides, we evaluated possible correlation ( $P > |0.7|$ ) among the predictors, using Pearson correlation test of *R* package base. We also assessed the Variance Inflation Factor (VIF) using *VIF* function of *USDM* package (Naimi et al., 2014) and we excluded any variables with VIF values higher than 3 (Zuur et al., 2010). We scaled all explanatory variables (mean = 0 and SD = 1) to enable models to converge and aid variable effect size comparisons (Harrison et al., 2018).

Due to the great range of our sampling effort by CT (0-62 [range];  $42.3 \pm 12.4$  [mean  $\pm$  SD]), we filtered the photos recorded from 20 up to 39 days of sampling in order to reduce potentially overdispersion and to increase convergence of models, since in our previously inspection we observed very distinct detection histories to a major part of species. Our filtered data restricted our 720 CT to 697, which comprised a total sampling effort of 24,826 camera.days.

We first created detection histories based on detection-non detection records in intervals of 5, 7, 10, 12 and 15 days for all species using the function *detectionHistory* of the package *camtrapR* (Niedballa et al., 2016). Based on these histories, we fitted Royle-Nichols N-mixture occupancy models (*hereafter* RN models; Kéry and Royle, 2015; Royle and Nichols, 2003) using the function *occuRN* of the R package *unmarked* (Fiske and Chandler, 2011) by each detection history for each species. Each one of these models included two and six explanatory variables affecting the detection probability ( $r$ ) and the relative abundance ( $\lambda$ ), respectively (see Table 2). We assumed the relative abundance estimated as the individuals available for detection around the camera trap sites. We compared the lack of independence (overdispersion) among sites of these five models by species, using the goodness-of-fit test (MacKenzie and Bailey, 2004) through the function *mb.gof.test* of *AICcmodavg* package (Mazerolle, 2020). The least overdispersed models of each species were used in the following analyses (see Table S1), and we corrected for Quasi-AIC (QAIC) when the best model selected showed overdispersion ( $\hat{c} > 1$ ;  $p < 0.05$ ).

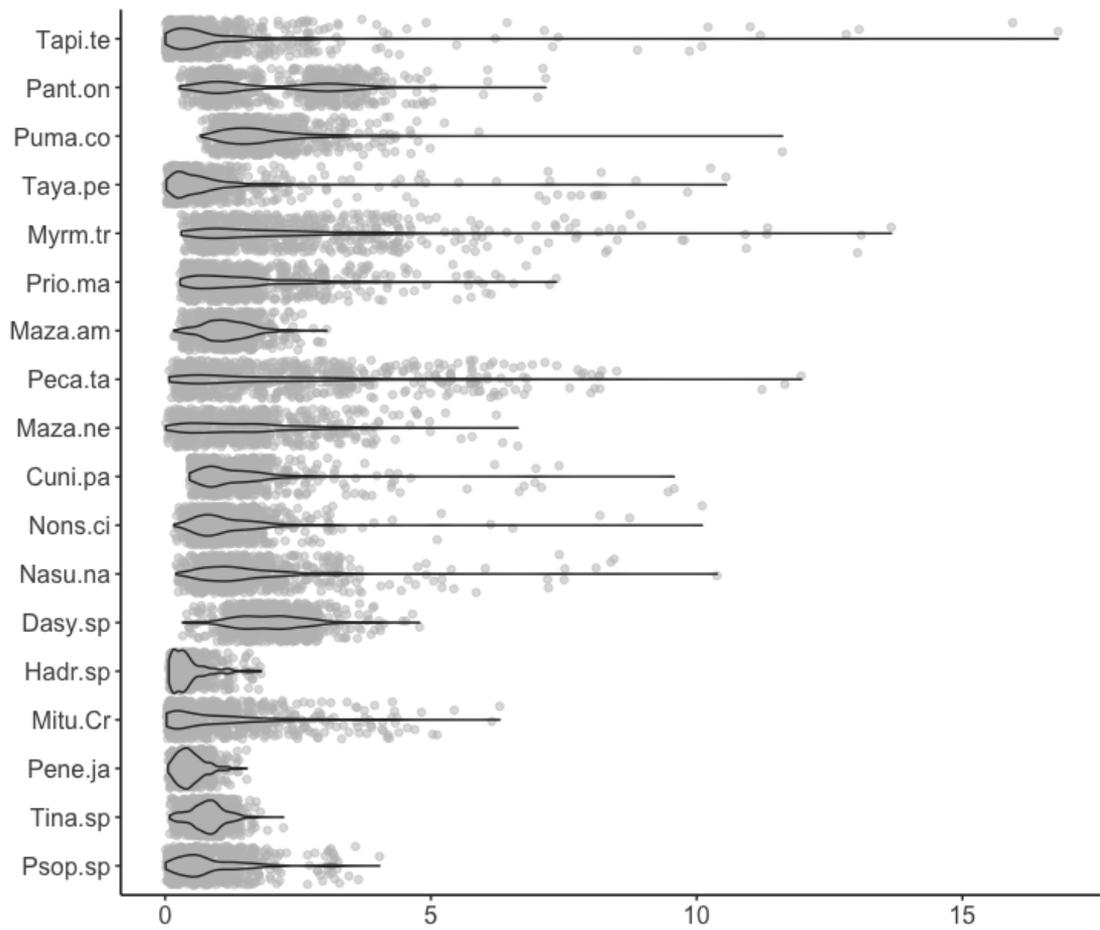
In a second stage, we used the structure of the least overdispersed model by species selected at first stage, to created 29 new models with all possible combination in up two variables affecting the detection probability and keeping constant the six predictors affecting the relative abundance, using the function *dredge* of *MuMIn*

package (Barton, 2020), in order to select the most parsimonious detection structure for each species using AIC or QAIC criterium values (see Table S2).

In the third and final stage, we refitted the best model selected by species at second stage using Bayesian approach, using the function *stan\_occuRN* of the *ubms* package (Kellner, 2021). In order to control for spatial correlation among our CT, due to the nested nature of our sampling design, where several CTs were deployed around each one of the 100 human communities studied (see Figure 1 and Table 2), we specified the name of the human community where CT was deployed as a categorical random effect variable. We used non-informative priors for all the parameters and ran four Markov Chain Monte Carlo (MCMC), with 100,000 iterations by chain. We evaluated chains convergence considering the Gelman-Rubin convergence diagnostic ( $R_{hat}$ ; Brooks and Gelman, 1998)  $\leq 1.1$ , and we assume a profitable accuracy in parameters estimation when the effective sample size was larger than 100 by parameter (Kéry and Royle, 2015) and we also made visual inspection of trace plots. We considered evidence of explanatory variable effect support when the estimated 95% posterior credible interval (CI) did not include zero (see Table S3). As we only are interesting into evaluate the effect of our six predictive variables on local abundance of species, we opted to show only their effects on this abundance parameter estimate by occupancy modelling.

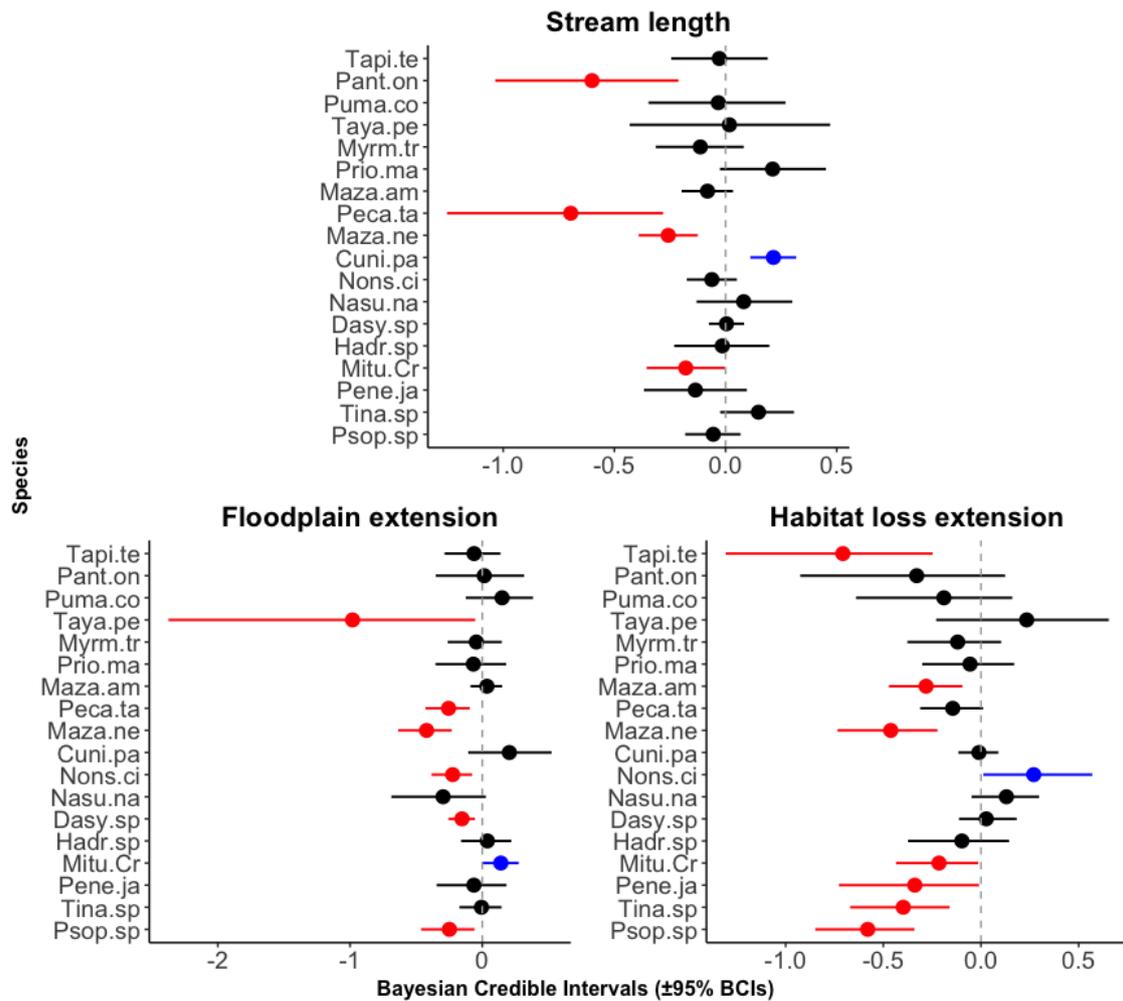
## **Results**

The mean relative abundance estimated by the Bayesian RN models ranged from 0.43 to 2.2 ( $1.33 \pm 0.55$ ; mean  $\pm$  SD) individuals available for detection around the camera trap sites for our 18 focal species and, in general, site-level abundance variation were similar across all species (Fig. 2).



**Figure 2** - Violin plot comparing estimated site-level focal species predicted relative abundance. See Table 1 for species' abbreviations.

The stream length around CT reduced the average relative abundance of most species (Fig. 3), however these effects were significantly only for jaguar (*Panthera onca*), collared peccary (*Pecari tajacu*), grey brocket deer (*Mazama nemorivaga*) and curassow (*Mitu* or *Crax* spp.). On the other hand, stream length increased the abundance of lowland paca (*Cuninulus paca*) and had a marginally significant increase on the abundance of large tinamou (*Tinamus* spp.) and the giant anteater (*Prionomys maximus*).

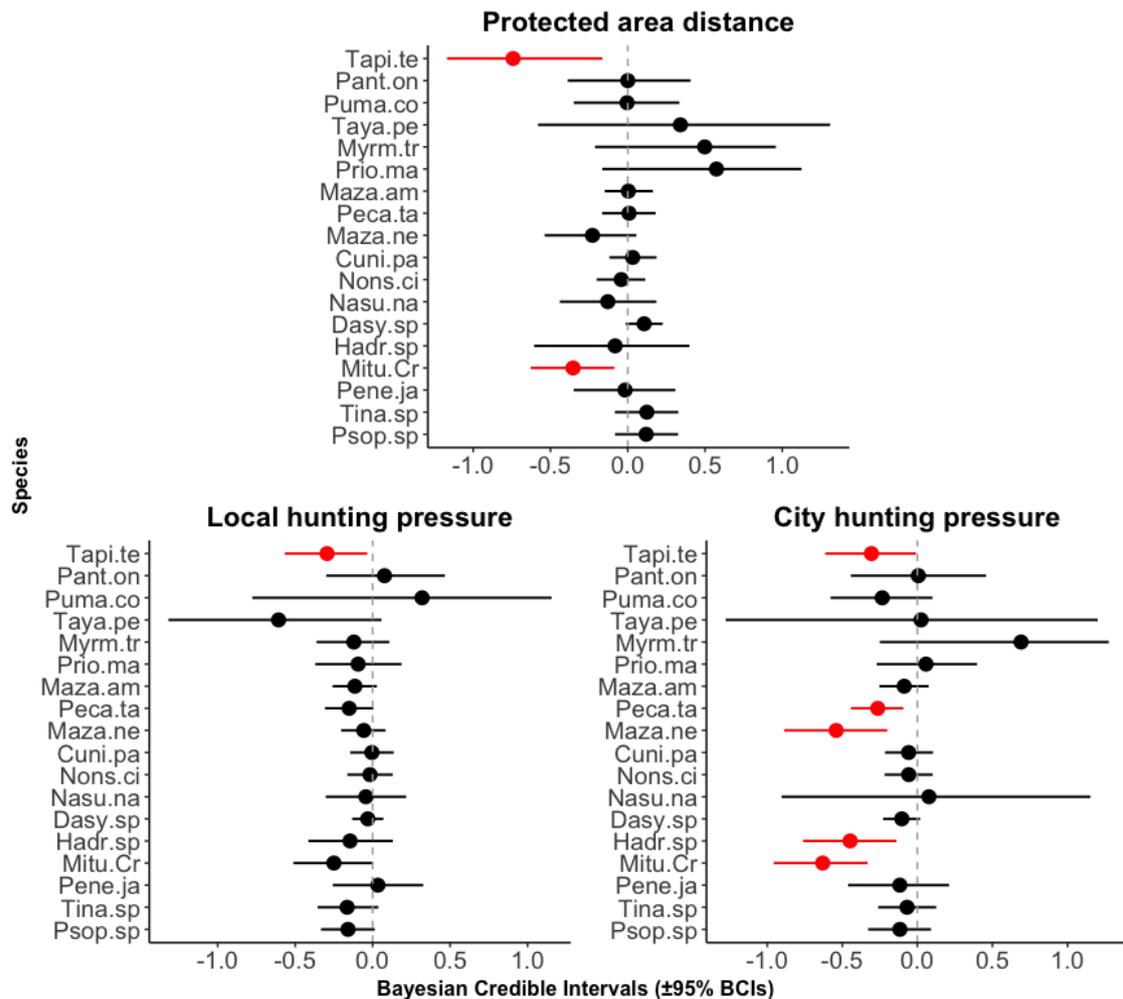


**Figure 3** – Panels synthesizing results of the Royle-Nichols occupancy models, showing the magnitude and direction effects (Bayesian means  $\pm$  95% credible intervals) for the posterior distribution of predictor effects on the relative abundance of 18 focal species for the habitat quality of predictors (Stream length, Floodplain extension and Habitat loss extension). Species were ordered by size and taxonomic order. See Figure 1 for species abbreviation.

The increasing of floodplain extension around CT reduced the mean relative abundance of the most species, however the relationship was significant only for the white lipped peccary (*Tayassu pecari*), collared peccary; grey brocket deer; small armadillos; agouti, and; trumpeter (*Psophia* spp.). Floodplain extension also marginally reduced the abundance the South American coati (*Nasua nasua*), while it increased the abundance of curassow (*Mitu* or *Crax* spp.; Fig. 3).

Habitat loss extension around CTs was the predictor affecting the higher number of species (n=7), reducing the abundance of the Brazilian tapir (*Tapirus terrestris*), the two brocket deer species and the four bird species (curassow, spix's guan [*Penelope jacquacu*], large tinamou and trumpeter) and marginally reducing the abundance of the collared peccary (Fig. 3). In contrast, habitat loss increased the abundance of small armadillos (Fig. 3).

Protected area distance showed a balanced effect among species; however, it reduced the abundances of lowland tapir and curassow, and marginally increased the abundance of agouti (Fig. 4). Both sources of hunting pressure were negative for most of species. Local hunting pressure reduced the mean relative abundance of a single species, the lowland tapir and marginally reduced the abundance of 5 other species, the red brocket deer, collared peccary, curassow, large tinamou and trumpeter. On the other hand, city hunting pressure reduced the abundance of a greater number of species (n=5), namely the Brazilian tapir, collared peccary, grey brocket deer, the Southern Amazon red squirrel (*Hadroskiurus spadiceus*) and the curassow, and marginally reduced the abundance of the agouti (Fig. 4).



**Figure 4** – Panels synthesizing results of the Royle-Nichols occupancy models, showing the magnitude and direction effects (Bayesian means  $\pm$  95% credible intervals) for the posterior distribution of predictor effects on the relative abundance of 18 focal species for the habitat quality of predictors (Protected area distance, Local hunting pressure and City hunting pressure). Species were ordered by size and taxonomic order.

## Discussion

To our knowledge, this study is one of the most intensive camera trap efforts already implemented to assess hunting pressure impacts on forest vertebrate species populations under a wide range of local and city hunting pressure intensities and distinct levels of protection. This effort was conducted in some of the most pristine and less defaunated remaining tropical forests of the world (Benítez-López et al., 2019). Using a modelling

strategy that control for species detection heterogeneity induced by variation in site-level abundance, we evaluate the relative effect of main drivers affecting site level relative abundances of 18 species within and outside Amazon Sustainable-Used Protected Areas.

Our results indicated that the relative abundances of our focal species were negatively affected by hunting pressures driven by urban areas and, to a lower extent, by local communities. The environmental quality variables also depleted populations, with habitat loss around CT impacting the highest number of game species. On the other hand, the expected protection induced by the protected area limits were not corroborated by our results since species responded differently to protect area distance and two game-sensitive species were less abundant inside than outside protected areas.

#### *The impacts of hunting on local game abundance*

Human population density is recognized as the main driver of game depletion in tropical forests (Abernethy et al., 2013; Benítez-López et al., 2017; Fa et al., 2002; Peres and Palacios, 2007; Ripple et al., 2016). Although our hunting pressure metrics related negatively with local abundances of most studied species, significant effects were mostly restricted to larger and sensitive species: lowland tapir, brocket deer and collared peccary among mammals and curassow among birds. The city hunting pressure significantly depleted a higher number of game species than local hunting pressure, as previously reported in the Amazon (Abrahams et al., 2017; Ricardo Sampaio et al., n.d.).

The local hunting pressure is governed mainly by the local consumption and local sharing within or between human communities (Nielsen et al., 2018; Nunes et al., 2019a) and our data showed signals that this pressure is specially affecting the largest

game species (lowland tapir, red brocket deer and curassow [larger bird species], the latter two with a marginally significant effect) as well as gregarious species (collared peccary and trumpeters, both with a marginal effect), for which the potential return in terms of protein biomass to local hunters can be higher.

Nonetheless, hunting pressure effects on local population occurring at the vicinities of rural communities can be mediated by urban demand and trade, since this demand is high and widespread in Brazilian Amazon (Chaves et al., 2017; El Bizri et al., 2019; Parry et al., 2014). It has been reported that the price of bushmeat kilogram traded by rural hunters is highest in urban areas (El Bizri et al., 2020). We can expect, therefore, that the greater the accessibility to urban areas the greater is the trade and consequently the defaunation intensity, as previously reported by Morton et al., (2021), affecting local game population even inside protected areas (Rija et al., 2020). This pattern is confirmed by our results, since urban trade (i.e., city hunting pressure) depleted the local abundances of a larger number of species, even those species that are more tolerant such as the grey brocket deer and/or are smaller, such as the Southern Amazon red squirrel and the agouti, the latter showing a marginally significant response.

Despite tropical protected areas has contributed to increase local population of game species (Benítez-López et al., 2017) and local hunters living inside the SURs studied by us reported a perceived a recent improvement of overall game abundance (R. Sampaio et al., n.d.), our data showed no positive effect of protection status in reducing the impacts of local and urban demands on populations of game species when it was compared with the populations outside SURs. Rather, only two species varied abundance in response to distance to protected area borders and these, the curassow and the lowland tapir, had lower rather than higher abundance inside the SURs limits.

Lowland tapir and curassow are game sensitive species since they are frequently depleted or locally extinct in overhunted Amazonian sites (Bodmer et al., 1994; Peres and Palacios, 2007; Sampaio et al., 2010). Although we observed wildlife management arrangements in some local communities living inside the SURs studied by us (R. Sampaio et al., n.d.), these are ad hoc in nature as there is no clear policy of community-based wildlife management in Brazilian SURs (Antunes et al., 2019). We believe this lack of regulatory policy is the main reason behind the absence of a PA effect in mitigating local game depletion.

Bushmeat trade is known to increase the impacts of hunting on local game abundances in tropical forests (Morton et al., 2021) and perhaps hunters living inside our SURs can be more dependent on bushmeat trade for their livelihood than hunters from outside. In general restriction on human land use is higher inside SURs than outside. So, local communities living in the surrounding areas of Amazonian SURs might increase their income through a greater range of possible economic activities than communities living inside SURs (Camilotti et al., 2020; Haddad et al., 2019), however, this is not a general rule (Campos-Silva et al., 2021). This translate to a reduced range of options for inhabitants living within the limits of the SURs and probably a lower income compared to households outside these protected areas, leading the SUR inhabitants to an increased reliance on bushmeat, as has been observed in tropical forests (Nielsen et al., 2018; Rija et al., 2020).

A second explanation for the absence of strong effect of PA limits, might relate to some unmeasured environmental factors with effect on population abundance, such as the local soil fertility (Ferreira Neto et al., 2021) and/or below canopy forest degradation (Aparecido et al., 2020). Search for additional and more accurate proxies of soil forest productivity or forest degradation and supplementary refinements such as

incorporating analyses of scale of effect (Jackson and Fahrig, 2015) might be some alternatives. Nevertheless, appealing as they might be, both explanations need further investigation.

#### *Habitat quality affecting the vertebrate species abundance*

We can expect a positive relationship among our stream length metric and the local relative abundance of large frugivore-herbivores vertebrate species (Paredes et al., 2017). However, the negative effects of stream length on the abundances of four game species can be related to hunting pressure near small streams which facilitates the hunter's accessibility, particularly near human settlements (Abrahams et al., 2017; Michalski et al., 2015; Peres and Lake, 2003; Ricardo Sampaio et al., n.d.), since hunt trails and temporary camps were usually established near to perennial streams in our study (R.S. pers. obs). Collared peccaries, grey brocket deer and curassow were frequently consumed by local people and were also affected by city hunting pressure in our study, and the same can be said for jaguars, which are frequently slaughtered by local people (R. Sampaio et al., n.d.). For these, the increased accessibility to hunters promoted by the web of streams translates to higher hunting pressure upon them. On the other hand, the lowland paca, which normally are more abundant near small perennial streams (Boron et al., 2019; Ferreguetti et al., 2017; Figueroa-De-León et al., 2016; Paredes et al., 2017) increased abundance in sites with high stream length. Although this species is the most locally consume in our study (R. Sampaio et al., n.d.), it has a higher reproductive rate compared to the other species, and has been observed persist even in overhunted sites (Peres and Palacios, 2007; Sampaio et al., 2010).

According to our predictions, the seasonally flooded areas around the camera traps function as an environmental filter structuring the local abundances of Amazonian

forested vertebrate species (Haugaasen and Peres, 2005). The most “terra-firme” specialized species such as white lipped peccaries, collared peccaries, grey brocket deer, agoutis, small cingulates, agoutis and trumpeters had reduced abundance in the more floodable sites, while the semi-arboreal curassow increased its abundance with floodplain extension. The negative association between these species and flooded forests has already been observed in other Amazonian sites (Alvarenga et al., 2018; Boron et al., 2019; Costa et al., 2018; Haugaasen and Peres, 2005).

Nevertheless, the most important environmental quality variable affecting the site-level game abundance in our study was the habitat loss around camera traps. The game species most affected by habitat loss were frugivorous and we believe that local scale deforestation possibly represents loss of important fruit source resources for them. Habitat loss negatively impacted local diversity of game frugivore species in our study (Ricardo Sampaio et al., n.d.), and the amount of remaining forest habitat is known to be determinant for the persistence of frugivorous mammal species in neotropical fragmented forests (Magioli et al., 2021). Although tapirs and red brocket deer can benefit from secondary forests in Amazon (Abrahams et al., 2017; Parry et al., 2007), in our study the coverage of deforested areas included secondary forests as well other land cover classes, such as agricultural fields and cattle pastures, these habitat alterations favoured only species with lower forest habitat specificity in Amazon (Zimbres et al., 2017). In fact, only small armadillos increased abundance in the more deforested sites, which is rather expected since these insectivorous-omnivorous species have already been noticed as persisting in disturbed sites in the Amazon (Sampaio et al., 2010; Zimbres et al., 2017).

### *Conclusion and conservation considerations*

Our study pointed out that the urban centres and habitat loss were the main drivers of local abundances reduction of game species inhabiting the catchment areas around human communities in nine Amazon Human-Occupied Protected Area and their surroundings, while the local demand of bushmeat showed lower but significant depletion effects. Unexpectedly though, the local level of protection didn't reduce the hunting pressure effect on local game abundances. In fact, the local abundances of two game-sensitive species were less abundant inside SURs than outside.

Our study corroborates that evidence-based conservation strategies need to be implemented in SURs in order to achieve sustainable hunting. Tropical forest stakeholders should prioritize conservation planning focused on reducing or restraining the bushmeat urban trade and demand. In addition to the increase the surveillance of this activity, strategies should also promote alternative sources of animal protein (aquatic and domestic) for urban consumption. At local level, strategies that encourage the establishment of community-based management of subsistence hunting should be prioritized, mainly in human communities closer to urban areas, with high levels of habitat loss around them and those inside tropical SURs. These local-level strategies should focus on: (1) to ban bushmeat trade with urban areas or even to promote the regulation of wild meat surplus sales (van Vliet et al., 2019); (2) to protect or to reduce the local consumption of sensitive species, such as lowland tapir and curassow, and; (3) to encourage the increasing of local availability of fruit resources in those human communities with larger proportion of deforestation in their vicinities, systems such as agroforestry can benefit the local abundance of game species. All these strategies certainly will contribute to improve the sustainability of hunting on vertebrates

inhabiting tropical sustainable-use reserves, increasing their conservation effectiveness beyond its “paper park” stigma.

## **General discussion**

All the results presented in this thesis clearly showed the negative impacts of hunting on exploited species in one of the most pristine and less defaunated remaining tropical forests of the world (Benítez-López et al., 2019). The main drivers of species depletion were related to the regional demand that urban areas exerted on forested game species, which were invariably extracted from the surrounding forests around human communities inside the Amazonian's SURs and their vicinities.

The TEK data (Chapter I) pointed out that the fast-breeding species (high-lambda) and those more persistent to hunt, such as agouti, lowland paca, collared peccary, and red brocket deer, were the most locally consumed species overall. However, reduced levels of game depletion were reached only in human communities having more access to extensive floodplains and those farther from the cities. The effects of legal protection status per se (distance to the border of PA) were seen only in the perceived on local change of overall game abundance. Likewise, community demographic configuration (age and size), only impacted the depletion of few species.

The local occurrences of our focal species (Chapter II) also showed signals of reduced depletion in sites with lower hunting pressure, while increasing the city hunting pressure, habitat loss and flooded area extension reduced the local diversity and assembly integrity of game species. The species replacement (turnover dissimilarity) was the principal component of pairwise dissimilarities among sites. The total and turnover dissimilarities of the non-game species assemblies were affected only by environmental variables, while all environmental covariates and city hunting pressure increased the total dissimilarity of game species, and all of them, excepting city hunting pressure, also increased the replacement of game species among sites.

The relative abundance of the 18 largest forested vertebrate species (Chapter III) also indicated that reduced depletion only was observed farther from urban areas and in communities with low habitat loss extension in their vicinities. The effects afforded by the distance from protected area borders didn't mitigate the hunting pressure effects, besides, two sensitive game species showed reduced relative abundances inside protected areas. In general, our environmental quality variables reduce the local population of species, however the habitat loss around CT impacted a large number of game species.

### **The effects of habitat quality affecting game species depletion**

The floodplain extension showed distinct effects depending on the scale of analyses presented in the three chapters. The increasing amount of floodplain extension around human communities reduced the game depletion, mediated by the higher availability of aquatic protein to local communities. On the other hand, the increased of floodplain at camera-trap site-level reduced the local diversity and the relative abundances of the strictly terrestrial and "terra-firme" specialized game species.

It has been recognized that fishing has greater cost-effective protein in relation to hunting for local dwellers in rural Amazon (Endo et al., 2016). Thus, for these communities that have access on both flooded and in-flooded forests, protein acquisition from terrestrial game species is essential only in during wet season, when the fish stocks are dispersed through the floodplain extension (Vieira et al., 2015). Thus, human communities with larger floodplain extension possibly were less dependent on game protein throughout the year, reducing the perceived game depletion of local hunters. Furthermore, in the regions of middle Juruá and Purus rivers, local community-based management of aquatic protein showed co-benefits effects increasing local

populations of non-target aquatic or semi aquatic vertebrate species (Campos-Silva and Peres, 2016; Campos-Silva et al., 2018), which could possibly result in more local availability of aquatic resources for local communities and consequently increasing the hunters perception about the recovery of game abundance in the catchment areas around their local communities.

On the other hand, the amount of seasonal floodplain extension around camera trap acted as an environmental filter to species not adapted to this kind of habitat (Alvarenga et al., 2018; Costa et al., 2018; Haugaasen and Peres, 2005). Floodplain extension reduced the site-level local diversity and assembly integrity of game species; besides it increased the turnover of species among sites. The extension of floodplain around camera trap also reduced the game species abundances of “terra-firme” habitat specialists such as white lipped and collared peccaries, grey brocket deer, agoutis, small cingulate and trumpeters; only one species increased abundance (curassow).

The metrics of perennial stream length around camera traps, contrary to the expectations (see Paredes et al., 2017), reduced the site-level diversity and local abundances of game species. This process can be related to the local hunters’ increased accessibility near perennial stream in Amazon (Abrahams et al., 2017; Michalski et al., 2015; Peres and Lake, 2003). Despite this effect, the local abundance of lowland paca a high tolerant to hunt species (Peres and Palacios, 2007; Sampaio et al., 2010), was still higher in sites with more perennial streams, corroborating other studies (Boron et al., 2019; Figueroa-De-León et al., 2016; Michalski et al., 2015).

The negative effect of amount of habitat loss around cameras traps on game local has been evidenced in tropical forests (Abrahams et al., 2017; Whitworth et al., 2019). Habitat loss promotes the reduction of important local availability of fruit resources and is determinant to the persistence of frugivorous species in fragmented

landscapes (Magioli et al., 2021). Increasing the extension of habitat loss around camera traps was detrimental for species diversity and assembly integrity, but only for game species. While the majority of our focal game species are frugivorous, less than the half of the non-game species are frugivorous. The abundance of frugivorous species such as Brazilian tapir (*Tapirus terrestris*), the two brocket deer species and all the focal bird species (curassow, spix's guan [*Penelope jacquacu*], large tinamou and trumpeter) reduced with habitat loss. Only the small armadillo increased abundance in the more deforested sites. Insectivorous-omnivorous species such as this armadillo have already been described as persistent in disturbed sites in Amazon (Sampaio et al., 2010; Zimbres et al., 2017). In the studied communities, local deforestation around them resulted in secondary forests, agricultural fields and cattle pastures, depending on the regional context of them (Ricardo Sampaio nonpublished data). This variation contributed to regionally distinct patterns of species incidence in and around this modified habitats, increasing the replacement of species of more deforested sites, a pattern already identified for Neotropical small mammals (Püttker et al., 2015).

### **Anthropogenic features modulating the game species depletion**

The results pointed here clearly showed that urban centers in Brazilian Amazon forests acted as the main sources of game species depletion in and around sustainable-use reserves, and evidence of depletion were detected in the catchment areas around human communities both from the hunter's perception level and at the camera trap level.

The consumption of bushmeat in Brazil is legally allowed only for subsistence purposes (Bragagnolo et al., 2019), but despite that, urban bushmeat consumption is high throughout the Amazon (Chaves et al., 2019; El Bizri et al., 2019; Parry et al., 2014), since most of local rural hunters in central Amazon reported wildmeat trade with

urban areas (El Bizri et al., 2020). This current urban oriented demand is clearing reducing the potential value of SURs for biodiversity conservation and is reducing the availability of bushmeat to local people. Only the local dwellers located farther from cities showed prey profiles that included sensitive, slow-reproducing game species, and the areas surrounding these communities showed reduced level of local depletion of several species. Therefore, with the current exploitation levels, hunting sustainability could only occur in the most isolated human communities distant from the cities.

The city hunting pressure also reduced the number of species recorded by camera traps around human communities, but rather unexpectedly, this species losses was not deterministic. We argue that this is likely related to the fact that our sampling sites are immersed in relatively vast tracts of continuous primary forests. In comparison with more disturbed regions of the Amazon, our study areas exhibit reduced accessibility and potentially lower hunting pressure. We also argue that dispersal rates of game species individuals from pristine to hunted sites are still possibly high. Under this framework, dynamics population and community processes such as the “source-sink”, “mass effect” and “rescue effect” (see Leibold *et al.* 2004) are likely contributing to the random game species loss induced by city hunting pressure. We caution that this “best-case” scenario could only make sense in the catchment areas of our study, surrounded by large tracts of mostly pristine forests. Such is not the case in more disturbed regions of the Amazon having regionally higher deforestation rates (Constantino, 2016; Sampaio et al., 2010).

It is recognized that local hunting pressures in tropical forests results from local consumption and sharing of wildmeat (Nielsen et al., 2018; Nunes et al., 2019a), and also by the configuration of the local settlements (Jerozolimski and Peres, 2003). Indeed, in our study settlement size and distance only depleted few species (jaguar,

collared peccary and spider monkey) considering the hunter perception, and the lowland tapir considering the site-level abundances estimated by camera traps. Comparing the effect sizes of game depletion of local and city hunting pressures, local communities had a relatively lower contribution in our study, contradicting the generalized concern of game species depletion by local human population in tropical forests (Robinson and Bennett, 2000), specially inside SURs (see Terborgh and Peres, 2017). Nevertheless, the unregulated and unsustainable exploitation of sensitive game species should concern both local communities and stakeholders of wildlife management in tropical forests.

The local level of protection showed positive effects in mitigating the hunting pressure effects but only considering the local hunters' perception about changes in the local aggregate abundances game species over the past ten years. This positive perception can result from local recovery and/or increase of game stock inside SURs, due to the reduced pressure from outsiders over game species population. This pattern is likely mediated by increased restrictions in land use together with surveillance activities inside PA (Gray et al., 2016), and also by greater inaccessibility of Amazonian PAs (Peres and Lake, 2003, Kauano et al., 2017) might influenced this pattern.

However, the analysis of the current local abundances at site-level of individual species (camera trap data) showed that two sensitive game species (lowland tapir and curassow) exhibited lower abundances inside SURs. Despite of the absence of a clear policy of wildlife management in Brazilian SURs (Antunes et al., 2019) that certainly contributes to this local depletion pattern, we advance two other hypothesis to explain this heterogeneity on site-level abundances: (1) the existence of unmeasured environmental covariate(s) affecting local abundances of these species, such as the local soil fertility (Ferreira Neto et al., 2021) and/or below canopy forest degradation (Aparecido et al., 2020), and; (2) the increased hunting pressure upon these sensitive

species (the larger mammal and bird species) inside SURs, resulting from a relatively lower income of people living inside SURs compared to outside (Camilotti et al., 2020; Haddad et al., 2019) and a consequent higher reliance on wildmeat for livelihoods of inside communities (Nielsen et al., 2018; Rija et al., 2020). The latter would translate into increased local wildmeat consumption and/or trade with urban areas by the communities in the interior of the SURs leading to higher levels of sensitive species depletion.

### **Final considerations and conservation recommendations**

The results presented in this thesis provide relevant information to the design of conservation strategies in tropical forests in general and sustainable-use reserves in particular. Sustainable-use protected areas comprehends a great portion of the aggregated protected territory in tropical forests (Schmitt et al., 2009), they are considered essential for biodiversity conservation (Peres, 2011) and they ensure the necessary territory for the livelihoods of countless tropical forests dwellers. However, this kind of protected area will only be effective for biodiversity conservation and local people livelihood if they were properly managed and supported by evidence-base strategies. Under this perspective and considering my main results, I proposed three main conservation strategies that should be prioritized by all stakeholders involved in local and regional tropical conservation.

First and foremost, to reduce the urban wildmeat pressure on local game populations, that can prioritizing the following conservation actions: i) implementation of a more efficient surveillance strategy of urban bushmeat trade in tropical cities, including the ban of bushmeat urban trade in countries where it is not permitted, or banning the trade of bushmeat of game sensitive species in countries where it is not

allowed; ii) to stimulate policies that provide alternative and cheap source of protein (aquatic and domestic) for urban consumption, that can potentially reduce the urban demand on wildmeat; iii) more aggressive education campaigns alarming about the negative effects of urban bushmeat consumption on game biodiversity, in order to reduce the urban wildmeat demand.

Secondly, to encourage the aquatic protein community-based management plans on local communities with access on large extension of floodplain areas around them. The management of aquatic or semi-aquatic focal species has been shown to be efficient in increasing of local availability of aquatic protein for local communities, including non-target species (see Campos-Silva and Peres, 2016; Campos-Silva et al., 2018). Strategies such as (i) the establishment of quotas to target species, well-defined no take zones and fishing rules and agreements in oxbow lakes, floodplains or portions of rivers, and; (ii) the protection of aquatic turtle nesting sites should also be prioritized. These strategies might be well accepted by local communities in floodplain areas of tropical forests, increasing the local availability of aquatic protein and consequently reducing the pressure on game terrestrial species.

Third, to prioritize subsistence hunting community-based management plans in larger human communities (i) inside protected areas; (ii) closer to urban areas; (iii) with lower availability of aquatic protein, and; (iv) with higher levels of habitat loss in the catchment areas around them. At these communities, the local-level strategies should prioritize the: (a) protection and/or reduction of local level of consumption of sensitive species such as lowland tapir and curassow; (b) the banishment of urban bushmeat trade or, alternatively, to promote an effective regulation of wild meat surplus sales with urban areas (van Vliet et al., 2019), and; (c) the increasing of local availability of fruit

resources for game species, such as agroforestry system in the communal harvesting deforested areas around communities.

Community-based management plans has empowered of local communities creating opportunities for self-development and biodiversity protection the first instance within SURs overflowing their boundaries in Amazon (Campos-Silva et al., 2021). These local communities can be encouraged to adopt community-based management if they can benefit from payments on global avoided carbon dioxide emission agreements if the local consumption of wildmeat reaches sustainable levels (Nunes et al., 2021) and if the conversion of deforested areas around communities into agroforestry systems area successful. Besides that, co-management strategies probably will be well accepted by local communities facing high levels of game species depletion, that consequently have increased their local concern about the need to increase local wildlife protein availability to their future generations. Scientific evidence supporting the sustainability of local arrangement of wildlife managements are extremely necessary in tropical forests and tend to be well accepted by local communities (see Annex I for an example).

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## **Annex I – When science touches the ground**

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In this note I present an unexpected and yet valuable scientific contribution for a local community-oriented “hunting agreement” inside a Sustainable Use Protected Area in the heart of Brazilian Amazon. I believe this contribution could really change local practices concerning subsistence hunting. The community in particular is named “Periquito” and is located inside the Riozinho da Liberdade Extractive Reserve, near the city of Cruzeiro do Sul in the Brazilian state of Acre. According to the locals, the village was founded around 45 years ago and is composed by *ribeirinhos* i.e. former rubber-tapper semi-subsistence communities of mixed-descent.

Influenced by a reduction of game supply in the forests near their community, the *ribeirinhos* created in 2016 an agreement to regulate local practices of subsistence hunting. The most important regulation was the use of domestic dogs to assist hunting to be allowed on the right bank of Liberdade river only and not on the left bank aiming to “preserve” the left bank. Because of enhanced hunting success, the use of domestic

dogs for hunting is a common practice in the Reserve. However, there was a debate in Periquito community about the impacts of dog-assisted hunting and whether the new agreement was efficient to preserve the game supply. Some believed that using dogs was not only very predatory but also repelled animals from nearby forests while others were skeptical and very resistant comply with the agreement.

In 2018, I visited the community to sample data for my PhD thesis that evaluated the subsistence hunting inside and surrounding Extractive Reserves. In agreement with the Periquito community, I installed 20 camera traps (motion-triggered automatic cameras) near the community in both banks of the Liberdade river, which operated around 45 days.

After 45 days I came back to retrieve the cameras and the community could not wait to see the photos. On my last night in the Reserve, we gathered the whole community in the local school and presented them all the 5621 photos. In a presentation of two hours (that I remember), I only inserted the memory cards in the computer and told them where that camera trap was installed. The diversity and abundance of game species observed in those photos brought so much excitement for that community and soon I realized that the excitement was mainly for two reasons: (1) the hunters were amazed to see that especially because game species are the principal protein source to their community; (2) except for the hunters, children and women may had ever seen those species alive in their habitat.

After the initial excitement, the most surprising thing for me was at the end of the presentation when they spontaneously started a very rich discussion about the biology of the game species and the effectiveness of their hunting agreement. The community unanimously concluded (including the skeptical most resisting hunters) that a higher number of game species was recorded when hunting without dogs (left bank of

Liberdade river). During the whole time I was a mere spectator, and I was “allowed” to express my opinion only at the end of their discussion, which of course, I agreed with all. A relevant information must be included here: the average formal education is very low, as it is common in the rural Amazon. Children and young people attend the school where we were holding the meeting, but the vast majority of adults, who are hunters and local leaders, are illiterate and some of them attend, when they can, to a form of adult education. This presentation, showing my raw data without parameters estimation, graphs, tables was presumably better for people without formal education or scientific background to create their own conclusions about the patterns of game species near their houses. Seeing their world in a raw format, was easier for them to conclude how it operates.

In 2019 I have received a letter containing the official minute of a meeting in the Periquito community. In this letter it was recorded their perceptions about the currently stock of game species, and the discussion of their perception about “my” photo presentation. All of them agreed to stop the breeding of hunting dogs and after one year they will finally stop the hunting with the assistance using domestic dogs.

Had this presentation not taken place in 2018 and if I was invited to go to the Periquito community to assist in their hunting agreement, I would probably present tables, graphs and perhaps some parameters of diversity. I believe that the end result of this field assessment would not have been as effective and as concrete as the results we see. This experience led me to think that if we want science to really contribute to our community, it is necessary that we increasingly make scientific knowledge touch the ground, even if it is raw.

## Annex II – Supplemental material Chapter II

### Tables

**Table S1** – Pearson correlation among the independent variables used in the Generalized mixed models.

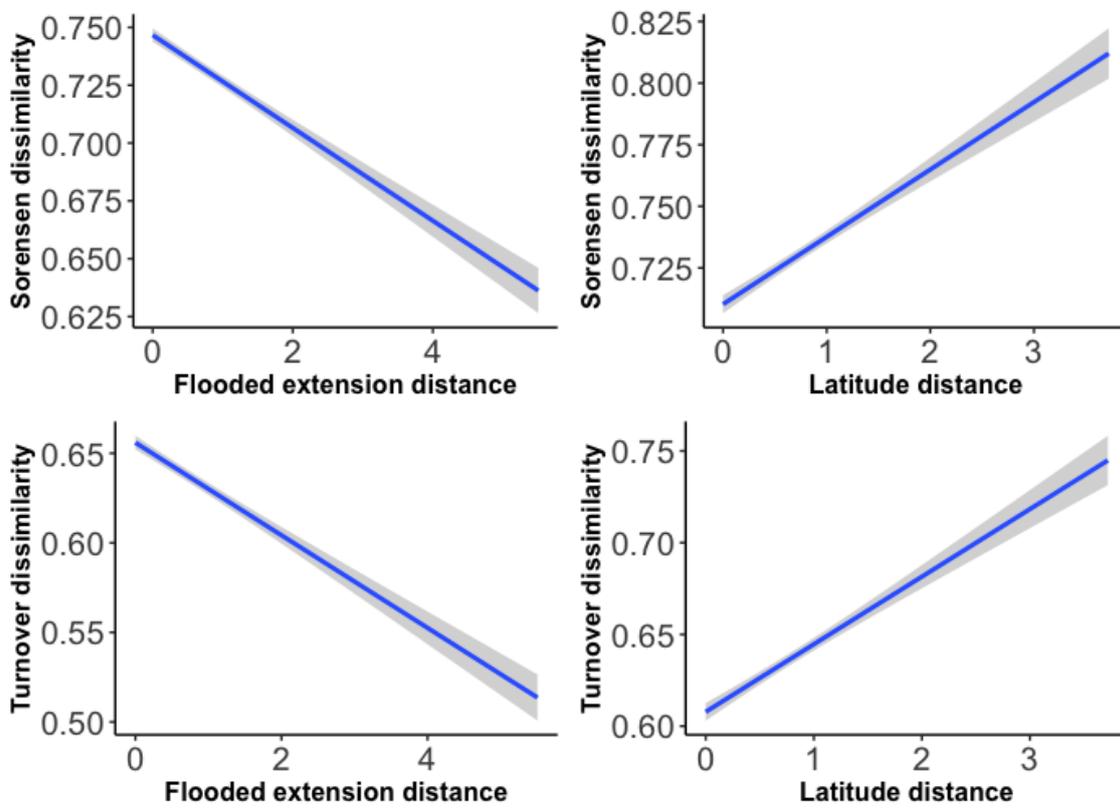
The last column shows the Variance Inflator Factor (VIF) of each predictor. FLOOD – Seasonally flooded area extension; STREAM – Stream density; HABITAT – Habitat loss extension; PROTE – Distance to PA limit; CITY.HP – City hunting pressure; COM.HP – Community hunting pressure.

	FLOOD	STREAM	HABITAT	PROTE	COM.HP	CITY.HP	VIF
FLOOD		-0.01	0.05	0.09	-0.01	-0.08	1.02
STREAM			0.11	-0.02	-0.02	0.15	1.04
HABITAT				-0.07	0.29	0.17	1.13
PROTE					0.04	-0.23	1.08
COM.HP						0.17	1.13
CITY.HP							1.13

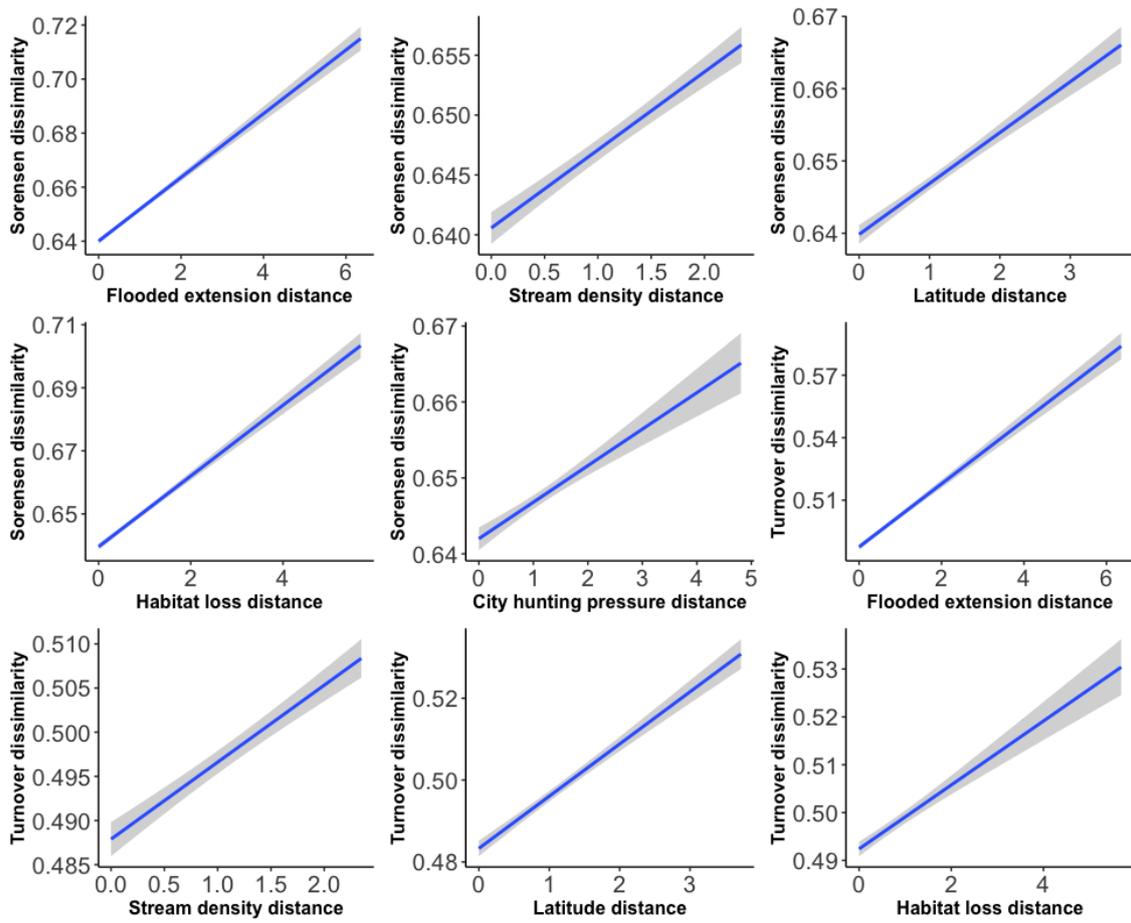
**Table S2** - Pearson and Spearman (Endemism) correlation among the pairwise value of independent variables (contrast of each variable) used in the multivariate distance-based mixed models. The last column shows the Variance Inflator Factor (VIF) of each predictor. The values in bold represents correlation ( $p > |0.7|$ ) and collinearity ( $VIF > 3$ ). The name of variables are described as FLOOD – Seasonally flooded extension area distance; STREAM – Stream density distance; HABITAT – Habitat loss extension distance; PROTE – Distance to PA limit distance; CITY.HP – City hunting pressure; COM.HP – Community hunting pressure; DIST – Geographic distance among cameras-traps (CT); END – Endemism; LAT – Latitude; LONG – Longitude.

	STREAM	HABITAT	PROTE	COM.HP	CITY.HP	DIST	END	LAT	LON	VIF
FLOOD	-0.02	0.02	-0.03	-0.01	-0.05	-0.06	-0.02	-0.05	-0.07	1.01
STREAM		0.02	0.01	0.00	0.05	0.06	-0.01	0.05	0.04	1.01
HABITAT			0.00	0.12	-0.01	-0.02	0.00	-0.03	0.02	1.02
PROTE				0.04	0.09	-0.05	-0.03	-0.10	0.05	1.08
COM.HP					-0.03	-0.04	-0.02	-0.06	0.01	1.03
CITY.HP						0.30	0.22	0.30	0.22	1.15
DIST							<b>0.75</b>	<b>0.97</b>	<b>0.85</b>	<b>198.22</b>
END								<b>0.75</b>	<b>0.71</b>	<b>7.44</b>
LAT									<b>0.70</b>	<b>130.15</b>
LON										<b>27.02</b>

## Figures



**Figure S1** – Plots showing the linear relation estimated (line blue) and confidence interval (95%; grey) among the pairwise Sorensen and Turnover dissimilarities of local non-game assemblies and the contrast of variables that showed significant effects (see Table 4).



**Figure S2** – Plots showing the linear relation estimated (line blue) and confidence interval (95%; grey) among the pairwise Sorensen and Turnover dissimilarities of local game assemblies and the contrast of variables that showed significant effects (see Table 4).

### Annex III - Supplemental material Chapter III

**Table S1.** Values of overdispersion (c-hat) and their respective level of significance (p) according to models with 5, 7, 10, 12 and 15 days of detection history (DH) by species. Model underlined were chosen for the posterior analyses.

<i>Tapirus terrestris</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.00	15.10
7 days	0.00	3.61
<u>10 days</u>	<u>0.51</u>	<u>0.68</u>
12 days	0.00	2.12
15 days	0.02	2.79
<i>Panthera onca</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.05	2.51
7 days	0.01	3.45
<u>10 days</u>	<u>0.54</u>	<u>0.85</u>
12 days	0.04	1.88
15 days	0.01	4.62
<i>Puma concolor</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.09	1.91
7 days	0.02	2.15
<u>10 days</u>	<u>0.32</u>	<u>0.93</u>
12 days	0.08	1.89
15 days	0.02	4.25
<i>Tayassu pecari</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.28	0.28
7 days	0.47	0.63
<u>10 days</u>	<u>0.39</u>	<u>1.01</u>
12 days	0.10	1.27
15 days	0.07	2.42
<i>Myrmecophaga tridactyla</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.81	0.35
7 days	0.58	0.74
<u>10 days</u>	<u>0.18</u>	<u>1.25</u>
12 days	0.02	2.04
15 days	0.00	3.66
<i>Priodontes maximus</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.73	0.59
7 days	0.72	0.55
<u>10 days</u>	<u>0.31</u>	<u>1.12</u>
12 days	0.05	1.91
15 days	0.00	3.26
<i>Mazama americana</i> (DH)	<b>c-hat</b>	<b>p</b>
5 days	0.13	1.32
<u>7 days</u>	<u>0.15</u>	<u>1.15</u>

10 days	0.00	3.10
12 days	0.00	3.78
15 days	0.00	6.94
<b><i>Pecari tajacu</i> (DH)</b>	<b>c-hat</b>	<b>p</b>
<u>5 days</u>	<u>0.00</u>	<u>1.82</u>
7 days	0.00	2.14
10 days	0.01	2.26
12 days	0.00	2.73
15 days	0.00	5.25
<b><i>Mazama nemorivaga</i> (DH)</b>	<b>c-hat</b>	<b>p</b>
5 days	0.04	1.38
<u>7 days</u>	<u>0.12</u>	<u>1.17</u>
10 days	0.07	1.48
12 days	0.00	3.60
15 days	0.00	7.72
<b><i>Cuniculus paca</i> (DH)</b>	<b>c-hat</b>	<b>p</b>
<u>5 days</u>	<u>0.10</u>	<u>1.24</u>
7 days	0.00	1.94
10 days	0.00	4.70
12 days	0.00	7.60
15 days	0.00	19.96
<b>Nonspecific cingulata small (DH)</b>	<b>c-hat</b>	<b>p</b>
5 days	0.01	1.39
<u>7 days</u>	<u>0.04</u>	<u>1.32</u>
10 days	0.00	2.08
12 days	0.00	5.52
15 days	0.00	9.47
<b><i>Nasua nasua</i> (DH)</b>	<b>c-hat</b>	<b>p</b>
5 days	0.05	2.41
7 days	0.01	3.33
<u>10 days</u>	<u>0.39</u>	<u>0.88</u>
12 days	0.08	1.85
15 days	0.01	4.97
<b><i>Dasyprocta</i> spp. (DH)</b>	<b>c-hat</b>	<b>p</b>
<u>5 days</u>	<u>0.05</u>	<u>1.21</u>
7 days	0.00	2.17
10 days	0.00	6.35
12 days	0.00	10.21
15 days	0.00	33.12
<b><i>Hadroskiurus spadiceus</i> (DH)</b>	<b>c-hat</b>	<b>p</b>
<u>5 days</u>	<u>0.37</u>	<u>1.02</u>
7 days	0.21	1.12
10 days	0.25	1.04

12 days	0.00	2.68
15 days	0.04	2.96
<b><i>Mitu or Crax spp. (DH)</i></b>	<b>c-hat</b>	<b>p</b>
5 days	0.00	2.70
<u>7 days</u>	<u>0.00</u>	<u>2.12</u>
10 days	0.03	2.61
12 days	0.01	2.94
15 days	0.00	8.47
<b><i>Penelope jacquacu (DH)</i></b>	<b>c-hat</b>	<b>p</b>
5 days	0.01	7.42
7 days	0.02	3.84
10 days	0.06	1.46
<u>12 days</u>	<u>0.12</u>	<u>1.32</u>
15 days	0.07	2.08
<b><i>Psophia spp. (DH)</i></b>	<b>c-hat</b>	<b>p</b>
<u>5 days</u>	<u>0.00</u>	<u>1.81</u>
7 days	0.00	2.13
10 days	0.00	4.80
12 days	0.00	4.22
15 days	0.00	10.93
<b><i>Tinamus spp. (DH)</i></b>	<b>c-hat</b>	<b>p</b>
5 days	0.00	13.24
7 days	0.04	1.15
<u>10 days</u>	<u>0.44</u>	<u>0.90</u>
12 days	0.02	2.92
15 days	0.00	4.29

**Table S3.** Model selection results by species (top 4 AIC or QAIC points) using up two predictors for the detection probability (p). Model selection was run using the global model in abundance parameter (lam). The predictors in each species best model were retained in the following Bayesian Royle-Nichols models. Predictor codes as follow: Eff – Effort; Hab – Habitat loss extension; Flo – Floodplain extension; Str – Stream length; PA – Protected area distance; C.HP – City hunting pressure; L.HP – Local hunting pressure.

<i>Tapirus terrestris</i>																			
p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-2.44	-0.68	NA	0.34	NA	NA	NA	NA	1.02	-0.75	0.03	-0.26	-0.26	-0.16	-0.94	10.00	-515.31	1050.94	0.00	0.49
-2.13	-0.95	NA	0.35	NA	NA	NA	0.52	NA	-0.75	0.03	-0.27	-0.24	-0.57	-0.05	10.00	-516.82	1053.97	3.03	0.11
-2.23	-0.76	NA	NA	NA	0.99	NA	NA	1.08	-0.83	0.03	-0.90	-0.25	-0.12	-0.88	10.00	-516.99	1054.31	3.37	0.09
<i>Panthera onca</i>																			
p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-4.39	-0.12	NA	0.32	NA	NA	NA	NA	NA	-0.26	0.04	0.01	0.05	-0.59	-0.01	9.00	-188.46	395.19	0.00	0.11
-4.19	-0.27	NA	NA	NA	NA	NA	NA	NA	-0.27	0.06	0.13	0.02	-0.56	0.02	8.00	-189.72	395.65	0.47	0.09
-3.88	-0.50	NA	NA	NA	1.70	NA	NA	NA	-0.26	0.05	-1.41	0.02	-0.53	0.03	9.00	-189.04	396.34	1.15	0.06
-4.11	-0.33	NA	0.29	NA	1.48	NA	NA	NA	-0.25	0.04	-1.34	0.04	-0.57	0.01	10.00	-188.09	396.49	1.30	0.06
-5.76	1.25	NA	0.32	NA	NA	NA	-2.05	NA	-0.25	0.05	0.01	0.05	1.44	-0.02	10.00	-188.22	396.76	1.57	0.05
-4.35	-0.15	NA	0.32	NA	NA	NA	NA	0.55	-0.26	0.04	0.01	0.06	-0.59	-0.55	10.00	-188.38	397.07	1.89	0.04
-4.33	-0.16	NA	0.31	-0.56	NA	NA	NA	NA	-0.25	0.59	0.01	0.05	-0.58	-0.01	10.00	-188.40	397.12	1.93	0.04
-3.74	-0.61	-0.46	NA	NA	1.91	NA	NA	NA	0.09	0.05	-1.53	0.03	-0.52	0.02	10.00	-188.42	397.15	1.96	0.04
-5.59	1.12	NA	NA	NA	NA	NA	-2.06	NA	-0.26	0.06	0.12	0.02	1.47	0.02	9.00	-189.45	397.16	1.97	0.04
-4.53	0.02	-0.51	0.31	NA	NA	NA	NA	NA	0.24	0.04	0.01	0.05	-0.59	-0.01	10.00	-188.44	397.20	2.01	0.04
-4.38	-0.12	NA	0.32	NA	NA	-0.34	NA	NA	-0.26	0.04	0.01	0.38	-0.59	-0.01	10.00	-188.46	397.23	2.05	0.04
-3.98	-0.48	NA	NA	-0.59	NA	NA	NA	NA	-0.26	0.64	0.12	0.02	-0.55	0.02	9.00	-189.57	397.41	2.22	0.04
-3.74	-0.59	NA	NA	NA	1.82	-0.87	NA	NA	-0.27	0.06	-1.44	0.75	-0.54	0.01	10.00	-188.57	397.46	2.27	0.04
-4.23	-0.23	NA	NA	NA	NA	NA	NA	0.42	-0.27	0.06	0.13	0.02	-0.56	-0.39	9.00	-189.68	397.61	2.42	0.03
-4.31	-0.15	-0.49	NA	NA	NA	NA	NA	NA	0.22	0.06	0.13	0.02	-0.56	0.02	9.00	-189.69	397.64	2.45	0.03
-4.19	-0.27	NA	NA	NA	NA	0.00	NA	NA	-0.27	0.06	0.13	0.03	-0.56	0.02	9.00	-189.72	397.71	2.52	0.03
-3.88	-0.48	NA	NA	NA	1.87	NA	NA	0.34	-0.26	0.05	-1.54	0.02	-0.52	-0.26	10.00	-188.74	397.80	2.61	0.03
-4.11	-0.29	NA	NA	NA	1.73	NA	-0.35	NA	-0.26	0.05	-1.45	0.01	-0.23	0.02	10.00	-188.97	398.26	3.07	0.02
-3.92	-0.46	NA	NA	-0.18	1.70	NA	NA	NA	-0.26	0.22	-1.41	0.02	-0.53	0.03	10.00	-189.01	398.34	3.15	0.02
-5.28	0.82	NA	NA	NA	NA	NA	-1.89	-0.39	-0.26	0.06	0.12	0.02	1.29	0.38	10.00	-189.41	399.15	3.96	0.02
-3.72	-0.70	NA	NA	NA	NA	-0.60	NA	0.69	-0.25	0.06	0.13	0.56	-0.55	-0.61	10.00	-189.43	399.18	3.99	0.02

*Puma concolor*

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-3.71	-0.36	NA	NA	NA	NA	-1.08	NA	NA	-0.14	0.16	-0.22	1.04	-0.05	0.00	9.00	-229.71	477.69	0.00	0.08
-3.74	-0.33	NA	NA	0.53	NA	-1.05	NA	NA	-0.13	-0.30	-0.21	0.98	-0.03	-0.01	10.00	-228.72	477.75	0.07	0.08
-4.47	0.34	NA	NA	NA	NA	NA	NA	NA	-0.16	0.17	-0.22	0.07	-0.04	-0.01	8.00	-230.79	477.80	0.11	0.08
-6.65	2.52	NA	NA	1.19	NA	NA	NA	NA	-0.16	-0.98	-0.21	0.05	-0.02	-0.04	9.00	-229.77	477.80	0.12	0.08
-4.22	0.11	NA	NA	NA	NA	NA	NA	1.04	-0.15	0.13	-0.23	0.08	-0.03	-1.02	9.00	-229.99	478.24	0.55	0.06
-5.55	1.44	NA	NA	1.13	NA	NA	1.15	NA	-0.16	-0.86	-0.22	0.07	-1.13	-0.04	10.00	-229.26	478.83	1.15	0.05
-3.87	-0.20	NA	NA	NA	0.84	NA	NA	1.18	-0.15	0.13	-0.99	0.06	-0.03	-1.10	10.00	-229.32	478.96	1.27	0.04
-3.63	-0.46	NA	NA	NA	NA	-0.65	NA	0.63	-0.13	0.14	-0.23	0.63	-0.04	-0.59	10.00	-229.51	479.35	1.66	0.04
-4.77	0.64	NA	NA	0.47	NA	NA	NA	0.78	-0.16	-0.31	-0.23	0.07	-0.02	-0.80	10.00	-229.55	479.43	1.74	0.03
-5.02	0.90	NA	NA	NA	NA	NA	1.09	NA	-0.16	0.18	-0.22	0.07	-1.11	-0.01	9.00	-230.60	479.46	1.77	0.03
-3.65	-0.41	NA	NA	NA	NA	-1.21	-0.29	NA	-0.13	0.15	-0.21	1.12	0.21	0.00	10.00	-229.63	479.58	1.90	0.03
-4.42	0.30	NA	NA	NA	0.59	NA	NA	NA	-0.16	0.17	-0.79	0.07	-0.05	-0.01	9.00	-230.67	479.59	1.91	0.03
-3.72	-0.35	NA	-0.04	NA	NA	-1.09	NA	NA	-0.14	0.16	-0.20	1.04	-0.04	0.00	10.00	-229.68	479.68	2.00	0.03
-6.46	2.33	NA	NA	1.11	-0.54	NA	NA	NA	-0.16	-0.90	0.32	0.06	-0.01	-0.04	10.00	-229.69	479.71	2.02	0.03
-3.71	-0.37	NA	NA	NA	0.11	-1.06	NA	NA	-0.14	0.16	-0.32	1.02	-0.05	-0.01	10.00	-229.70	479.73	2.04	0.03
-4.54	0.42	-0.62	NA	NA	NA	NA	NA	NA	0.45	0.17	-0.22	0.07	-0.04	-0.02	9.00	-230.74	479.74	2.06	0.03
-3.72	-0.36	-0.01	NA	NA	NA	-1.08	NA	NA	-0.12	0.16	-0.22	1.04	-0.05	0.00	10.00	-229.71	479.74	2.06	0.03
-4.50	0.38	NA	-0.05	NA	NA	NA	NA	NA	-0.16	0.17	-0.20	0.06	-0.04	-0.01	9.00	-230.76	479.78	2.09	0.03
-6.71	2.58	-0.21	NA	1.19	NA	NA	NA	NA	0.04	-0.98	-0.21	0.06	-0.02	-0.04	10.00	-229.74	479.81	2.12	0.03
-6.67	2.55	NA	-0.03	1.19	NA	NA	NA	NA	-0.16	-0.98	-0.19	0.05	-0.01	-0.03	10.00	-229.75	479.83	2.14	0.03
-3.98	-0.12	NA	NA	NA	NA	NA	0.48	1.00	-0.15	0.14	-0.24	0.08	-0.48	-0.97	10.00	-229.76	479.85	2.16	0.03
-4.21	0.10	-0.34	NA	NA	NA	NA	NA	1.08	0.16	0.13	-0.23	0.08	-0.03	-1.05	10.00	-229.79	479.90	2.21	0.03
-4.21	0.10	NA	-0.06	NA	NA	NA	NA	1.04	-0.15	0.14	-0.21	0.07	-0.03	-1.02	10.00	-229.93	480.19	2.50	0.02
-4.91	0.78	-0.42	NA	NA	NA	NA	1.00	NA	0.25	0.18	-0.22	0.08	-1.03	-0.01	10.00	-230.51	481.35	3.66	0.01
-5.04	0.91	NA	-0.05	NA	NA	NA	1.11	NA	-0.16	0.18	-0.20	0.07	-1.14	-0.01	10.00	-230.55	481.43	3.74	0.01
-4.93	0.81	NA	NA	NA	0.29	NA	0.90	NA	-0.16	0.18	-0.51	0.07	-0.93	-0.01	10.00	-230.56	481.45	3.76	0.01
-4.43	0.31	-0.41	NA	NA	0.58	NA	NA	NA	0.24	0.17	-0.78	0.07	-0.05	-0.02	10.00	-230.62	481.55	3.87	0.01
-4.43	0.31	NA	-0.05	NA	0.61	NA	NA	NA	-0.16	0.17	-0.79	0.07	-0.04	-0.01	10.00	-230.62	481.57	3.88	0.01

*Tayassu pecari*

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	AICc	delta	weight
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-5.22	-0.20	NA	1.41	NA	-2.20	NA	NA	NA	0.31	-0.57	1.42	-0.57	0.07	0.42	10.00	-132.74	285.80	0.00	0.348
-4.25	-1.04	NA	1.14	NA	NA	NA	NA	NA	0.27	-0.54	-0.44	-0.57	0.02	0.30	9.00	-134.46	287.18	1.38	0.175
-4.28	-1.09	NA	1.37	NA	NA	NA	NA	1.87	0.29	-0.54	-0.46	-0.54	0.01	-1.29	10.00	-133.64	287.59	1.79	0.142
-4.40	-0.89	NA	1.19	NA	NA	NA	-1.36	NA	0.28	-0.53	-0.42	-0.60	1.29	0.31	10.00	-133.89	288.11	2.31	0.11
-4.06	-1.22	-0.53	1.15	NA	NA	NA	NA	NA	0.77	-0.53	-0.43	-0.57	0.02	0.30	10.00	-134.21	288.73	2.93	0.08
-4.46	-0.84	NA	1.14	NA	NA	-0.48	NA	NA	0.27	-0.53	-0.44	-0.10	0.01	0.29	10.00	-134.37	289.05	3.25	0.068
-4.55	-0.75	NA	1.14	-1.11	NA	NA	NA	NA	0.27	0.54	-0.44	-0.57	0.02	0.30	10.00	-134.38	289.09	3.29	0.067

***Myrmecophaga tridactyla***

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-3.14	0.22	NA	NA	NA	-1.22	NA	NA	-1.05	-0.15	-0.01	1.10	-0.07	-0.14	0.88	10.00	-520.12	1060.56	0.00	0.40
-2.82	-0.16	NA	0.21	NA	NA	NA	NA	NA	-0.13	0.00	-0.04	-0.07	-0.15	-0.03	9.00	-522.88	1064.03	3.47	0.07

***Priodontes maximus***

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	AICc	delta	weight
-2.67	-0.68	NA	0.31	NA	NA	NA	NA	-0.64	0.00	-0.07	0.02	-0.12	0.17	0.48	10.00	-396.34	813.00	0.00	0.165
-2.60	-0.63	NA	NA	NA	-0.99	NA	NA	-0.93	0.00	-0.07	0.94	-0.12	0.21	0.76	10.00	-396.55	813.41	0.41	0.134
-2.84	-0.48	NA	NA	NA	NA	NA	0.67	-0.55	0.01	-0.07	0.13	-0.13	-0.39	0.43	10.00	-396.98	814.28	1.27	0.087
-2.89	-0.42	-0.89	NA	NA	NA	NA	0.81	NA	0.81	-0.07	0.13	-0.12	-0.51	-0.01	10.00	-397.23	814.78	1.78	0.068
-2.59	-0.72	NA	NA	NA	NA	NA	NA	-0.57	0.01	-0.07	0.13	-0.13	0.19	0.45	9.00	-398.44	815.14	2.14	0.057
-3.81	0.51	NA	NA	NA	NA	0.57	1.92	NA	0.03	-0.08	0.14	-0.61	-1.58	-0.03	10.00	-397.48	815.29	2.29	0.053
-2.70	-0.61	-0.74	NA	NA	NA	NA	NA	-0.53	0.68	-0.06	0.13	-0.13	0.19	0.43	10.00	-397.57	815.46	2.45	0.048
-3.02	-0.33	NA	0.23	NA	NA	NA	0.88	NA	0.00	-0.08	0.05	-0.11	-0.62	-0.06	10.00	-397.60	815.51	2.51	0.047
-2.91	-0.41	NA	NA	NA	NA	NA	0.93	NA	0.01	-0.07	0.13	-0.12	-0.64	-0.03	9.00	-398.80	815.87	2.87	0.039
-2.68	-0.65	-0.85	0.26	NA	NA	NA	NA	NA	0.78	-0.07	0.03	-0.11	0.17	-0.06	10.00	-397.97	816.26	3.26	0.032
-2.55	-0.79	NA	0.27	NA	NA	NA	NA	NA	-0.01	-0.07	0.03	-0.10	0.17	-0.06	9.00	-399.01	816.29	3.28	0.032
-2.62	-0.67	NA	NA	0.35	NA	NA	NA	-0.66	0.01	-0.34	0.13	-0.13	0.19	0.53	10.00	-398.01	816.34	3.34	0.031
-2.66	-0.65	NA	NA	NA	NA	-0.23	NA	-0.60	0.01	-0.06	0.13	0.07	0.19	0.47	10.00	-398.23	816.78	3.78	0.025

***Mazama americana***

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-1.77	-0.02	0.16	0.41	NA	NA	NA	NA	NA	-0.29	0.04	-0.08	-0.07	-0.08	-0.03	10.00	-1475.21	2970.74	0.00	0.33
-1.77	-0.02	NA	0.41	0.14	NA	NA	NA	NA	-0.18	-0.06	-0.07	-0.08	-0.09	-0.02	10.00	-1475.76	2971.84	1.11	0.19
-1.77	-0.02	NA	0.41	NA	NA	NA	NA	NA	-0.19	0.03	-0.07	-0.07	-0.09	-0.02	9.00	-1476.84	2971.95	1.21	0.18
-1.77	-0.02	NA	0.42	NA	NA	NA	-0.08	NA	-0.19	0.03	-0.08	-0.07	-0.03	-0.03	10.00	-1476.56	2973.45	2.71	0.08

-1.78	-0.01	NA	0.42	NA	NA	NA	NA	0.09	-0.19	0.03	-0.08	-0.07	-0.09	-0.09	10.00	-1476.61	2973.55	2.81	0.08
-1.77	-0.02	NA	0.42	NA	NA	0.07	NA	NA	-0.19	0.03	-0.08	-0.12	-0.09	-0.02	10.00	-1476.74	2973.80	3.06	0.07
-1.77	-0.02	NA	0.42	NA	-0.01	NA	NA	NA	-0.19	0.03	-0.07	-0.07	-0.09	-0.02	10.00	-1476.84	2974.00	3.26	0.06

***Pecari tajacu***

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	QAIC	delta	weight
-2.35	-0.08	NA	NA	NA	NA	NA	0.45	NA	-0.13	-0.23	-0.19	-0.15	-0.48	0.03	9.00	-1394.85	1552.80	0.00	0.171
-2.37	-0.07	NA	NA	NA	-0.24	NA	0.44	NA	-0.13	-0.22	-0.01	-0.15	-0.47	0.03	10.00	-1393.29	1553.09	0.29	0.148
-2.36	-0.07	-0.17	NA	NA	NA	NA	0.46	NA	0.00	-0.23	-0.19	-0.15	-0.48	0.03	10.00	-1393.84	1553.70	0.90	0.109
-2.38	-0.06	NA	0.08	NA	NA	NA	0.45	NA	-0.13	-0.23	-0.22	-0.15	-0.48	0.02	10.00	-1394.24	1554.13	1.33	0.088
-2.35	-0.08	NA	NA	0.12	NA	NA	0.46	NA	-0.13	-0.32	-0.19	-0.15	-0.49	0.03	10.00	-1394.48	1554.40	1.60	0.077
-2.37	-0.07	NA	NA	NA	NA	-0.09	0.45	NA	-0.13	-0.23	-0.20	-0.07	-0.48	0.02	10.00	-1394.64	1554.57	1.77	0.07
-2.34	-0.08	NA	NA	NA	NA	NA	0.45	-0.09	-0.13	-0.23	-0.19	-0.15	-0.48	0.10	10.00	-1394.70	1554.64	1.84	0.068
-2.26	-0.17	NA	NA	NA	NA	NA	NA	NA	-0.13	-0.21	-0.19	-0.16	-0.12	0.03	8.00	-1399.88	1556.32	3.52	0.029
-2.32	-0.13	NA	NA	NA	-0.28	NA	NA	NA	-0.12	-0.22	0.02	-0.16	-0.11	0.04	9.00	-1398.29	1556.58	3.78	0.026
-2.36	-0.10	NA	0.14	NA	-0.34	NA	NA	NA	-0.12	-0.22	0.02	-0.16	-0.13	0.03	10.00	-1396.63	1556.75	3.95	0.024

***Mazama nemorivaga***

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	AICc	delta	weight
-1.93	-0.16	NA	NA	NA	0.51	NA	NA	0.29	-0.44	-0.42	-0.57	-0.04	-0.26	-0.22	10.00	-1108.00	2236.39	0.00	0.245
-2.04	-0.08	-0.39	NA	NA	0.53	NA	NA	NA	-0.11	-0.42	-0.58	-0.06	-0.27	0.01	10.00	-1108.42	2237.22	0.83	0.161
-1.92	-0.19	NA	NA	NA	0.42	NA	NA	NA	-0.43	-0.42	-0.50	-0.05	-0.27	0.00	9.00	-1110.01	2238.33	1.94	0.093
-1.90	-0.20	NA	NA	NA	0.39	NA	0.20	NA	-0.43	-0.42	-0.48	-0.05	-0.42	0.00	10.00	-1109.24	2238.86	2.47	0.071
-1.91	-0.18	NA	NA	0.15	0.45	NA	NA	NA	-0.43	-0.52	-0.54	-0.05	-0.27	0.00	10.00	-1109.48	2239.35	2.96	0.056
-1.92	-0.18	NA	NA	NA	0.44	-0.05	NA	NA	-0.43	-0.41	-0.52	-0.01	-0.27	0.00	10.00	-1109.96	2240.30	3.91	0.035
-1.91	-0.22	NA	NA	NA	NA	NA	NA	NA	-0.42	-0.41	-0.20	-0.04	-0.27	-0.02	8.00	-1112.06	2240.37	3.98	0.033
-1.92	-0.19	NA	-0.01	NA	0.42	NA	NA	NA	-0.43	-0.42	-0.50	-0.05	-0.27	0.00	10.00	-1109.99	2240.37	3.98	0.033

***Cuniculus paca***

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-1.61	0.01	NA	0.21	-0.18	NA	NA	NA	NA	-0.01	0.05	-0.08	0.04	0.22	0.01	10.00	-2084.74	4189.81	0.00	0.29
-1.60	0.00	NA	0.23	NA	NA	NA	NA	NA	-0.01	-0.07	-0.08	0.04	0.22	0.01	9.00	-2086.14	4190.55	0.74	0.20
-1.60	0.00	NA	0.24	NA	NA	-0.13	NA	NA	-0.01	-0.07	-0.08	0.12	0.21	0.01	10.00	-2085.21	4190.74	0.93	0.18
-1.60	0.00	-0.05	0.24	NA	NA	NA	NA	NA	0.03	-0.07	-0.08	0.03	0.21	0.01	10.00	-2085.91	4192.13	2.33	0.09
-1.60	0.00	NA	0.24	NA	NA	NA	NA	0.03	-0.01	-0.07	-0.08	0.04	0.22	-0.02	10.00	-2086.06	4192.44	2.64	0.08

-1.60	0.00	NA	0.24	NA	-0.03	NA	NA	NA	-0.01	-0.07	-0.06	0.04	0.22	0.01	10.00	-2086.06	4192.45	2.64	0.08
-1.60	0.00	NA	0.23	NA	NA	NA	0.01	NA	-0.01	-0.07	-0.08	0.04	0.21	0.01	10.00	-2086.12	4192.57	2.76	0.07

**Nonspecific cingulata small**

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	QAIC	delta	weight
-1.85	-0.14	-0.24	NA	NA	NA	NA	NA	NA	0.21	-0.21	-0.04	0.01	-0.05	-0.02	9.00	-1720.77	2627.23	0.00	0.084
-1.88	-0.12	-0.24	0.10	NA	NA	NA	NA	NA	0.21	-0.22	-0.07	0.01	-0.05	-0.03	10.00	-1719.61	2627.47	0.24	0.074
-1.86	-0.13	-0.22	NA	NA	NA	-0.15	NA	NA	0.20	-0.21	-0.04	0.12	-0.04	-0.01	10.00	-1719.62	2627.48	0.24	0.074
-1.87	-0.12	-0.24	NA	NA	NA	NA	NA	0.17	0.22	-0.21	-0.04	0.00	-0.05	-0.14	10.00	-1719.66	2627.54	0.31	0.072
-1.85	-0.13	-0.31	NA	0.15	NA	NA	NA	NA	0.27	-0.30	-0.04	0.01	-0.05	-0.01	10.00	-1719.77	2627.71	0.48	0.066
-1.86	-0.13	NA	NA	NA	NA	-0.21	NA	0.22	0.03	-0.21	-0.04	0.15	-0.04	-0.17	10.00	-1719.78	2627.73	0.49	0.065
-1.86	-0.13	-0.23	NA	NA	NA	NA	-0.12	NA	0.21	-0.21	-0.04	0.01	0.04	-0.01	10.00	-1719.98	2628.03	0.79	0.056
-1.88	-0.12	NA	0.11	NA	NA	-0.20	NA	NA	0.03	-0.22	-0.07	0.16	-0.05	-0.03	10.00	-1720.14	2628.28	1.04	0.05
-1.85	-0.14	NA	NA	NA	NA	-0.18	NA	NA	0.03	-0.22	-0.04	0.14	-0.04	-0.01	9.00	-1721.52	2628.36	1.12	0.048
-1.85	-0.15	NA	NA	NA	NA	NA	NA	NA	0.04	-0.22	-0.04	0.01	-0.04	-0.02	8.00	-1723.22	2628.94	1.70	0.036
-1.86	-0.13	-0.25	NA	NA	0.04	NA	NA	NA	0.22	-0.21	-0.07	0.01	-0.05	-0.02	10.00	-1720.67	2629.07	1.84	0.033
-1.86	-0.13	NA	NA	NA	NA	NA	-0.17	0.21	0.03	-0.22	-0.05	0.00	0.07	-0.17	10.00	-1720.67	2629.08	1.85	0.033
-1.85	-0.14	NA	NA	NA	NA	-0.17	-0.12	NA	0.03	-0.22	-0.04	0.13	0.04	-0.01	10.00	-1720.77	2629.22	1.99	0.031
-1.85	-0.14	NA	NA	NA	NA	NA	NA	0.17	0.04	-0.22	-0.05	0.00	-0.04	-0.14	9.00	-1722.11	2629.25	2.02	0.03
-1.87	-0.13	NA	0.10	NA	NA	NA	NA	NA	0.04	-0.22	-0.08	0.01	-0.05	-0.03	9.00	-1722.14	2629.30	2.07	0.03
-1.85	-0.15	NA	NA	NA	NA	NA	-0.14	NA	0.03	-0.22	-0.05	0.01	0.06	-0.02	9.00	-1722.19	2629.39	2.15	0.028
-1.84	-0.14	NA	NA	0.09	NA	-0.20	NA	NA	0.03	-0.27	-0.04	0.15	-0.04	-0.01	10.00	-1721.12	2629.76	2.53	0.024
-1.88	-0.12	NA	0.10	NA	NA	NA	NA	0.17	0.03	-0.22	-0.08	0.01	-0.05	-0.16	10.00	-1721.14	2629.79	2.56	0.023
-1.87	-0.13	NA	0.10	NA	NA	NA	-0.13	NA	0.03	-0.22	-0.08	0.01	0.05	-0.03	10.00	-1721.22	2629.92	2.68	0.022
-1.85	-0.14	NA	NA	NA	0.04	-0.19	NA	NA	0.03	-0.22	-0.07	0.14	-0.04	-0.01	10.00	-1721.42	2630.21	2.98	0.019
-1.84	-0.15	NA	NA	0.05	NA	NA	NA	NA	0.04	-0.25	-0.04	0.01	-0.04	-0.02	9.00	-1723.11	2630.77	3.54	0.014
-1.85	-0.15	NA	NA	NA	0.01	NA	NA	NA	0.04	-0.22	-0.05	0.01	-0.04	-0.02	9.00	-1723.21	2630.93	3.70	0.013
-1.85	-0.14	NA	NA	0.06	NA	NA	NA	0.18	0.04	-0.25	-0.05	0.00	-0.04	-0.15	10.00	-1721.96	2631.03	3.80	0.013
-1.87	-0.13	NA	0.10	0.06	NA	NA	NA	NA	0.04	-0.26	-0.08	0.01	-0.05	-0.03	10.00	-1721.99	2631.08	3.84	0.012
-1.84	-0.15	NA	NA	0.06	NA	NA	-0.15	NA	0.03	-0.26	-0.05	0.01	0.06	-0.02	10.00	-1722.00	2631.09	3.86	0.012
-1.86	-0.14	NA	NA	NA	0.04	NA	NA	0.18	0.04	-0.22	-0.07	0.00	-0.04	-0.15	10.00	-1722.03	2631.13	3.90	0.012
-1.87	-0.13	NA	0.11	NA	-0.03	NA	NA	NA	0.04	-0.22	-0.06	0.01	-0.05	-0.03	10.00	-1722.09	2631.23	4.00	0.011

***Nasua nasua***

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-3.52	0.20	NA	0.54	NA	1.41	NA	NA	NA	0.18	-0.32	-0.97	-0.04	0.14	-0.09	10.00	-461.94	944.19	0.00	0.24
-2.55	-0.74	NA	0.61	NA	NA	NA	NA	NA	0.19	-0.32	0.21	-0.04	0.12	-0.13	9.00	-463.09	944.45	0.25	0.21
-2.60	-0.69	NA	0.60	NA	NA	-0.41	NA	NA	0.20	-0.32	0.21	0.30	0.11	-0.14	10.00	-462.31	944.94	0.74	0.17
-2.70	-0.60	NA	0.57	NA	NA	NA	0.36	NA	0.19	-0.31	0.22	-0.03	-0.18	-0.12	10.00	-462.62	945.56	1.37	0.12
-2.53	-0.75	NA	0.61	NA	NA	NA	NA	0.24	0.19	-0.32	0.21	-0.03	0.12	-0.34	10.00	-462.94	946.20	2.01	0.09
-2.56	-0.73	NA	0.61	-0.09	NA	NA	NA	NA	0.19	-0.25	0.21	-0.04	0.12	-0.13	10.00	-463.06	946.43	2.24	0.08
-2.54	-0.75	-0.03	0.61	NA	NA	NA	NA	NA	0.21	-0.32	0.21	-0.04	0.12	-0.13	10.00	-463.08	946.49	2.29	0.08

*Dasyprocta spp.*

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	QAIC	delta	weight
-1.16	0.53	-0.13	0.32	NA	NA	NA	NA	NA	0.04	-0.18	-0.09	-0.01	0.01	0.12	10.00	-2995.00	4931.83	0.00	0.34
-1.16	0.53	NA	0.31	NA	NA	NA	NA	NA	-0.06	-0.18	-0.09	0.00	0.01	0.11	9.00	-2997.07	4933.24	1.40	0.17
-1.16	0.54	NA	0.32	0.09	NA	NA	NA	NA	-0.05	-0.24	-0.10	-0.01	0.01	0.11	10.00	-2995.94	4933.38	1.55	0.16
-1.16	0.54	NA	0.31	NA	NA	NA	NA	0.09	-0.06	-0.18	-0.09	0.00	0.01	0.05	10.00	-2996.36	4934.06	2.23	0.11
-1.16	0.54	NA	0.31	NA	NA	-0.05	NA	NA	-0.06	-0.18	-0.09	0.03	0.01	0.11	10.00	-2996.80	4934.78	2.95	0.08
-1.15	0.53	NA	0.32	NA	-0.05	NA	NA	NA	-0.06	-0.18	-0.06	0.00	0.01	0.11	10.00	-2996.80	4934.79	2.96	0.08
-1.16	0.53	NA	0.31	NA	NA	NA	-0.02	NA	-0.06	-0.18	-0.09	0.00	0.02	0.11	10.00	-2997.04	4935.18	3.35	0.06

*Hadrosaurus spadicus*

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	AICc	delta	weight
-2.67	-0.68	NA	0.31	NA	NA	NA	NA	-0.64	0.00	-0.07	0.02	-0.12	0.17	0.48	10.00	-396.34	813.00	0.00	0.165
-2.60	-0.63	NA	NA	NA	-0.99	NA	NA	-0.93	0.00	-0.07	0.94	-0.12	0.21	0.76	10.00	-396.55	813.41	0.41	0.134
-2.84	-0.48	NA	NA	NA	NA	NA	0.67	-0.55	0.01	-0.07	0.13	-0.13	-0.39	0.43	10.00	-396.98	814.28	1.27	0.087
-2.89	-0.42	-0.89	NA	NA	NA	NA	0.81	NA	0.81	-0.07	0.13	-0.12	-0.51	-0.01	10.00	-397.23	814.78	1.78	0.068
-2.59	-0.72	NA	NA	NA	NA	NA	NA	-0.57	0.01	-0.07	0.13	-0.13	0.19	0.45	9.00	-398.44	815.14	2.14	0.057
-3.81	0.51	NA	NA	NA	NA	0.57	1.92	NA	0.03	-0.08	0.14	-0.61	-1.58	-0.03	10.00	-397.48	815.29	2.29	0.053
-2.70	-0.61	-0.74	NA	NA	NA	NA	NA	-0.53	0.68	-0.06	0.13	-0.13	0.19	0.43	10.00	-397.57	815.46	2.45	0.048
-3.02	-0.33	NA	0.23	NA	NA	NA	0.88	NA	0.00	-0.08	0.05	-0.11	-0.62	-0.06	10.00	-397.60	815.51	2.51	0.047
-2.91	-0.41	NA	NA	NA	NA	NA	0.93	NA	0.01	-0.07	0.13	-0.12	-0.64	-0.03	9.00	-398.80	815.87	2.87	0.039
-2.68	-0.65	-0.85	0.26	NA	NA	NA	NA	NA	0.78	-0.07	0.03	-0.11	0.17	-0.06	10.00	-397.97	816.26	3.26	0.032
-2.55	-0.79	NA	0.27	NA	NA	NA	NA	NA	-0.01	-0.07	0.03	-0.10	0.17	-0.06	9.00	-399.01	816.29	3.28	0.032
-2.62	-0.67	NA	NA	0.35	NA	NA	NA	-0.66	0.01	-0.34	0.13	-0.13	0.19	0.53	10.00	-398.01	816.34	3.34	0.031
-2.66	-0.65	NA	NA	NA	NA	-0.23	NA	-0.60	0.01	-0.06	0.13	0.07	0.19	0.47	10.00	-398.23	816.78	3.78	0.025

*Mitu or Crax spp.*

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	QAIC	delta	weight
-1.92	-0.77	NA	NA	NA	NA	NA	NA	NA	-0.20	0.29	-0.47	-0.06	-0.30	-0.30	8.00	-883.21	718.96	0.00	0.13
-1.83	-0.78	NA	NA	NA	0.60	NA	NA	0.34	-0.19	0.28	-0.90	-0.07	-0.30	-0.54	10.00	-879.91	720.34	1.39	0.06
-1.98	-0.72	-0.24	NA	NA	NA	NA	NA	NA	-0.01	0.29	-0.47	-0.06	-0.30	-0.30	9.00	-882.48	720.38	1.42	0.06
-1.87	-0.79	NA	NA	NA	0.20	NA	NA	NA	-0.20	0.28	-0.62	-0.06	-0.30	-0.30	9.00	-882.49	720.39	1.43	0.06
-1.97	-0.74	NA	NA	NA	NA	NA	-0.15	NA	-0.20	0.29	-0.47	-0.06	-0.20	-0.30	9.00	-882.82	720.65	1.69	0.05
-1.92	-0.77	NA	NA	NA	NA	NA	NA	0.09	-0.20	0.29	-0.47	-0.06	-0.31	-0.37	9.00	-882.90	720.71	1.75	0.05
-1.94	-0.76	NA	NA	0.05	NA	NA	NA	NA	-0.20	0.25	-0.47	-0.06	-0.30	-0.30	9.00	-883.14	720.91	1.95	0.05
-1.91	-0.78	NA	0.03	NA	NA	NA	NA	NA	-0.20	0.28	-0.48	-0.06	-0.31	-0.31	9.00	-883.14	720.91	1.95	0.05
-1.93	-0.76	NA	NA	NA	NA	-0.03	NA	NA	-0.20	0.29	-0.47	-0.04	-0.30	-0.30	9.00	-883.19	720.94	1.99	0.05
-1.93	-0.75	-0.29	NA	NA	0.26	NA	NA	NA	0.03	0.28	-0.66	-0.07	-0.30	-0.30	10.00	-881.34	721.47	2.52	0.04
-2.03	-0.68	-0.26	NA	NA	NA	NA	-0.17	NA	0.01	0.29	-0.47	-0.06	-0.18	-0.30	10.00	-881.99	721.99	3.04	0.03
-1.97	-0.73	-0.22	NA	NA	NA	NA	NA	0.06	-0.03	0.29	-0.47	-0.06	-0.31	-0.35	10.00	-882.34	722.27	3.31	0.02
-1.88	-0.78	NA	NA	NA	0.22	-0.09	NA	NA	-0.20	0.28	-0.63	0.00	-0.30	-0.30	10.00	-882.34	722.27	3.31	0.02
-1.90	-0.78	NA	NA	NA	0.17	NA	-0.09	NA	-0.20	0.28	-0.60	-0.06	-0.24	-0.30	10.00	-882.37	722.29	3.33	0.02
-2.00	-0.71	-0.24	NA	0.06	NA	NA	NA	NA	-0.01	0.24	-0.47	-0.06	-0.30	-0.30	10.00	-882.37	722.29	3.33	0.02
-1.96	-0.74	-0.24	0.04	NA	NA	NA	NA	NA	-0.01	0.28	-0.49	-0.06	-0.31	-0.31	10.00	-882.39	722.31	3.35	0.02
-1.89	-0.78	NA	NA	0.06	0.21	NA	NA	NA	-0.19	0.24	-0.62	-0.06	-0.30	-0.30	10.00	-882.40	722.32	3.36	0.02
-1.98	-0.72	-0.26	NA	NA	NA	0.04	NA	NA	0.00	0.29	-0.47	-0.09	-0.30	-0.30	10.00	-882.45	722.35	3.40	0.02
-1.97	-0.73	NA	NA	NA	NA	NA	-0.15	0.09	-0.20	0.29	-0.47	-0.06	-0.19	-0.37	10.00	-882.49	722.39	3.43	0.02
-1.87	-0.79	NA	0.00	NA	0.20	NA	NA	NA	-0.20	0.28	-0.62	-0.06	-0.30	-0.30	10.00	-882.49	722.39	3.43	0.02
-1.97	-0.73	NA	NA	0.04	NA	NA	-0.14	NA	-0.20	0.26	-0.47	-0.06	-0.20	-0.30	10.00	-882.78	722.62	3.66	0.02
-1.97	-0.73	NA	NA	NA	NA	-0.04	-0.15	NA	-0.20	0.29	-0.47	-0.03	-0.19	-0.30	10.00	-882.78	722.62	3.66	0.02
-1.96	-0.74	NA	0.01	NA	NA	NA	-0.14	NA	-0.20	0.29	-0.48	-0.06	-0.20	-0.30	10.00	-882.80	722.64	3.68	0.02
-1.91	-0.78	NA	0.03	NA	NA	NA	NA	0.09	-0.20	0.28	-0.48	-0.06	-0.31	-0.37	10.00	-882.85	722.68	3.72	0.02
-1.93	-0.76	NA	NA	0.03	NA	NA	NA	0.09	-0.20	0.26	-0.47	-0.06	-0.31	-0.37	10.00	-882.87	722.69	3.74	0.02
-1.92	-0.76	NA	NA	NA	NA	-0.02	NA	0.09	-0.20	0.29	-0.47	-0.04	-0.31	-0.37	10.00	-882.89	722.71	3.75	0.02
-1.92	-0.77	NA	0.03	0.04	NA	NA	NA	NA	-0.20	0.25	-0.48	-0.06	-0.31	-0.31	10.00	-883.09	722.87	3.91	0.02
-1.95	-0.75	NA	NA	0.06	NA	-0.05	NA	NA	-0.20	0.24	-0.47	-0.02	-0.30	-0.30	10.00	-883.10	722.87	3.92	0.02
-1.91	-0.77	NA	0.04	NA	NA	-0.04	NA	NA	-0.20	0.28	-0.48	-0.03	-0.31	-0.31	10.00	-883.11	722.88	3.92	0.02

*Penelope jacquacu*

p(Int)	lam(Int)	p(Def)	p(Eff.3)	p(Flo)	p(HP.C)	p(HP.L)	p(Hyd)	p(UC)	lam(Def)	lam(Flo)	lam(HP.C)	lam(HP.L)	lam(Hyd)	lam(UC)	df	logLik	AICc	delta	weight
-2.10	-1.04	NA	0.48	NA	NA	NA	NA	NA	-0.39	-0.06	-0.07	0.06	-0.14	0.04	9.00	-397.69	813.68	0.00	0.22
-2.13	-1.02	NA	0.56	0.42	NA	NA	NA	NA	-0.39	-0.28	-0.08	0.06	-0.14	0.03	10.00	-396.90	814.18	0.50	0.171
-2.14	-1.00	NA	0.48	NA	NA	-0.32	NA	NA	-0.39	-0.05	-0.06	0.30	-0.14	0.04	10.00	-396.97	814.30	0.63	0.161
-2.11	-1.02	NA	0.48	NA	NA	NA	0.22	NA	-0.39	-0.06	-0.07	0.06	-0.30	0.04	10.00	-397.34	815.06	1.38	0.11
-2.12	-1.02	NA	0.48	NA	0.12	NA	NA	NA	-0.39	-0.06	-0.16	0.05	-0.13	0.04	10.00	-397.62	815.61	1.93	0.084
-2.09	-1.04	NA	0.48	NA	NA	NA	NA	-0.07	-0.39	-0.06	-0.07	0.05	-0.13	0.09	10.00	-397.63	815.64	1.96	0.083
-2.11	-1.03	-0.03	0.48	NA	NA	NA	NA	NA	-0.37	-0.06	-0.07	0.06	-0.14	0.04	10.00	-397.68	815.73	2.06	0.079

*Psophia spp.*

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	QAIC	delta	weight
-1.52	-0.62	NA	NA	NA	NA	NA	NA	NA	-0.58	-0.32	-0.08	-0.06	-0.01	0.11	8.00	-1532.36	1875.40	0.00	0.10
-1.54	-0.60	NA	0.10	NA	NA	NA	NA	NA	-0.57	-0.32	-0.11	-0.05	-0.01	0.11	9.00	-1531.34	1876.17	0.77	0.07
-1.53	-0.61	NA	NA	NA	NA	-0.12	NA	NA	-0.59	-0.32	-0.08	0.02	-0.01	0.11	9.00	-1531.43	1876.27	0.87	0.06
-1.52	-0.62	NA	NA	NA	NA	NA	-0.09	NA	-0.59	-0.32	-0.08	-0.06	0.05	0.11	9.00	-1531.76	1876.68	1.28	0.05
-1.53	-0.62	NA	NA	NA	-0.08	NA	NA	NA	-0.59	-0.32	-0.03	-0.05	-0.01	0.12	9.00	-1531.85	1876.79	1.39	0.05
-1.55	-0.60	NA	0.13	NA	-0.12	NA	NA	NA	-0.58	-0.32	-0.04	-0.05	-0.02	0.11	10.00	-1530.35	1876.97	1.57	0.05
-1.56	-0.59	NA	0.10	NA	NA	-0.13	NA	NA	-0.58	-0.32	-0.11	0.02	-0.02	0.10	10.00	-1530.36	1876.98	1.58	0.04
-1.51	-0.62	NA	NA	0.08	NA	NA	NA	NA	-0.59	-0.36	-0.08	-0.06	-0.01	0.11	9.00	-1532.02	1876.99	1.59	0.04
-1.55	-0.60	NA	0.11	NA	NA	NA	-0.11	NA	-0.57	-0.32	-0.11	-0.06	0.05	0.11	10.00	-1530.53	1877.18	1.78	0.04
-1.54	-0.60	NA	NA	NA	NA	-0.14	-0.11	NA	-0.59	-0.33	-0.08	0.02	0.06	0.11	10.00	-1530.57	1877.23	1.83	0.04
-1.52	-0.62	NA	NA	NA	NA	NA	NA	0.00	-0.58	-0.32	-0.08	-0.06	-0.01	0.11	9.00	-1532.35	1877.40	2.00	0.04
-1.52	-0.62	0.01	NA	NA	NA	NA	NA	NA	-0.59	-0.32	-0.08	-0.06	-0.01	0.11	9.00	-1532.35	1877.40	2.00	0.04
-1.53	-0.61	NA	0.11	0.09	NA	NA	NA	NA	-0.57	-0.37	-0.11	-0.05	-0.01	0.11	10.00	-1530.92	1877.66	2.26	0.03
-1.52	-0.61	NA	NA	0.08	NA	-0.12	NA	NA	-0.59	-0.36	-0.08	0.02	-0.01	0.11	10.00	-1531.08	1877.86	2.46	0.03
-1.54	-0.61	NA	NA	NA	-0.07	-0.11	NA	NA	-0.59	-0.32	-0.04	0.01	-0.01	0.11	10.00	-1531.10	1877.88	2.48	0.03
-1.53	-0.61	0.05	0.11	NA	NA	NA	NA	NA	-0.59	-0.32	-0.11	-0.05	-0.01	0.11	10.00	-1531.29	1878.11	2.71	0.03
-1.54	-0.60	NA	0.10	NA	NA	NA	NA	-0.01	-0.57	-0.32	-0.11	-0.05	-0.01	0.11	10.00	-1531.33	1878.16	2.76	0.02
-1.52	-0.62	0.06	NA	NA	NA	-0.13	NA	NA	-0.62	-0.32	-0.08	0.02	-0.01	0.11	10.00	-1531.36	1878.19	2.79	0.02
-1.53	-0.62	NA	NA	NA	-0.07	NA	-0.09	NA	-0.59	-0.32	-0.04	-0.06	0.04	0.12	10.00	-1531.37	1878.20	2.80	0.02
-1.53	-0.61	NA	NA	NA	NA	-0.12	NA	0.00	-0.59	-0.32	-0.08	0.02	-0.01	0.11	10.00	-1531.43	1878.27	2.87	0.02
-1.51	-0.62	NA	NA	0.07	NA	NA	-0.09	NA	-0.59	-0.36	-0.08	-0.06	0.05	0.11	10.00	-1531.53	1878.40	3.00	0.02
-1.51	-0.62	NA	NA	0.08	-0.08	NA	NA	NA	-0.59	-0.36	-0.04	-0.05	-0.01	0.12	10.00	-1531.57	1878.45	3.05	0.02

-1.52	-0.62	0.01	NA	NA	NA	NA	-0.09	NA	-0.59	-0.32	-0.08	-0.06	0.05	0.11	10.00	-1531.76	1878.68	3.28	0.02
-1.52	-0.62	NA	NA	NA	NA	NA	-0.09	0.00	-0.59	-0.32	-0.08	-0.06	0.05	0.11	10.00	-1531.76	1878.68	3.28	0.02
-1.52	-0.62	NA	NA	NA	-0.08	NA	NA	-0.01	-0.59	-0.32	-0.03	-0.05	-0.01	0.12	10.00	-1531.84	1878.78	3.38	0.02
-1.53	-0.62	-0.01	NA	NA	-0.08	NA	NA	NA	-0.59	-0.32	-0.03	-0.05	-0.01	0.12	10.00	-1531.85	1878.79	3.39	0.02
-1.51	-0.62	NA	NA	0.08	NA	NA	NA	-0.01	-0.59	-0.36	-0.08	-0.06	-0.01	0.12	10.00	-1532.01	1878.99	3.59	0.02
-1.50	-0.62	0.01	NA	0.08	NA	NA	NA	NA	-0.59	-0.36	-0.08	-0.06	-0.01	0.11	10.00	-1532.02	1878.99	3.59	0.02
-1.52	-0.62	0.01	NA	NA	NA	NA	NA	0.00	-0.59	-0.32	-0.08	-0.06	-0.01	0.11	10.00	-1532.35	1879.40	4.00	0.01

*Tinamus spp.*

p(Int)	lam(Int)	p(Hab)	p(Eff)	p(Flo)	p(C.HP)	p(L.HP)	p(Str)	p(PA)	lam(Hab)	lam(Flo)	lam(C.HP)	lam(L.HP)	lam(Str)	lam(PA)	df	logLik	AICc	delta	weight
-2.18	-0.39	NA	0.61	NA	NA	NA	NA	NA	-0.38	0.01	-0.08	-0.15	0.14	0.11	9.00	-710.40	1439.06	0.00	0.25
-2.20	-0.38	NA	0.64	NA	-0.43	NA	NA	NA	-0.39	0.01	0.27	-0.15	0.13	0.12	10.00	-709.42	1439.15	0.09	0.24
-2.20	-0.37	NA	0.61	NA	NA	NA	0.15	NA	-0.37	0.01	-0.07	-0.15	0.02	0.11	10.00	-710.13	1440.57	1.51	0.12
-2.20	-0.37	NA	0.60	-0.23	NA	NA	NA	NA	-0.38	0.20	-0.08	-0.15	0.14	0.11	10.00	-710.21	1440.74	1.68	0.11
-2.19	-0.38	NA	0.61	NA	NA	NA	NA	0.14	-0.38	0.01	-0.08	-0.14	0.14	0.00	10.00	-710.31	1440.95	1.89	0.10
-2.17	-0.39	NA	0.61	NA	NA	0.04	NA	NA	-0.38	0.01	-0.08	-0.18	0.14	0.12	10.00	-710.39	1441.09	2.03	0.09
-2.19	-0.38	-0.04	0.61	NA	NA	NA	NA	NA	-0.35	0.01	-0.08	-0.15	0.14	0.11	10.00	-710.39	1441.10	2.04	0.09

**Table S3.** Posterior credible intervals (Mean, 2.50% and 95.5%) of the values of the effects of all variables affecting the relative abundance estimated by Bayesian Royle-Nichols models by each focal species. Values of convergence considering sample size (n\_eff) and the MCMC chains convergence (Rhat) are indicated by each variable.

<i>Tapirus terrestris</i>					
	Mean	2.5%	97.5%	n_eff	Rhat
Intercept	-0.95	-1.57	-0.34	4485.36	1.00
Habitat loss	-0.71	-1.31	-0.25	7485.60	1.00
Floodplain extension	-0.06	-0.29	0.14	8094.92	1.00
Stream length	-0.03	-0.24	0.19	5680.02	1.00
City hunting pressure	-0.31	-0.61	-0.01	7450.49	1.00
Community hunting pressure	-0.29	-0.57	-0.03	8428.42	1.00
Protected area distance	-0.74	-1.17	-0.17	4512.67	1.00
Random [1 Comunidade]	0.76	0.44	1.14	1079.72	1.00
<i>Panthera onca</i>					
	Mean	2.5%	97.5%	n_eff	Rhat
Intercept	-0.20	-2.01	1.76	1581.50	1.01
Habitat loss	-0.33	-0.93	0.12	7684.50	1.00
Floodplain extension	0.02	-0.35	0.32	9522.65	1.00
Stream length	-0.60	-1.04	-0.21	8918.52	1.00
City hunting pressure	0.01	-0.44	0.46	10194.30	1.00
Community hunting pressure	0.08	-0.30	0.47	8816.49	1.00
Protected area distance	0.00	-0.39	0.41	9829.34	1.00
Random [1 Comunidade]	0.55	0.09	1.27	165.83	1.02
<i>Puma concolor</i>					
	Mean	2.5%	97.5%	n_eff	Rhat
Intercept	-0.12	-1.55	1.73	2224.36	1.00
Habitat loss	-0.19	-0.64	0.16	4425.06	1.00
Floodplain extension	0.15	-0.12	0.38	4635.07	1.00
Stream length	-0.03	-0.35	0.27	5979.41	1.00
City hunting pressure	-0.23	-0.58	0.10	5684.75	1.00
Community hunting pressure	0.32	-0.78	1.15	2170.87	1.00
Protected area distance	0.00	-0.35	0.33	4763.25	1.00
Random [1 Comunidade]	0.50	0.06	1.16	95.88	1.03
<i>Tayassu pecari</i>					
	Mean	2.5%	97.5%	n_eff	Rhat
Intercept	-2.39	-4.66	-0.39	858.91	1.01
Habitat loss	0.23	-0.23	0.65	6788.01	1.00
Floodplain extension	-0.98	-2.37	-0.05	6465.97	1.00
Stream length	0.02	-0.43	0.47	9057.88	1.00
City hunting pressure	0.02	-1.28	1.20	4292.53	1.00
Community hunting pressure	-0.61	-1.32	0.06	5067.30	1.00
Protected area distance	0.34	-0.58	1.31	6086.20	1.00
Random [1 Comunidade]	2.00	1.04	3.37	566.81	1.01

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***Myrmecophaga tridactyla***

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	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	0.14	-0.62	1.07	3037.15	1.00
Habitat loss	-0.12	-0.38	0.10	4361.59	1.00
Floodplain extension	-0.04	-0.26	0.15	3994.54	1.00
Stream length	-0.11	-0.31	0.08	4141.33	1.00
City hunting pressure	0.69	-0.25	1.27	2008.13	1.00
Community hunting pressure	-0.12	-0.36	0.11	3215.39	1.00
Protected area distance	0.50	-0.21	0.96	1877.61	1.00
Random [1 Comunidade]	0.59	0.20	0.96	244.01	1.00

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***Priodontes maximus***

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	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.24	-1.20	0.90	5996.01	1.00
Habitat loss	-0.06	-0.30	0.17	14432.63	1.00
Floodplain extension	-0.07	-0.35	0.18	13534.30	1.00
Stream length	0.21	-0.03	0.45	15692.55	1.00
City hunting pressure	0.06	-0.27	0.40	10168.44	1.00
Community hunting pressure	-0.09	-0.37	0.19	12747.67	1.00
Protected area distance	0.57	-0.17	1.12	5364.43	1.00
Random [1 Comunidade]	0.77	0.30	1.23	516.28	1.01

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***Mazama americana***

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	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.01	-0.25	0.25	9602.74	1.00
Habitat loss	-0.28	-0.47	-0.10	10974.26	1.00
Floodplain extension	0.04	-0.09	0.15	16158.12	1.00
Stream length	-0.08	-0.20	0.03	19243.99	1.00
City hunting pressure	-0.09	-0.25	0.08	10401.90	1.00
Community hunting pressure	-0.11	-0.26	0.03	12469.06	1.00
Protected area distance	0.00	-0.15	0.16	12321.21	1.00
Random [1 Comunidade]	0.44	0.25	0.63	1345.89	1.01

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***Pecari tajacu***

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	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	0.14	-0.30	0.72	7026.55	1.00
Habitat loss	-0.14	-0.31	0.01	34362.64	1.00
Floodplain extension	-0.25	-0.43	-0.09	29229.58	1.00
Stream length	-0.70	-1.25	-0.28	7403.65	1.00
City hunting pressure	-0.26	-0.44	-0.09	12853.09	1.00
Community hunting pressure	-0.15	-0.31	0.00	20563.78	1.00
Protected area distance	0.01	-0.17	0.18	16770.67	1.00
Random [1 Comunidade]	0.57	0.38	0.77	3336.09	1.00

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***Mazama nemorivaga***

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	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.14	-0.47	0.22	7111.38	1.00

Habitat loss	-0.46	-0.74	-0.22	13554.76	1.00
Floodplain extension	-0.42	-0.64	-0.23	13302.99	1.00
Stream length	-0.26	-0.39	-0.13	15638.06	1.00
City hunting pressure	-0.54	-0.89	-0.20	7013.44	1.00
Community hunting pressure	-0.06	-0.20	0.08	9503.65	1.00
Protected area distance	-0.23	-0.54	0.06	8413.42	1.00
Random [1 Comunidade]	0.30	0.07	0.52	334.44	1.02
<b><i>Cuniculus paca</i></b>					
	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	0.07	-0.14	0.29	12415.54	1.00
Habitat loss	-0.01	-0.12	0.09	21818.52	1.00
Floodplain extension	0.21	-0.11	0.52	10591.13	1.00
Stream length	0.22	0.11	0.32	22554.27	1.00
City hunting pressure	-0.06	-0.22	0.10	13432.93	1.00
Community hunting pressure	-0.01	-0.14	0.14	15521.04	1.00
Protected area distance	0.03	-0.12	0.19	15284.55	1.00
Random [1 Comunidade]	0.54	0.39	0.71	3990.01	1.00
<b><i>Nonspecific cingulata small</i></b>					
	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.11	-0.35	0.15	8658.67	1.00
Habitat loss	0.27	0.01	0.57	8795.82	1.00
Floodplain extension	-0.22	-0.38	-0.08	19436.53	1.00
Stream length	-0.06	-0.17	0.05	19678.48	1.00
City hunting pressure	-0.06	-0.22	0.10	9925.75	1.00
Community hunting pressure	-0.02	-0.16	0.13	12929.67	1.00
Protected area distance	-0.04	-0.20	0.11	10289.36	1.00
Random [1 Comunidade]	0.55	0.40	0.73	3788.19	1.00
<b><i>Nasua nasua</i></b>					
	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.35	-1.34	0.82	6149.55	1.00
Habitat loss	0.13	-0.05	0.30	14056.66	1.00
Floodplain extension	-0.30	-0.69	0.03	15211.71	1.00
Stream length	0.08	-0.13	0.30	14182.38	1.00
City hunting pressure	0.08	-0.90	1.15	5045.11	1.00
Community hunting pressure	-0.04	-0.30	0.22	13284.12	1.00
Protected area distance	-0.13	-0.44	0.18	12101.09	1.00
Random [1 Comunidade]	0.82	0.52	1.21	1549.37	1.00
<b><i>Dasyprocta spp.</i></b>					
	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	0.56	0.41	0.72	13449.70	1.00
Habitat loss	0.03	-0.11	0.18	19915.16	1.00
Floodplain extension	-0.15	-0.26	-0.06	31381.57	1.00
Stream length	0.00	-0.08	0.08	33881.30	1.00

City hunting pressure	-0.10	-0.23	0.02	12859.19	1.00
Community hunting pressure	-0.03	-0.13	0.07	18830.94	1.00
Protected area distance	0.11	-0.01	0.23	13186.72	1.00
Random [1 Comunidade]	0.43	0.31	0.56	5077.28	1.00

***Hadroskiurus spadiceus***

	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-1.22	-1.66	-0.77	7104.61	1.00
Habitat loss	-0.10	-0.37	0.14	19038.29	1.00
Floodplain extension	0.04	-0.16	0.22	18548.53	1.00
Stream length	-0.01	-0.23	0.20	20506.42	1.00
City hunting pressure	-0.45	-0.76	-0.14	10017.54	1.00
Community hunting pressure	-0.15	-0.41	0.13	14558.48	1.00
Protected area distance	-0.08	-0.61	0.40	9914.70	1.00
Random [1 Comunidade]	0.81	0.48	1.19	1770.00	1.00

***Mitu or Crax spp.***

	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.81	-1.31	-0.27	9673.14	1.00
Habitat loss	-0.21	-0.44	-0.01	21059.16	1.00
Floodplain extension	0.14	0.00	0.28	13379.46	1.00
Stream length	-0.18	-0.35	0.00	14594.39	1.00
City hunting pressure	-0.63	-0.96	-0.33	8024.67	1.00
Community hunting pressure	-0.25	-0.51	0.00	6782.01	1.00
Protected area distance	-0.35	-0.63	-0.09	10732.45	1.00
Random [1 Comunidade]	1.08	0.77	1.47	2840.53	1.00

***Penelope jacquacu***

	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-1.11	-1.68	-0.42	8915.01	1.00
Habitat loss	-0.34	-0.73	-0.01	14998.97	1.00
Floodplain extension	-0.06	-0.35	0.18	19482.03	1.00
Stream length	-0.14	-0.37	0.10	20797.49	1.00
City hunting pressure	-0.12	-0.46	0.21	13146.78	1.00
Community hunting pressure	0.03	-0.26	0.33	18999.93	1.00
Protected area distance	-0.02	-0.35	0.31	13896.19	1.00
Random [1 Comunidade]	0.71	0.30	1.15	978.81	1.00

***Psophia spp.***

	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.67	-0.94	-0.40	9518.05	1.00
Habitat loss	-0.58	-0.85	-0.34	28116.80	1.00
Floodplain extension	-0.25	-0.46	-0.06	24017.92	1.00
Stream length	-0.06	-0.18	0.07	27151.68	1.00
City hunting pressure	-0.12	-0.33	0.09	8912.44	1.00
Community hunting pressure	-0.16	-0.33	0.01	14483.76	1.00
Protected area distance	0.12	-0.08	0.33	10531.50	1.00

Random [1 Comunidade]	0.80	0.60	1.05	4413.42	1.00
<b><i>Tinamus spp.</i></b>					
	<b>Mean</b>	<b>2.5%</b>	<b>97.5%</b>	<b>n_eff</b>	<b>Rhat</b>
Intercept	-0.42	-0.81	0.01	1186.18	1.00
Habitat loss	-0.40	-0.67	-0.16	2934.34	1.00
Floodplain extension	-0.01	-0.17	0.15	2035.16	1.00
Stream length	0.15	-0.02	0.31	1261.68	1.00
City hunting pressure	-0.07	-0.26	0.13	1889.80	1.00
Community hunting pressure	-0.16	-0.36	0.04	1542.43	1.00
Protected area distance	0.12	-0.08	0.33	2559.94	1.00
Random [1 Comunidade]	0.25	0.03	0.61	52.82	1.07