# Terrestrial herbivorous mammals in a mosaic of Cerrado, Atlantic Forest and land-use changes

Cyntia Cavalcante Santos

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# Terrestrial herbivorous mammals in a mosaic of Cerrado, Atlantic Forest and land-use changes

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Dr. Pierre-Cyril Renaud

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Ao primeiro olhar, nada mais é que solidão,
Terra infértil, seca, perdida no meio do nada.
Ao segundo, no entanto: que terra abençoada!
Quanta riqueza é gerada pelo seu queimado chão!

Amarelo do ipê, do capim dourado,
E do sol a brilhar por toda parte.
E vem da cigana o tom avermelhado
Que colore as araras com tamanha arte.

Desse sagrado encontro da natureza
Surge o alaranjado do entardecer;
Deixa para traz mais um dia dessa beleza
Reafirmando a maravilha de viver.

Somente com um olhar mais atento, mais profundo
Percebe-se a magia de todas essas cores
O cerrado, com o fogo, supera suas dores
Renasce, outra vez, para a sobrevivência desse nosso mundo.

*“As cores do fogo da vida” – Aline Bassoli*

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# PRESENTATION AND THESIS STRUCTURE

The native vegetation of the Cerrado and Atlantic forest tropical forest ecosystem hotspots in Brazil have been suffered their most intense deforestation rates and experienced their most rapid land-use changes in the last five decades. Major impacts have been recorded, such as loss and fragmentation of habitats, loss of biodiversity and invasion of exotic species, soil erosion, water contamination and to changes in burning regimens, which have consequences for the carbon cycle and possible climatic changes at the regional level (Klink & Machado 2005, Gardner et al. 2009, Rocha et al. 2011).

The Bodoquena Plateau region, in the Paraguay River Basin (BAP, in Portuguese) (Figure 1), in Mato Grosso do Sul state, southern Brzil, is part of this transformation, and has been the site of government incentives to increase regional development, most notably over the last decade (MMA-PPCerrado 2015, Rocha et al. 2011, Imasul-ZEE 2015, Roque et al. 2016). Agricultural monocultures (*e.g.* soy and maize) and cattle production have been gradually replacing the native vegetation and changing local landscape dynamics. This fact deserves attention given that such landscape changes may lead biodiversity loss at different scales (Alves et al. 2012, Barreto et al. 2012, Phalan et al. 2013, Grecchi et al. 2014, Brum et al. 2016, Arvor et al. 2017).

This region is a natural system housing a highly diverse flora and fauna. Native regional vegetation is dominated by Cerrado, interspersed with remnants of Atlantic Forest and a small portion of Pantanal vegetation. There are also species adapted to highly-specialized habitats, such as submerged aquatic plants in crystal clear waters, lithophylic species often endemic to rock outcrops (especially bromeliads and cacti), species adapted to shallow soil, and to moist forests and dry forests (Scremin-Dias et al.

2009, Pott et al. 2014, Scremin-Dias et al. 2016). There fauna has been inventoried for fish (Froehlich 1999, Severo-Neto et al. 2018), amphibians (Uetanabaro et al. 2007, Souza et al. 2017), insects (Koroiva et al. 2017), birds (Pivatto et al. 2006), and mammals (Cáceres et al. 2007, Lopes et al. 2015, Tomas et al. 2017).

Among the terrestrial mammals present on this plateau, the herbivores, which differ in body size and eating habits, likely perceive and response to landscape changes in different ways (Manning et al. 2004, Metzger 2006, Boscolo & Metzger 2009, Hansbauer et al. 2009, Lyra-Jorge et al. 2009, Villard & Metzger 2014, Moreira et al. 2015). Herbivorous mammals are a key functional group with which to investigate the how of land-use changes cause biodiversity decline, because the species are directly influenced by landscape composition and configuration, and they themselves are regulators of landscape environments as a result of their biological, functional and ecological characteristics (Fritz et al. 2002, Durant et al. 2003, Bueno et al. 2013, Foster et al. 2014). Ripple et al. (2015) states that the roles of large herbivores cannot be adopted by or compensated for by smaller herbivores, because large herbivores not only directly and indirectly affect other animal species across the entire food chain, including their predators and small herbivores, but also modify abiotic processes involving nutrient cycles, soil properties, fire regimes, and primary production. At the same time, the large herbivores are under intense pressure from the threat of hunting, defaunation, competition with livestock, and such land-use changes as habitat loss, human encroachment, agricultural and forestry cultivation and deforestation (Huntly 1991, Ripple et al. 2015, Berzaghi et al. 2018).

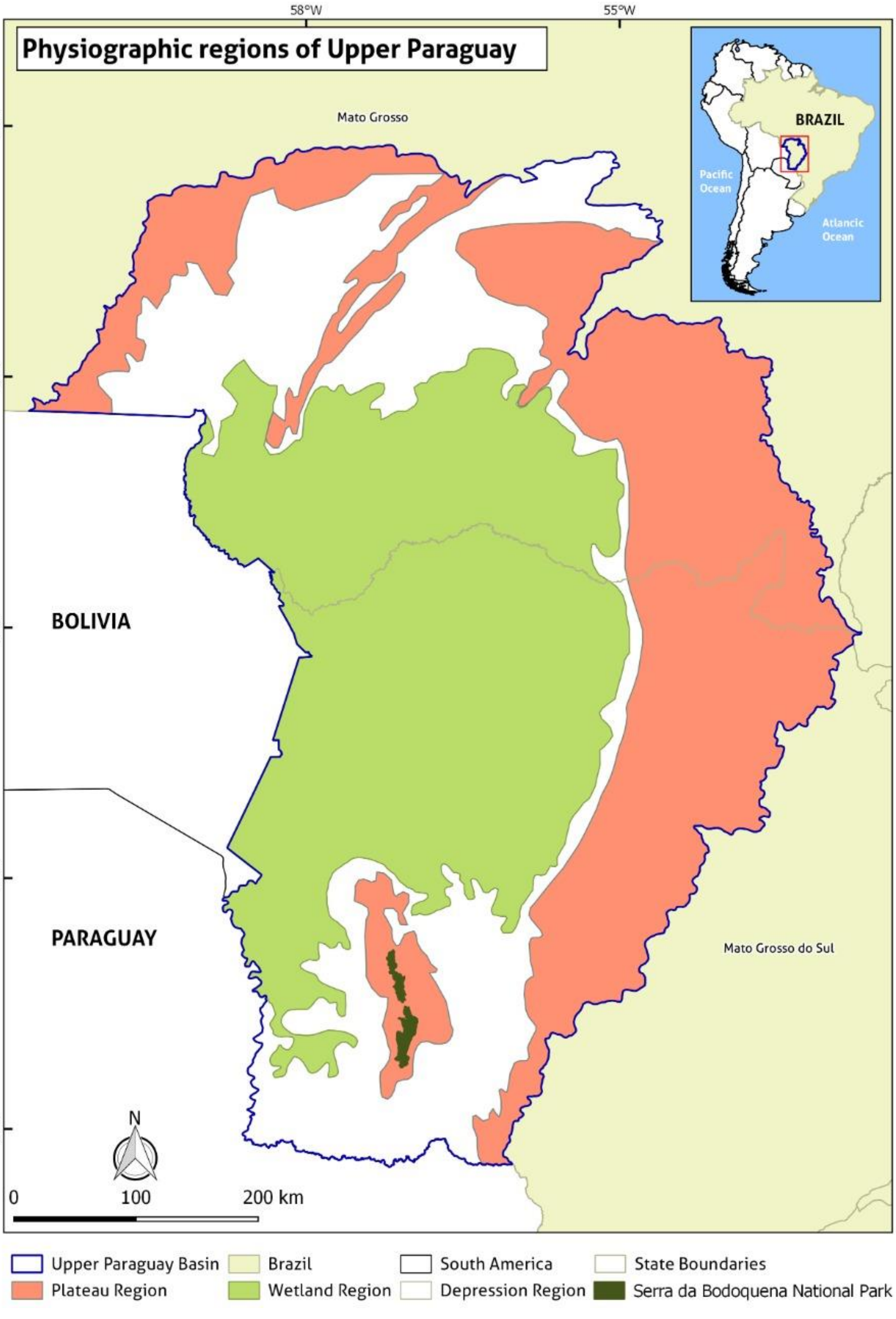

**Figure 1.** Map of the Physiographic regions of Upper Paraguay River (BAP) showing the relief macroforms surrounding plateau and the Pantanal plain (wetland region) and showing the Serra da Bodoquena National Park insert in Bodoquena Plateu range study area.

To understand the distribution of terrestrial herbivorous mammals across land-use change gradients on the Bodoquena Plateau, a region characterized by a mosaic of Atlantic Forest and Cerrado, I collected data on the small, medium and large herbivore mammal assemblage using camera traps and live traps along a gradient of native vegetation loss on the Bodoquena Plateau, Mato Grosso do Sul state, southern Brazil, between February 2016 and December 2017.

In my *first chapter*, I present a review of articles published in the last 16 years (2002 - 2018) involving responses by the Brazilian Cerrado non-volant mammal community to land-use change. Included species were analyzed for their functional characteristics and responses to different land-uses changes. The results showed that the species negative responses were mainly associated with agriculture, livestock, roads and urban areas. Additionally, large knowledge gaps were revealed so that, for example, more than half of the Brazilian states with Cerrado as a dominant native vegetation type do not have published studies about species responses.

In the *second chapter*, I analyze data on herbivorous mammals of Cerrado and Atlantic forest vegetational natural ecosystems, testing how three landscape metrics (percentage of forest cover, patch density and edge density) affect the occurrence of four herbivore species (*Dasyprocta azarae*, *Pecari tajacu, Mazama gouazoubira* and *Tapirus terrestris*). Multi-scale landscape structure analysis shows that metric variability is best explained at the 5,000 meters scale. Nevertheless, when species occurrences were analysed, results showed species-specific variation at the scale at which responses to different landscape metrics occurred. Therefore, based on landscape structure alone, I was not be able to establish a specific scale that could be applied for all species. Considering the species individually, for all metrics, a smaller 500 m scale spatial best explained the distribution of the smaller-sized mammalian herbivore, Azara's agouti. As expected, scale effects for the two larger generalist species (*Mazama gouazoubira* and *Tapirus terrestris*) were only demonstrated for percent forest cover at larger scales (> 750 m). Collared peccary (*Pecari tajacu*) was the only species not to demonstrate any scale of response to our selected metrics.

Finally, in the *third chapter*, using combined data from camera traps and live traps, I attempted to see how herbivorous mammal species occupy the Bodoquena Plateau landscape. I used sample units with a 5 km bufferextension, with transects and camera points separated by at least 1.5 km and 400 meters, respectively. I recorded 23 species that responded idiosyncratically to land-use changes. Six species responded to the percentage of forest cover in the landscape within 5,000 m. *Tayassu pecari*, *Mazama americana*, and *Mazama gouazoubira* responded negatively to forest loss, while *Sus scrofa* and *Hydrochoerus hydrochaeris* showed positive responses, preferring open areas. In terms of conservation and management, a major issue emerging from our findings and other recent studies is: how should we optimize community conservation where most species respond idiosyncratically to changes in land-use? In this chapter, are recommended different and complementary strategies for conserving herbivorous mammals on the Bodoquena Plateau.

I hope you enjoy reading this!

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# CHAPTER I

# GENERAL INTRODUCTION

## Effect of land-use change on terrestrial mammals of the Cerrado: large knowledge deficits in a biodiversity hotspot

Human activities have drastically changed the structure and function of landscapes worldwide (Foley et al. 2005). The conversion of native vegetation to cultivated and urban lands is the most prevalent driver of such changes (Brannstrom et al. 2007, Gibbs et al. 2009, Radda 2012, Laurance et al., 2014). Nevertheless, human-dominated areas are important for food security and economic development, leading to the creation of very complex landscapes dynamics. Currently, human-modified landscapes cover a big extension of the world's terrestrial area (Ramankutty et al. 2008) and constitute critical assets for fulfilling human percieved needs while maintaining functional ecosystems and biodiversity (Brooks et al. 2002).

Biodiversity has a certain resilience to landscape modifications. Recent studies have demonstrated that biodiversity decline does not necessarily follow a linear trend along a gradient of habitat loss (Andrén 1994, Fahrig, 2002, Pardini et al. 2010, Roque et al. 2018). Most surveyed species, taxa or communities tend to be resistand at the early stages of natural vegetation modification and will collapse only after a vegetation modification threshold is reached (Radford et al. 2005, Hanski, 2011). Since the effect of fragmentation on landscape structure and configuration is insuffecient to effectively model the biodiversity response to anthropogenic activities, it is important to consider the matrix with its own ecological properties (Pardini et al. 2010). Such newly created landscapes will play an important role in animal mobility and survival according to matrix permeability in areas connecting natural vegetation patches (Kupfer at al. 2006). Because of this interplay between fragmentation and connectivity processes, it is expected that specific animal ecological and biological traits will play a critical role in explaining resilience (Estavillo et al. 2013, Magioli et al. 2016). Indeed, large body mass can improve an animal's capacity to move through a fragmented landscape. Specialized diets requirements can narrow species flexibility if landscape change implies destruction of a specific habitat type and resource (With & Crist 1995). Therefore, a clear understanding on how biological and ecological traits structure animal communities is essential effects of land-use change on biodiversity are to be predicted with the accuracy required for effective management planning.

Terrestrial mammals form a key community for an ecosystem (Turkington, 2009). Carnivores act as top-down regulators, while herbivores are involved in both bottom-up and top-down processes (Estes et al. 2011). Both are influenced by human activities (Gandiwa 2013). Consequently, terrestrial mammals can be expected to show sensitivity to landscape changes.

Neotropical savanna (called "*Cerrado*" in Brazil) harbors a unique and endangered diversity of terrestrial mammals. It is also a threatened landscape under severe agricultural strain (Hoekstra et al., 2005, Rada 2013, MMA PPCerrado 2015, Strassburg et al. 2017). Deforestation rates in Cerrado tend to be higher than in Amazonian forest and recent paper stated that "*Cerrado is the most threatened biome in Brazil*" (Tollesfson, 2018). Despite this, the Cerrado biome remains poorly covered by protected areas when compared to Amazonian forest (Klink & Machado 2005). Furthermore, privately owned land covers most of the biome, so that nearly 53% of remaining native vegetation occurs on private lands (Soares-Filho et al. 2014) and, even if private conservation initiative arises, conflict between stakeholders can profoundly compromise conservation policies that might otherwise successfully mitigate of land-use change impacts on biodiversity. In a recent paper, Vieira et al. (2018) stated that, even if the existing Brazilian forest code is respected, this will not be sufficient to protect biodiversity in Brazil. In this context, conservation strategies urgently need scientific knowledge to guide public policies. Although mammals are the most studied animal group in terms of taxonomy and ecology around the world (Di Marco et al. 2017), for Brazilian Cerrado, information concerning species responses to land-use changes are scarce and fragmented (Marinho-Filho et al. 2002, Bonvicino et al. 2008, Paglia et al. 2012). This knowledge gap needs to be filled in order to tackle conservation issues in Cerrado ecosystems effectively.

Considering that monitoring biases and trends in conservation literature on Cerrado mammals is crucial to track knowledge progress, and to inform conservation strategies, in this chapter, we conducted a literature review, including published and gray literature, to assess the knowledge of mammal responses to land-use changes the Brazilian Cerrado.

## Methods

### *Study region*

The Brazilian Cerrado is a complex vegetation mosaic with varying canopy cover, with more than 2 million km$^2$ in extent, it is the largest open vegetation biome in South America, and one of the largest savanna-forest complexes in the world (Bonvicino et al.2005, Reynolds et al.2016). Its total area occupies 24% of Brazilian national territory, and occurs in 12 states (Borlaug 2002, MMA 2015). The biome it is also important hydrographically as it houses the headwaters of the three largest river basins in South

America (Tocantins, São Francisco and Prata) (MMA 2015). With 5 % of all the planet's biodiversity, is considered the most diverse tropical savanna in the world (Colli et al. 2002, Ratter et al. 2003, Aguiar et al. 2004, MMA PPCerrado 2015). In contrast, it is also considered one of the last major agricultural frontiers of the Earth (Borlaug 2002) (Figure 2).

The Brazilian Cerrado is a center of economic recently developed interest, where mean national production shares are greatest for cotton (48.8%), oranges (41.7%), soybeans (39.6%), cattle (37.0%), and sugar (32.0%) (Rada 2013). As a result, the Cerrado is becoming the target of an extensive and rapid removal of native vegetation cover process, mainly encouraged by agribusiness, the varying sectors of which have been in operation for the last 30 years (PPE-Cerrado 2015, Rada 2013). As a consequence of this increase in land-cover dedicated to agribusiness, many endemic species to South America and Brazil, present in the Cerrado (Mendonça et al. 1998), are suffering extreme population reduction and fragmentation (Strassburg et al. 2017). Additionally, negative impacts on the water cycle are already visible (Spera et al. 2016). This authors explain that one way in which these operate is via decrease in the annual amount of water recycled into the atmosphere by evapotranspiration, since satellite mapping of cultivated area from 2003 to 2013 shows that the cultivated area more than doubled from 1.2 to 2.5 million ha, with 74% of new lands of the Cerrado (Spera et al. 2016). The proportion of original native vegetation cover lost varies between the 12 States that are part of this ecosystem, with some states having lost more than 90% of the original area (e.g. Goiás, Minas Gerais and Mato Grosso do Sul), while others retain more than 83% of the original cover but have habitat loss in progresses (Mato Grosso, Maranhão, Tocantins, Bahia and Piauí) (MMA 2014). Legal measures to combat native habitat loss are the responsabillty of the Brazilian federal government, and include the creation of the Action Plan for Prevention and Control of Deforestation and Burnings in the Cerrado (MMA-PPCerrado 2015, Decreto n° 7.390/2010), establishing as one of the targets, a reduction, by 2020, of 40% in annual native vegetation loss rates in the Cerrado in relation to the average rates between 1999 and 2008 (MMA-PPCerrado 2015).

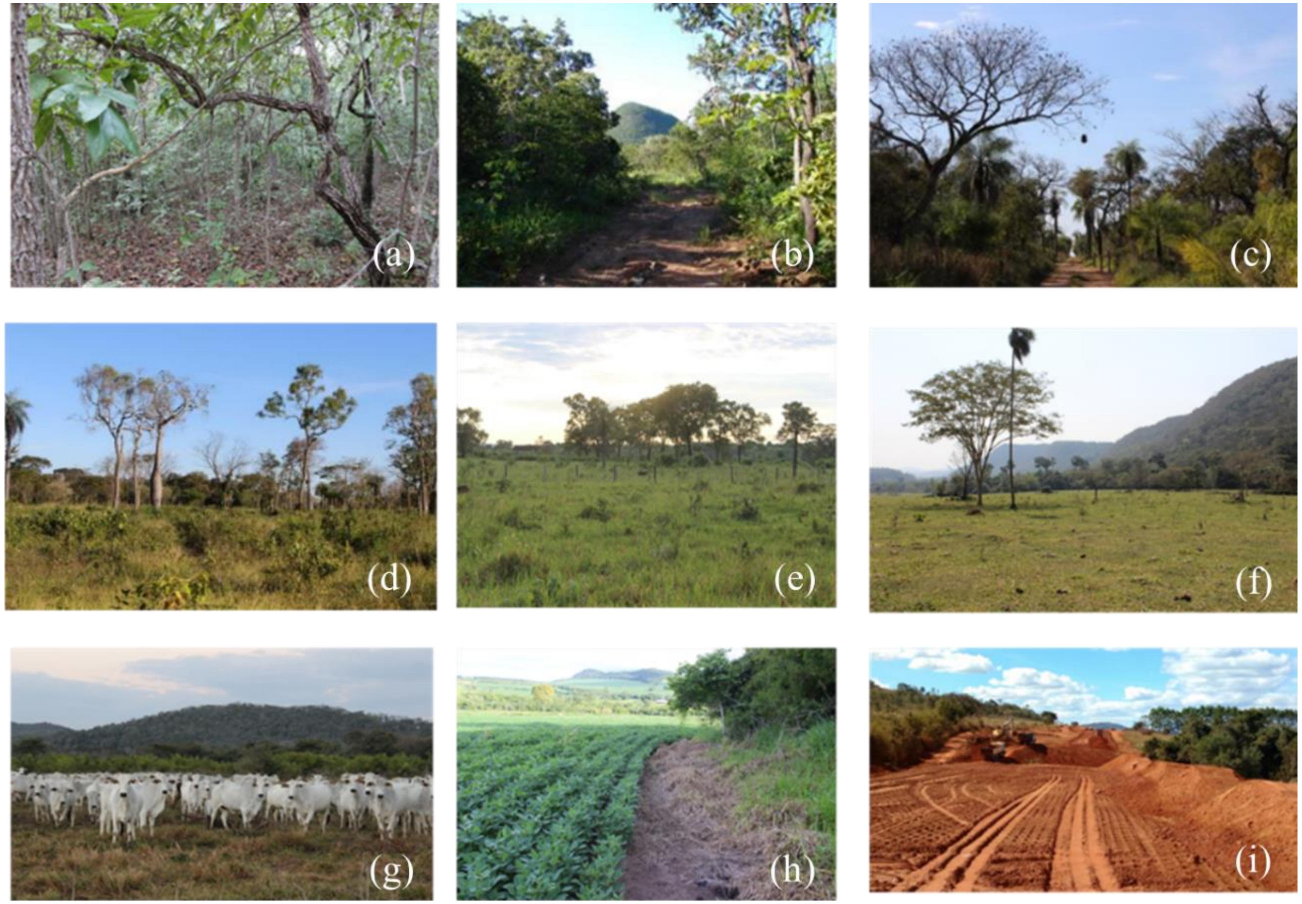

**Figure 2.** Some characteristic vegetation formations and anthropogenic transformations within an area of the Cerrado Biome, showing the great variation of habitats within the landscape. Legend: (a) Cerrado area; (b) nature trail through semi-deciduous forest; (c) farm access road through riparian forest; (d) 'campo sujo' and semi-deciduous seasonal forest; (e) and (f) exotic pasture area (*Brachiaria* sp); (g) livestock; (h) agriculture (soy); (i) opening of new access road between the municipalities of Bonito and Jardim.

*Ecological characteristics of species and their responses to land-use change*

For the ecological and functional attributes of the species, we use the most updated lists on the different species of mammals in the Cerrado (body mass, activity cycle, diet, substrate use, behaviour or group size, geographic range and conservation status) (Bonvicino et al. 2008, Reis et al. 2006, Paglia et al. 2012, MMA 2014, IUCN 2017).

As the mammal community has great ecological variation, occupying a wide variety of niches and presenting a wide functional diversity, we extract as detailed data as possible, using specific literature information (Paglia et al. 2012), separating the community into feeding guilds from ‘carnivores’, ‘insectivores’, and ‘herbivores’. For the latter categories, which represents 82% of the mammal community, we consider herbivore species in two distinct groups: a) “only plants/specialists” - those that ingest only plants (‘preferably fruits’, ‘preferably leaves’, ‘preferably grains’, ‘mixed feed’ including fruits, leaves and or grains); b) “omnivores/generalists” - those who in addition to eating plant also use in their diet insects and other types of protein. For the carnivorous and insectivorous categories, we consider a single group called “meet eater/generalists”.

By convention, small mammals are represented mainly by species of the orders Rodentia and Didelphimorphia (Paglia et al. 2012), however, when we analysed the functional traits of the species and observed the average weight of the marsupials *Didelphis aurita*, *D. albiventris* and the rodent *Coendou spinosus*, we observed that they have a mean body mass between 1,200 and 1,900 Kg, and that five other species of the orders Carnivora (*Conepatus chinga*), Cingulata (*Tolypeutes tricinctus*, *T. matacus*, *Dasypus septemcinctus*) and Lagomorpha (*Sylvilagus brasiliensis*), on average, the same pattern. Thus, because of this variation, in this paper we consider for this community of terrestrial mammals of the Cerrado that small mammals are those species with up to 1,900 kg, medium mammals, animals weighing between 2,000 kg and 80 kg, and large weighing more animals than 81 kg.

To evaluate the literature on the mammal responses to different types of land-use change, we used the terms "[(fragment- * OR land) AND use AND mammal * AND Cerrado]" in Scopus (http: //www.scopus.com/), Web of Science (https://apps.webofknowledge.com/) and Scielo (http://www.scielo.br/). Additionally, we looked for articles in a Google Web Search (https://www.google.com) and ResearchGate (https://www.researchgate.net/), always using the same terms. We searched for papers pubkished between 2002 to 2018 (search conducted, 31/01/2018).

Based on land use information from this research, I classified the articles in three different groups: 1- Human Activities other than agriculture = IM (Iron mining) and RU (Road & Urban area); 2 – Agriculture, livestock and forestry = Agr (Agriculture only), Li (Livestock only), For (Forestry only), ALi (Agriculture & Livestock), AFor (Agriculture & Forestry), ALiFor (Agriculture, Livestock & Forestry); and 3 - Native habitats and connectivity = CF (Corridor & Fragments), in order to gain an understanding of mammalian responses in each case analyzed (for descriptions of types of land-use, see Tables 1a and 1b).

Articles were analyzed for the following information: year, area of study, habitat configuration, type of the land-use, geographical coordinates, community and species proxy, study duration (months), and taxonomic indentity, at the levels of family, genus and species. After reading the articles, the response of each species was classified as: negative, positive or neutral.

## Results

### *Mammalian responses*

The analysed papers included responses of 99 species of the 150 non-volant terrestrial mammals present in Cerrado (Table 2). I found 37 papers covering the topic of non-volant mammal responses to land-use changes in the Cerrado (Table 3). Most of these studies were conducted at community level, but 13 were at species level, *e.g.*, Maned Wolf (*Chrysocyon brachyurus*) (20 papers), Giant Anteater (*Myrmecophaga tridactyla*) (17 papers), Cougar (*Puma concolor*) (14 papers), Jaguar (*Panthera onca*) (8 papers), White-lipped Peccary (*Tayassu pecari*), and Bush Dog (*Speothos venaticus*). There were significantly more papers focussing = on carnivorous/insectivorous species (t= -3.1452, df = 21, p-value = 0.004886).

### *Herbivore community organization*

The multivariate analysis found dimensions 1 and 2 explained 42.44% of the total variance (Figure 3b). The third axis, alone, explained 17.79%, but when plotted with the first axis we found no significant changes to community structuration. The first dimension was positively correlated with mean body mass and negatively correlated with forest use. The second dimension was strongly correlated with use of open and forested areas. This axis is also largely due to the generalist (negative correlation)/specialist antagonism. Finally, the use of open or forested area contributed to both axes being positively correlation with dimension 1 and negatively correlate with dimension 2. Dimension 1 allow the clear differentiation of two families (*Suidae* and *Tapiridae*) from other taxa due to their high body mass. The family *Cervidae* was also part of the large-bodied Cerrado mammal group, but seperated out due to their preferential use of open areas (Figure 3a). The other 16 families were more discriminated by their diet than by use of natural habitat. Some families (*Caviidae, Cricetidae, Dasypodidae, Echimyidae*), overlapped substantially in diet. In terms of percentage of generalist or specialized species among herbivorous mammals, the first group represented 55% of the total community, while specialists represented 31%. However, when plotted species, were recorded a slight overlap between generalist and specialist species (Figure 3c), although, generalist species tended to have higher body masses, with the Cervid *Blastocerus dichotomus* being the only specialist species group to have a high bodymass. Specialist species also tend to use open areas. We found a clear segregation of species by use of natural habitat (Figure 3d).

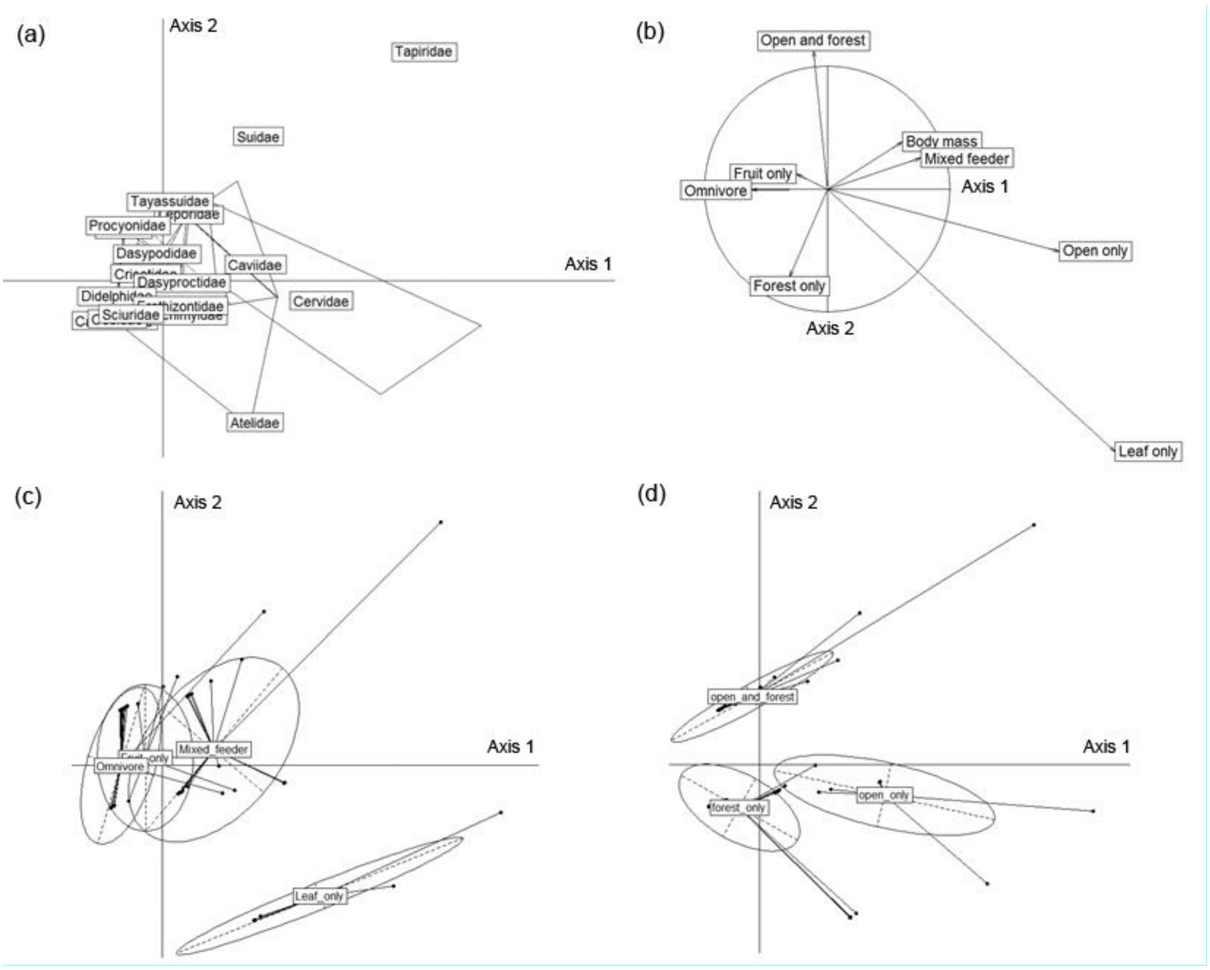

**Figure 3.** Multivariate analysis of functional traits for the herbivore community. In (a) distribution of families on the axes, in (b) relationship of species of mixed feeding habit and

body size, for two families (*Suidae* and *Tapiridae*), in (c) the food guilds of a well-defined mammalian herbivore community, in (d) evidence of presence of species inhabiting regions with or without forest by diet category.

### *Carnivore community organization*

The two first axes of the multivariate analysis (dimensions 1 and 2) explain 68.21% of the total variance (Figure 4a). Compared to the herbivore community, that of the carnivores seems more structured. The first dimension is positively correlated with the use of open areas and, to a lesser extent, by body mass (Figure 4b). The second dimension is positively correlated with species from open areas and negatively correlated to species with a preference for open/forest areasThe diet vectors are antagonistic for carnivores and insectivores participate either for Dimension 1 and 2 separately. Were see that dimension two separated off five of the seven carnivorous families (*Canidae, Dasypodidae, Mephitidae, Mustelidae* and *Procyonidae*). The use of natural habitat is, therefore, a strongly structuring variable. The family Felidae, whose carnivores have a larger body size, used mainly forest areas. When plotting species, we saw a clear structuring between insectivorous and carnivorous species. Insectivores are mainly structured by the dimension 2 and use open areas most extensively. Most carnivorous species use forested areas and have the greatest body masses.

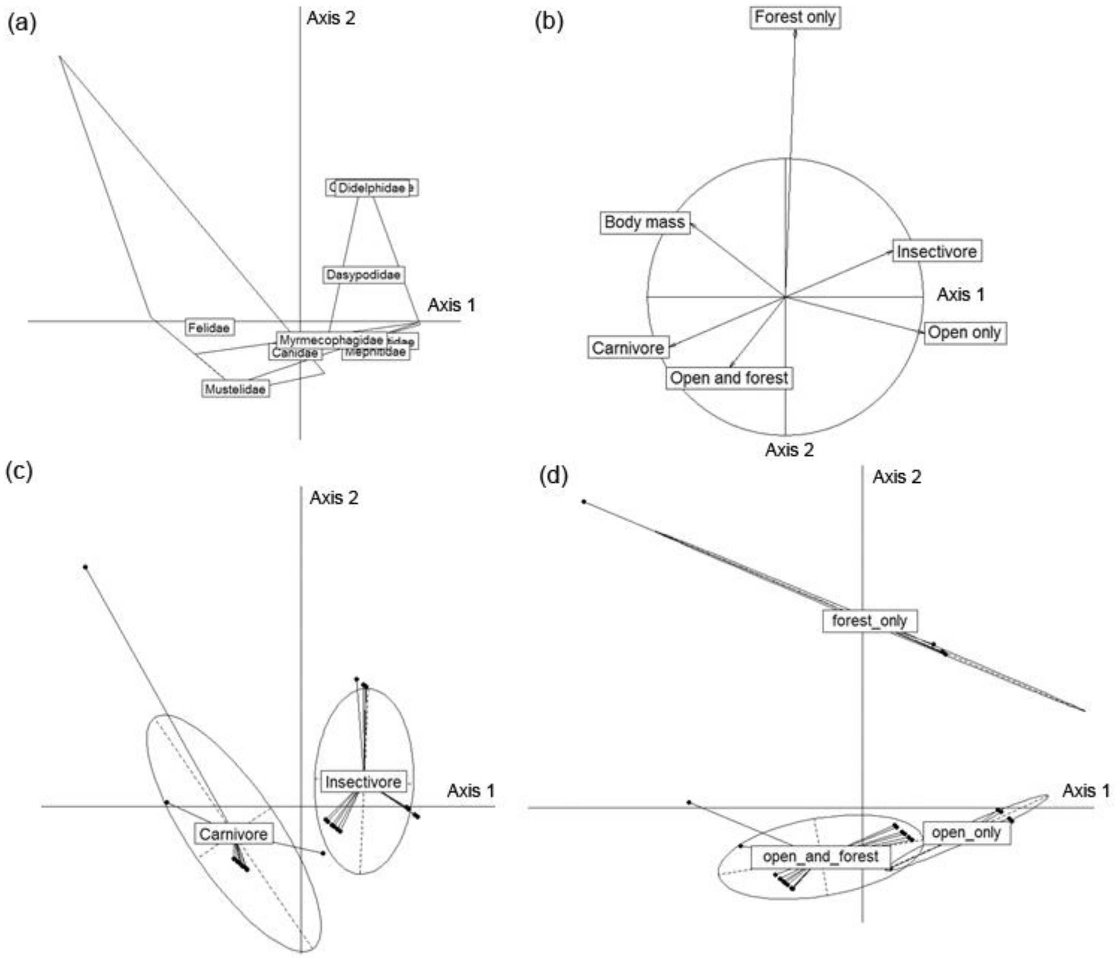

**Figure 4.** Multivariate analysis of functional traits in the carnivore community. In (a) the distribution of the families, in (b) the insectivores more associated with open areas, in (c) the food guilds of well-defined carnivores and insectivores, in (d) concentration of these species in open or intermediate areas.

Substantial variation in the scale of each study was observed, ranging from, *e.g.*, 900 ha to 400.000 ha, ranging from a single farm, via several municipalities, to the entire Cerrado domain. The extent of this variation resulted from the different objectives and methods applied in the various studies used, including the use of traps for capture and recapture, camera traps, collection of biological material for genetic analysis, and analysis of occurrence of species using satellite images.

The land-use categories with the highest number of articles were ‘Agriculture only’ (N=8), followed by ‘Agriculture and Livestock’ and ‘Road and Urban areas’ (N=7 each) (Table 4a). This did not allow us to compare the responses of the species found by land-use category, since the other categories all had only one or two articles. At the family level, 60% of the species showed a negative response to land-use changes, while for 17% the response was positive (185 and 53, respectively). Of the investigated species 56 % were herbivores, and 44% carnivores.

Two types of land-uses were always associated with negative impacts on mammals: ‘Roadkill & urban areas’ and ‘Agriculture only’. On the other hand, ~~the~~ ‘Corridor & Fragments’ had a neutral effect on the focal herbivore species, contrary to our expectation of a positive effect. Some types of land-use, such abandoned pastures, had a variable effect, as half of the studied species showed a positive response. Species responses to the ‘Forestry only’ land-use class showed similar variation, but it is important to note that, for this category, researchers mostly investigated responses by carnivores. Interestingly, carnivores and herbivores did not have the same response to ‘Agriculture & Livestock’ land-use change, while herbivores displayed a mostly negative trend, carnivores exhibited positive or neutral trends. This land-use change is the most studied in the Cerrado ecosystem. This opposing response was not found by studies investigating the impact of ‘Agriculture, Livestock & Forestry’ (the second most studied land-use change) as carnivores and herbivores both how mostly negative trends.

‘Iron-ore Mining’ and ‘Roadkill & Urban area’, which are land-uses with direct impacts, yielded negative responses for species from 20 families. We also observed that some species of these families seemed to be more sensitive to such changes, such as *Leopardus pardalis*, *Panthera onca*, *Dasypus novemcinctus*, *Euphractus sexcinctus*, *Cerdocyon thous*, *Chrysocyon brachyurus* and *Lycalopex vetulus*, where strong negative responses were observed (Table 4a).

For land-use types that involved activities classified under ‘Agriculture & Livestock’, the responses varied according to the specific activity (*e.g.* Lyra-Jorge et al. 2009, Barreto et al. 2012, Lessa et al. 2012, Jácomo et al. 2013, Hunke et al. 2015, Oliveira et al. 2017). In the case of ‘Agriculture only’, responses were negative for 19 families, but with greater expressiveness of negative responses for families *Felidae, Cricetidae, Canidae*, *Dasypodidae* and *Didelphidae*. The negative responses of species of the two small mammal families (*Cricetidae* and *Didelphidae*) suggest that these groups are sensitive to the loss of forested environments (Table 4b), except for some species of *Didelphidae* that do quite well in anthropic environments, under moderate disturbance.

In addition to landscape changes, the characteristics of each species seem to influence the response form associated with the type of matrix. For the larger-bodied species from the families *Felidae*, *Dasypodidae* and *Canidae*, responses depended on the regeneration vegetation stage in which the study had occurred. This was readily observed in areas of native forest or eucalypt and coffee plantations. These areas of forestry generally cover large tracts of land and are often associated with remnants of other vegetation types, providing species-friendly habitats for those forms with nocturnal habits, broad home ranges, and which can temporarily adapt to the management and dynamics of human activities.

Neutral responses in the 'Agriculture & Livestock' areas appeared to be more associated with generalist small mammal species such members of the *Didelphidae* and *Cricetidae*, as well as armadillos (*Dasypodidae*) and the Giant anteaters (*Myrmecophagidae*), this both last which preferentially use more open landscapes or edges of fragments. Species that showed negative responses to land use changes, included: carnivores (*Chrysocyon brachyurus, Leopardus pardalis, Leopardus tigrinus,* *Leopardus wiedii, Procyon cancrivorus, Panthera onca, Puma concolor, Puma yagouaroundi* and *Speothos venaticus,*), herbivores (*Cavia aperea, Calomys callosus, Cuniculus paca, Hydrochoerus hydrochaeris, Mazama gouazoubira* and *Mazama* sp., *Oligoryzomys nigripes, Pecari tajacu, Sylvilagus brasiliensis, Tapirus terrestris*), the omnivores (*Akodon montensis, Callithrix penicillata, Cerdocyon thous, Dasypus novemcinctus, Didelphis albiventris, Eira barbara, Euphractus sexcinctus, Nasua nasua,*), and one insectivore (*Myrmecophaga tridactyla*).

## Discussion

In both African and Australian savannas, mammals have been the target group of many studies of how land-use affects biodiversity (Schuette et al. 2012, Okullo et al. 2013, Wilkerson et al. 2013, Radford et al. 2014, Wigley et al. 2014). However, in South America, most mammalian studies have occurred in forested ecosystems, such as the Amazonian and Atlantic Forest (*e.g.* Jorge et al. 2013, Cruz et al. 2014, Galetti et al. 2015, Dias & Bocchiglieri 2016, Bogoni et al. 2016). My review, focused on the Cerrado hotspot, shows an increasing number of papers concerning land-use effects on mammals in the last decade. However, I also found that pronounced knowledge gaps, especially for small mammals, remain.

The low number of papers on the response of mammals to land-use changes in the Cerrado causes concern because it is a group that plays a variety of important roles in both material and non-material ecological services (Reider et al. 2013, Young et al. 2013, Song et al. 2014, Cadotte et al. 2015, González-Maya et al. 2017). Moreover, the Cerrado is one of the most threatened tropical ecosystems (Klink & Machado 2005, Strassburg et al. 2017). The results showed that 60% of all non-volant Cerrado mammal species were reported to have negative responses to land-use changes, mainly related to agriculture, livestock and mining activities (Table 4b). Small mammals (*Didelphidae* and *Cricetidae*), some species of which depend on forested environments (Dalmagro & Vieira 2005, Cáceres et al. 2010, Hannibal & Neves-Godoi 2015); herbivores (*Cervidae*) with specialized diets, mainly herbs and shrubby plants (*e.g.* Richard & Juliá et al. 2001, Tomas & Salis 2000); and predators (*e.g. Felidae*) (Lyra-Jorge et al. 2008), were the groups where species showed the greatest number of negative responses to such activities (Table 4a and 4b).

I found that the responses of some species to 'Forestry only' activities and 'Agriculture & Livestock' were in some cases neutral and positive. It is possible that some mammal species that live in these areas are habitat generalists. Moreover, the occurrence of the mammals in such systems can be attributed to the enchanced availability of resources, such as insects, snails or worms and also fruits, leaves, fibers, flowers, roots, bark, shoots, stalks, twigs, minerals, fungi, and small vertebrates (*e.g.* Bachand et al. 2009, Fernandes et al. 2013), as well as matrix items, such as maize and soybean (Bradham et al. 2019), which may attract such herbivorous native species as *Dasyprocta azarae*, *Mazama gouazoubira*, *Pecari tajacu*, *Tapirus terrestris* and *Tayassu pecari*. In these cases, the landscape composition and arrangement, as it occurs in Cerrado regions, where there is t great spatial variability in vegetation (29 categories of native plant cover: Probio 2002), may favor the dispersion of certain species that prefer heterogeneous landscapes (Redon et al. 2014).

In the process of extracting the data, one of the difficulties I found was to separate the effects of fragmentation and habitat extent. This is a problem already discussed in the landscape ecology literature (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019), but recently Melo et al. (2017) presented data consistent with the hypothesis that habitat extent can be used to predict small mammal species richness in the Cerrado. Through it remains to be seen if this is the case for other groups.

In the Cerrado, exotic species have been shown to share spaces with the native species (Paolino et al. 2016). One of the most relevant cases is the contact between *Tayassu pecari* and *Pecari tajacu*, with the feral pig *Sus scrofa* (Trovati & Munerato 2013), but their interactions are still poorly understood in these areas, compared to other areas such as Pantanal, mainly because feral pigs are typically generalists and effective foragers (Oliver & Brisbin 1993, Galetti et al. 2015).

Improving the inclusion of information concerning Cerrado biodiversity in regional planning is at the heart of conservation and sustainability strategies. Part of this challenge is related to overcoming knowledge shortfalls, including those for species taxonomy (Linnean), distribution (Wallacean), abundance (Prestonian), evolutionary patterns (Darwinian), abiotic tolerances of species (Hutchinsonian), species traits (Raunkiæran) and biotic interactions (Eltonian) (Hortal et al. 2015). As shown, the Hutchinsonian shortfall in terms of tolerances and responses to land-use changes is applied for mammals in the Cerrado. I also found a strong geographical, taxonomical and environmental system bias in studies involving Cerrado mammals. Although the Cerrado is present in 12 Brazilian states, most studies came from just three states, São Paulo, Goiás (9 each), and Minas Gerais (8). The variability in focus, taxonomic groups and methods does not allow the application of any formal meta-analysis thus complicating knowledge synthesis. Despite the increasing number of investigations in recent decades, studies on the responses of mammals to habitat change are still poorly connected with conservation science and conservation priorities. As outlined by Di Marco et al. (2017), overcoming this challenge may require improving the integration of conservation agendas and biodiversity studies, but more importantly, these agendas should be clearly connected with real world demands in terms of landscape planning and species management.

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**Table 1a**. Types of land-use found in the 37 papers between 2002 and 2018 and following the classification of land-use changes in Cerrado Domain used here.

| **Category** | **Land Cover Class** | **Land Cover Description in papers** |
|---|---|---|
| Native habitats and connectivity | Corridors and Fragments | Linked fragments that facilitate species gene flow<br>Areas of native vegetation present in the Cerrado. Heterogeneous environments with diversity of plant species. |
| Agriculture and livestock | Agriculture only. | Crops under annual rotation ~~system~~. May include soybean, corn, sugarcane or sorghum. Permanent crops not under a rotation system that provide repeated harvests and occupy the land for an entended period before being ploughed up and replanted. Row Crops. |
| | Livestock | Areas of pasture planted with African grasses (*Brachiaria* spp.) that is intensively managed for livestock grazing: includes, 'pasto limpo' (pasture) and 'pasto sujo' (abandoned/degraded pasture).<br>Areas of intensive and extensive use to raise cattle |
| | Forestry | Areas planted with species of *Eucalyptus* or *Pinus* for pulp and wood industries.<br>May include rubber trees. |
| | Agriculture & Livestock | Rural properties that combine both activities. |
| | Agriculture & Forestry | Rural properties that combine both activities. |
| | Agriculture, Livestock & Forestry | Rural properties that combine both activities. Silvipastoril farms. |
| Human activities (other than agriculture) | Iron-ore Mining | Specific area for the extraction of soil and subsoil material. |
| | Roads & Urban areas | Areas of intensive use around population centers (villages and cities), covered by buildings and road systems, with predominance of non-agricultural artificial surfaces.<br>Transportation infrastructure, including both paved and dirt roads |

**Table 1b.** Land-use characterization for each analysed article from the period 2002 to 2018.

| Land-use group | Land-use types | Selected Papers | | |
|---|---|---|---|---|
| Human Activities other than agriculture | Iron-ore Mining | 2013 | Morcatty et al. | Iron-ore mining |
| | Road & Urban area | 2010 | da Cunha et al. | roadkill, pasture, seasonal plantation |
| | | 2012 | Cáceres et al. | roadkill and anthropogenic areas |
| | | 2013 | Diniz e Brito | roadkill and anthropogenic fire |
| | | 2015 | Diniz e Brito | roadkill in agricultural mosaic |
| | | 2016 | Saranholi et al. | roadkill in agricoltural mosaic |
| | | 2017 | Silveira Miranda et al. | roadkill in agricoltural mosaic |
| | | 2017 | Brum et al. | roadkill in agricoltural mosaic |
| Agriculture & Livestock + Forestry | Agriculture only | 2012 | Barreto et al. | agriculture |
| | | 2013 | De Almeida Jácomo et al. | agriculture (crops) |
| | | 2014 | Vynne et al. | agriculture |
| | | 2014 | Rocha et al. | agriculture |
| | | 2014 | Magioli et al. | agriculture |
| | | 2015 | Hardt et al. | agriculture |
| | | 2016 | Magioli et al. | agriculture, urbanized areas and road network |
| | | 2016 | Paolino et al. | agriculture (sugarcane) |
| | Livestock only | 2002 | Bonvicino et al. | planted pasture |
| | | 2008 | Santos-Filho et al. | pasture matrix |
| | | 2010 | Cáceres et al. | cattle ranching |
| | | 2011 | Lemos et al. | pasture |
| | | 2018 | de Souza et al. | pasture |
| | Forestry only | 2008 | Lyra-Jorge et al. | Eucalyptus |
| | | 2009 | Oliveira | silviculture |
| | | 2010 | Lyra-Jorge et al. | Eucalyptus |
| | | 2012 | Martin et al. | Eucalyptus |
| | | 2014 | Timo et al. | Eucalyptus |
| | Agriculture & Livestock | 2007 | Trolle et al. | agriculture and livestock |
| | | 2007 | Trolle et al. | agriculture and livestock |
| | | 2011 | Vynne et al. | agriculture and pasture (farms with soy, corn, cotton, cattle pasture) |
| | | 2012 | Lessa et al. | pastures and sugar-cane plantations |
| | | 2014 | Zeilhofer et al. | agriculture and livestock farms |
| | | 2016 | Kennedy et al. | agriculture, pasture |
| | | 2017 | Melo et al. | agriculture and livestock |
| | Agriculture & Forestry | 2017 | Rodrigues et al. | agriculture (sugarcane) and forestry (Eucalyptus) |
| | Agriculture, Livestock & Forestry | 2014 | Do Passo Ramalho et al. | agriculture (sugarcane), pasture and Eucalyptus plantation (forestry) |
| Native habitats and Connectivity | Corridor & Fragments | 2008 | Coelho et al. | fragmentation and mosaic land-use (buildings + roads + farmland + Eucalyptus) |
| | | 2012 | Zimbres et al. | Fragmentation |

**Table 2.** Nine orders with the 150 terrestrial mammal species extracted from Paglia et al. (2012) were considered in this study: Artiodactyla (3 family and 7 species), Carnivora (5 family and 19 species, except *Lontra longicaudis* and *Pteronura brasiliensis* which are semi-aquatic species), Cingulata (1 family and 8 species), Didelphimorphia (1 family and 24 species, except *Chironectes minimus* and *Lutreolina crassicaudata* which are semi-aquatic species and eat fish and substantial quantities of aquatic invertebrates), Lagomorpha (1 family and 2 species, including an exotic species, *Lepus europaeus*), Perissodactyla (1 family and 1 species), Pilosa (2 family and 3 species), Primates (3 families and 5 species) and Rodentia (9 families and 81 species, including, in this case, two exotic species: *Rattus rattus* and *Sus scrofa*).

| **Order** | **Family** | ***Species*** | **Common name** | **mean body mass adult (g)** | **diet** | **forest use** |
|---|---|---|---|---|---|---|
| Artiodactyla | Cervidae | *Blastocerus dichotomus* | Marsh Deer | 125000 | SpecialistL | open areas |
| Artiodactyla | Cervidae | *Mazama americana* | South American Red Brocket | 36500 | Mixed feeder | forest |
| Artiodactyla | Cervidae | *Mazama gouazoubira* | South American Brow Brocket | 21000 | Mixed feeder | both |
| Artiodactyla | Cervidae | *Ozotoceros bezoarticus* | Pampas Deer | 30000 | SpecialistL | open areas |
| Artiodactyla | Suidae | *Sus scrofa* | Feral pig | 97500 | Omnivore | both |
| Artiodactyla | Tayassuidae | *Pecari tajacu* | Collared Peccary | 22000 | SpecialistF | both |
| Artiodactyla | Tayassuidae | *Tayassu pecari* | White-lipped Peccary | 35000 | SpecialistF | both |
| Carnivora | Canidae | *Cerdocyon thous* | Crab-eating Fox | 6250 | Insectivore | open areas |
| Carnivora | Canidae | *Chrysocyon brachyurus* | Maned Wolf | 22000 | Carnivore | both |
| Carnivora | Canidae | *Lycalopex vetulus* | Hoary Fox | 3250 | Insectivore | both |
| Carnivora | Canidae | *Speothos venaticus* | Bush Dog | 5900 | Carnivore | both |
| Carnivora | Felidae | *Leopardus braccatus* | Pantanal Cat | 2950 | Carnivore | open areas |
| Carnivora | Felidae | *Leopardus pardalis* | Ocelot | 9500 | Carnivore | both |
| Carnivora | Felidae | *Leopardus tigrinus* | Oncilla | 2250 | Carnivore | both |
| Carnivora | Felidae | *Leopardus wiedii* | Margay | 5500 | Carnivore | both |
| Carnivora | Felidae | *Panthera onca* | Jaguar | 90500 | Carnivore | forest |

| | | | | | | |
|---|---|---|---|---|---|---|
| Carnivora | Felidae | *Puma concolor* | Cougar | 48000 | Carnivore | both |
| Carnivora | Felidae | *Puma yagouaroundi* | Jaguarundi | 4300 | Carnivore | both |
| Carnivora | Mephitidae | *Conepatus chinga* | Molina's Hog-nosed Skunk | 1375 | Insectivore | open areas |
| Carnivora | Mephitidae | *Conepatus semistriatus* | Striped Hot-nosed Skunk | 3000 | Carnivore | open areas |
| Carnivora | Mustelidae | *Eira barbara* | Tayra | 7400 | Carnivore | both |
| Carnivora | Mustelidae | *Galictis cuja* | Lesser Grison | 2000 | Carnivore | both |
| Carnivora | Mustelidae | *Galictis vittata* | Greater Grison | 2550 | Carnivore | both |
| Carnivora | Procyonidae | *Nasua nasua* | South American Coati | 6350 | Omnivore | both |
| Carnivora | Procyonidae | *Potos flavus* | Kinkajou | 2600 | Omnivore | forest |
| Carnivora | Procyonidae | *Procyon cancrivorus* | Crab-eating Raccoon | 4250 | Omnivore | both |
| Cingulata | Dasypodidae | *Cabassous tatouay* | Greater Naked-tailed Armadillo | 5350 | Insectivore | forest |
| Cingulata | Dasypodidae | *Cabassous unicinctus* | Southern Naked-tailed armadillo | 4900 | Insectivore | open areas |
| Cingulata | Dasypodidae | *Dasypus novemcinctus* | Nine-banded armadillo | 3650 | Omnivore | both |
| Cingulata | Dasypodidae | *Dasypus septemcinctus* | Seven-banded armadillo | 1500 | Insectivore | both |
| Cingulata | Dasypodidae | *Euphractus sexcinctus* | Yellow armadillo | 4850 | Omnivore | open areas |
| Cingulata | Dasypodidae | *Priodontes maximus* | Giant armadillo | 7900 | Insectivore | both |
| Cingulata | Dasypodidae | *Tolypeutes matacus* | Southern trhee-banded armadillo | 1250 | Omnivore | both |
| Cingulata | Dasypodidae | *Tolypeutes tricinctus* | Brazilian Three-banded armadillo | 1530 | Insectivore | forest |
| Didelphimorphia | Didelphidae | *Caluromys lanatus* | Brown-eared Woolly Opossum | 435 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Caluromys philander* | Bare-tailed Woolly Opossum | 265 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Cryptonanus agricolai* | Moojen's Dwarf Mouse Opossum | 14 | Insectivore | forest |
| Didelphimorphia | Didelphidae | *Didelphis albiventris* | Guaiba Dwarf Mouse Opossum | 1850 | Omnivore | both |
| Didelphimorphia | Didelphidae | *Didelphis aurita* | Big-eared Opossum | 1235 | Omnivore | both |
| Didelphimorphia | Didelphidae | *Gracilinanus agilis* | Agile Gracile Opossum | 26 | Omnivore | both |
| Didelphimorphia | Didelphidae | *Marmosa murina* | Linnaeus's Mouse Opossum | 51 | Omnivore | forest |

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|---|---|---|---|---|---|---|
| Didelphimorphia | Didelphidae | *Marmosops incanus* | Gray Slender Opossum | 80 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Marmosops ocellatus* | Santa Cruz Slender Opossum | 31 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Metachirus nudicaudatus* | Guianan Brown Four-eyed Opossum | 390 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Micoureus constantiae* | White-bellied Woolly Mouse Opossum | 79 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Micoureus demerarae* | Woolly Mouse Opossum | 120 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Micoureus paraguayanus* | Tate's Woolly Mouse Opossum | 147 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Monodelphis americana* | Northern Three-striped Opossum | 29 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Monodelphis domestica* | Gray Short-tailed Opossum | 108 | Omnivore | both |
| Didelphimorphia | Didelphidae | *Monodelphis kunsi* | Pygmy Short-tailed Opossum | 19 | Omnivore | both |
| Didelphimorphia | Didelphidae | *Monodelphis sorex* | Southern Red-sided Opossum | 48 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Monodelphis umbristriata* | Red Three-striped Opossum | 90 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Monodelphis unistriata* | One-striped Opossum | 50 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Philander frenatus* | Southerastern Four-eyed Opossum | 450 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Philander opossum* | Gray Four-Eyed Opossum | 490 | Omnivore | both |
| Didelphimorphia | Didelphidae | *Thylamys karimii* | Karimi's Fat-tailed Mouse Opossum | 29 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Thylamys macrurus* | Paraguayan Fat-tailed Mouse Opossum | 42 | Omnivore | forest |
| Didelphimorphia | Didelphidae | *Thylamys velutinus* | Dwarf Fat-tailed Mouse Opossum | 24 | Omnivore | forest |
| Lagomorpha | Leporidae | *Lepus europaeus* | Hare | 3800 | Mixed feeder | both |
| Lagomorpha | Leporidae | *Sylvilagus brasiliensis* | Tapeti (Brazilian rabbit) | 1100 | Mixed feeder | both |
| Perissodactyla | Tapiridae | *Tapirus terrestris* | South American Tapir | 170000 | Mixed feeder | both |
| Pilosa | Cyclopedidade | *Cyclopes didactylus* | Silky Anteater | 400 | Insectivore | forest |
| Pilosa | Myrmecophagidae | *Myrmecophaga tridactyla* | Giant anteater | 30000 | Insectivore | both |
| Pilosa | Myrmecophagidae | *Tamandua tetradactyla* | Southern tamandua | 6900 | Insectivore | both |
| Primates | Atelidae | *Alouatta caraya* | Black-and-gold howler monkey | 6000 | SpecialistF | forest |
| Primates | Callitrichidae | *Callithrix penicillata* | Black-pencilled marmoset | 125 | Omnivore | forest |

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|---|---|---|---|---|---|---|
| Primates | Callitrichidae | *Mico melanurus* | Black-tailed marmoset | 275 | Omnivore | forest |
| Primates | Cebidae | *Sapajus cay* | Azara's Capuchin | 2900 | Omnivore | forest |
| Primates | Cebidae | *Sapajus libidinosus* | Bearded Capuchin | 2750 | Omnivore | forest |
| Rodentia | Caviidae | *Cavia aperea* | Brazilian Guinea Pig | 774 | Mixed feeder | open areas |
| Rodentia | Caviidae | *Cavia fulgida* | Shiny Guinea Pig | 283 | Mixed feeder | open areas |
| Rodentia | Caviidae | *Galea flavidens* | Brazilian Yellow-toothed Cavy | 247 | Mixed feeder | open areas |
| Rodentia | Caviidae | *Galea spixii* | Spix's Yellow-toothed Cavy | 350 | Mixed feeder | open areas |
| Rodentia | Caviidae | *Hydrochoerus hydrochaeris* | Capybara | 48500 | Mixed feeder | both |
| Rodentia | Caviidae | *Kerodon acrobata* | Climbing Cavy | 950 | Mixed feeder | both |
| Rodentia | Cricetidae | *Akodon cursor* | Cursorial Grass Mouse | 50 | Omnivore | both |
| Rodentia | Cricetidae | *Akodon lindberghi* | Lindbergh's Grass Mouse | 17 | Omnivore | both |
| Rodentia | Cricetidae | *Akodon montensis* | Montane Grass Mouse | 43 | Omnivore | both |
| Rodentia | Cricetidae | *Akodon paranaensis* | Paraná Grass Mouse | 35 | Omnivore | both |
| Rodentia | Cricetidae | *Calomys callidus* | Big Laucha | 37 | SpecialistF | both |
| Rodentia | Cricetidae | *Calomys callosus* | Big Laucha, Large Vesper Mouse | 30 | SpecialistF | both |
| Rodentia | Cricetidae | *Calomys cerqueirai* | Cerqueira's Laucha | 30 | SpecialistF | open areas |
| Rodentia | Cricetidae | *Calomys expulsus* | Caatinga Laucha | 32 | SpecialistF | both |
| Rodentia | Cricetidae | *Calomys tener* | Delicate Laucha | 20 | SpecialistF | both |
| Rodentia | Cricetidae | *Calomys tocantinsi* | Tocantins Laucha | 22 | SpecialistF | both |
| Rodentia | Cricetidae | *Cerradomys maracajuensis* | Maracaju Rice Rat | 114 | SpecialistF | both |
| Rodentia | Cricetidae | *Cerradomys marinhus* | Marinho's Rice Rat | 104 | SpecialistF | both |
| Rodentia | Cricetidae | *Cerradomys scotti* | Lindbergh's Rice Rat | 90 | SpecialistF | both |
| Rodentia | Cricetidae | *Cerradomys subflavus* | Flavescent Rice Rat | 92 | SpecialistF | both |
| Rodentia | Cricetidae | *Cerradomys vivoi* | De Vivo's Rice Rat | 77 | SpecialistF | both |
| Rodentia | Cricetidae | *Euryoryzomys lamia* | Buffy-sided Rice Rat | 57 | SpecialistF | forest |

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|---|---|---|---|---|---|---|
| Rodentia | Cricetidae | *Euryoryzomys nitidus* | Elegant Rice Rat | 62 | SpecialistF | forest |
| Rodentia | Cricetidae | *Gyldenstolpia fronto* | Fossorial Giant Rat | 230 | Mixed feeder | NA |
| Rodentia | Cricetidae | *Gyldenstolpia planaltensis* | Fossorial Giant Rat | 225 | Mixed feeder | both |
| Rodentia | Cricetidae | *Holochilus brasiliensis* | Brazilian Marsh Rat | 210 | Omnivore | both |
| Rodentia | Cricetidae | *Holochilus sciureus* | Amazonian Marsh Rat | 145 | Omnivore | both |
| Rodentia | Cricetidae | *Hylaeamys megacephalus* | Azara's Broad-headed Rice Rat | 59 | SpecialistF | both |
| Rodentia | Cricetidae | *Juscelinomys candango* | Candango Akodont | 90 | Omnivore | NA |
| Rodentia | Cricetidae | *Kunsia tomentosus* | Woolly Giant Rat | 430 | Mixed feeder | open areas |
| Rodentia | Cricetidae | *Microakodontomys transitorius* | Transitional Colilargo | 18 | SpecialistF | open areas |
| Rodentia | Cricetidae | *Neacomys spinosus* | Common Bristly Mouse | 31 | SpecialistF | forest |
| Rodentia | Cricetidae | *Necromys lasiurus* | Hairy-tailed Akodont | 60 | Omnivore | both |
| Rodentia | Cricetidae | *Nectomys rattus* | Amazonian Water Rat | 240 | Omnivore | forest |
| Rodentia | Cricetidae | *Nectomys squamipes* | Atlantic Forest Water Rat | 250 | Omnivore | NA |
| Rodentia | Cricetidae | *Oecomys bicolor* | White-bellied Arboreal Rice Rat | 26 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oecomys catherinae* | Atlantic Forest Arboreal Rice Rat | 70 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oecomys cleberi* | Cleber's Arboreal Rice Rat | 28 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oecomys mamorae* | Mamoré Arboreal Rice Rat | 118 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oecomys roberti* | Robert's Arboreal Rice Rat | 270 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oligoryzomys chacoensis* | Chacoan colilargo | 30 | SpecialistF | both |
| Rodentia | Cricetidae | *Oligoryzomys flavescens* | Flavescent Colilargo | 18 | SpecialistF | both |
| Rodentia | Cricetidae | *Oligoryzomys fornesi* | Forne's Colilargo | 13 | SpecialistF | both |
| Rodentia | Cricetidae | *Oligoryzomys moojeni* | Moojen's Colilargo | 17 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oligoryzomys nigripes* | Black-footed Colilargo | 29 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oligoryzomys rupestris* | Rochy Outcrop Colilargo | 15 | SpecialistF | forest |
| Rodentia | Cricetidae | *Oligoryzomys stramineus* | Straw-colored Colilargo | 26 | SpecialistF | forest |

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| Rodentia | Cricetidae | *Oxymycterus delator* | Paraguayan Hocicudo | 92 | Insectivore | open areas |
| Rodentia | Cricetidae | *Pseudoryzomys simplex* | Brazilian False Rice Rat | 50 | Omnivore | NA |
| Rodentia | Cricetidae | *Rhipidomys ipukensis* | Ipuka Climbing Mouse | 66 | SpecialistF | forest |
| Rodentia | Cricetidae | *Rhipidomys macrurus* | Long-tailed Climbing Mouse | 89 | Mixed feeder | forest |
| Rodentia | Cricetidae | *Rhipidomys mastacalis* | Atlantic Forest Climbing Mouse | 95 | SpecialistF | forest |
| Rodentia | Cricetidae | *Thalpomys cerradensis* | Cerrado Mouse | 27 | SpecialistF | open areas |
| Rodentia | Cricetidae | *Thalpomys lasiotis* | Hairy-eared Mouse | 21 | SpecialistF | open areas |
| Rodentia | Cricetidae | *Wiedomys cerradensis* | Cerrado Wiedomys | 40 | Omnivore | forest |
| Rodentia | Ctenomyidae | *Ctenomys boliviensis* | Bolivian Tuco-tuco | 535 | Mixed feeder | NA |
| Rodentia | Ctenomyidae | *Ctenomys brasiliensis* | Brazilian Tuco-tuco | 240 | Mixed feeder | NA |
| Rodentia | Ctenomyidae | *Ctenomys minutus* | Tiny Tuco-tuco | 240 | Mixed feeder | NA |
| Rodentia | Ctenomyidae | *Ctenomys nattereri* | Netterer's Tuco-tuco | 240 | Mixed feeder | NA |
| Rodentia | Cuniculidae | *Cuniculus paca* | Spotted Paca | 9300 | Mixed feeder | forest |
| Rodentia | Dasyproctidae | *Dasyprocta aurea* | Cope's Agouti | 2650 | Mixed feeder | forest |
| Rodentia | Dasyproctidae | *Dasyprocta azarae* | Azara's Agouti | 2900 | Mixed feeder | both |
| Rodentia | Dasyproctidae | *Dasyprocta nigriclunis* | Highland Black-rumped Agouti | 2500 | Mixed feeder | forest |
| Rodentia | Dasyproctidae | *Dasyprocta prymnolopha* | Black-rumped Agouti | 2500 | Mixed feeder | forest |
| Rodentia | Echimyidae | *Carterodon sulcidens* | Owl's Spiny Rat | 180 | Mixed feeder | NA |
| Rodentia | Echimyidae | *Clyomys laticeps* | Broad-headed Spiny-rat | 185 | Mixed feeder | open areas |
| Rodentia | Echimyidae | *Dactylomys dactylinus* | Amazon Bamboo Rat | 750 | SpecialistL | forest |
| Rodentia | Echimyidae | *Euryzygomatomys spinosus* | Guiara | 185 | Mixed feeder | NA |
| Rodentia | Echimyidae | *Kannabateomys amblyonyx* | Atlantic Bamboo Rat | 420 | SpecialistL | forest |
| Rodentia | Echimyidae | *Phyllomys brasiliensis* | Orange-brown Atlantic Tree-rat | 240 | SpecialistL | forest |
| Rodentia | Echimyidae | *Proechimys longicaudatus* | Long-tailed Spiny-rat | 200 | Omnivore | forest |
| Rodentia | Echimyidae | *Proechimys roberti* | Robert's Spiny-rat | 212 | SpecialistF | forest |

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| Rodentia | Echimyidae | *Thrichomys apereoides* | Common Punaré | 155 | Mixed feeder | both |
| Rodentia | Echimyidae | *Thrichomys fosteri* | Paraguayan Punaré | 310 | Mixed feeder | both |
| Rodentia | Echimyidae | *Thrichomys inermis* | Highlands Punaré | 185 | Mixed feeder | both |
| Rodentia | Echimyidae | *Trinomys albispinus* | White-spined Atlantic Spiny-rat | 140 | SpecialistF | forest |
| Rodentia | Echimyidae | *Trinomys moojeni* | Moojen's Atlantic Spiny-rat | 170 | SpecialistF | forest |
| Rodentia | Erethizontidae | *Coendou prehensilis* | Brazilian Porcupine | 4250 | Mixed feeder | forest |
| Rodentia | Erethizontidae | *Coendou spinosus* | Paraguayan Hairy Dwarf Porcupine | 1800 | Mixed feeder | forest |
| Rodentia | Muridae | *Rattus rattus* | Black rat, house rat | 230 | Omnivore | both |
| Rodentia | Sciuridae | *Guerlinguetus poaiae* | Moojen's Squirrel | 175 | SpecialistF | NA |

**Table 3**. Papers found on research bases for confirmed terrestrial mammals in Cerrado associated with land-use change (37 articles published between 2002 and 2018).

| # | Year | Paper | Scientific base |
|---|---|---|---|
| 1 | 2002 | Bonvicino CR, Lindbergh SM, Maroja LS. Small non-flying mammals from conserved and altered areas of Atlantic Forest and Cerrado: comments on their potential use for monitoring environment. Brazilian Journal of Biology, 62(4b):765 - 774 | Scielo |
| 2 | 2007 | Trolle M, Noss AJ, Lima EDS, Dalponte JC. Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. Biodiversity and Conservation, 16 (4), pp. 1197-1204 | Scopus |
| 3 | 2007 | Trolle M, Bissaro MC & Prado HM. Mammal survey at a ranch of the Brazilian Cerrado. Biodivers Conserv (2007) 16:1205–1211 | Scopus/ |
| 4 | 2008 | Lyra-Jorge MC, Ciocheti G, Pivello VR. Carnivore mammals in a fragmented landscape in northeast of São Paulo State, Brazil. Biodiversity and Conservation, 17 (7), pp. 1573-1580. | Web of Science<br>Scopus |
| 5 | 2008 | Coelho CM, De Melo LFB, Sábato MAL, Vaz Magni EM., Hirsch A., Young RJ. Habitat use by wild maned wolves (*Chrysocyon brachyurus*) in a transition zone environment. Journal of Mammalogy, 89 (1), pp. 97-104. | Scopus |
| 6 | 2008 | Santos-Filho et al. Edge effects and landscape matrix use by a small mammal comunity in fragments of semidesciduous submontane forest in Mato Grosso, Brazil. Braz. J. Biol., 68(4): 703-710 | Web of Science |
| 7 | 2009 | Oliveira TG. Distribution, habitat utilization and conservation of the Vulnerable bush dog Speothos venaticus in northern Brazil. Fauna & Flora International, Oryx, 43(2), 247–253 | Scopus |
| 8 | 2010 | da Cunha HF, Moreira FGA, Silva SS. Roadkill of wild vertebrates along the GO-060 road between Goiânia and Iporá, Goiás State, Brazil. Acta Scientiarum - Biological Sciences, 32 (3), pp. 257-263. | Scopus |
| 9 | 2010 | Lyra-Jorge MC, Ribeiro MC, Ciocheti G, Tambosi LR, Pivello VR. Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. European Journal of Wildlife Research, 56 (3), pp. 359-368. | Scopus/<br>Web of Science |
| 10 | 2010 | Cáceres NC, Hannibal W, Freitas DR, Silva EL, Roman C, & Casella J. Mammal occurrence and roadkill in two adjacent ecoregions (Atlantic Forest and Cerrado) in south-western Brazil. Zoologia (Curitiba), Out 2010, Volume 27 Nº 5 Páginas 709 - 717 | Scielo |
| 11 | 2011 | Lemos FG, Facure KG, de Azevedo FC. A first approach to the comparative ecology of the hoary fox and the crab-eating fox in a fragmented human altered landscape in the Cerrado Biome at Central Brazil. Middle-Sized Carnivores in Agricultural Landscapes, pp. 143-160. | Scopus |
| 12 | 2011 | Vynne C, Keim JL, Machado RB, Marinho-Filho J, Silveira L, Groom MJ, Wasser SK. Resource Selection and Its Implications for Wide-Ranging Mammals of the Brazilian Cerrado. PLoS ONE December 2011 \| Volume 6 \| Issue 12 \| e28939 | Scopus/<br>Web of Science |
| 13 | 2012 | Barreto L, Van Eupen M, Kok K, Jongman RHG, Ribeiro MC., Veldkamp A, Hass A, Oliveira TG. The impact of soybean expansion on mammal and bird, in the Balsas region, north Brasilian Cerrado. Journal for Nature Conservation, 20 (6), pp. 374-383. | Scopus/<br>Web of Science |
| 14 | 2012 | Lessa LG, Alves H, Geise L, Barreto RMF. Mammals of medium and large size in a fragmented cerrado landscape in northeastern Minas Gerais state, Brazil. Check List, 8 (2), pp. 192-196. | Scopus |
| 15 | 2012 | Martin PS, Gheler-Costa C, Lopes PC, Rosalino LM, Verdade LM. Terrestrial non-volant small mammals in agro-silvicultural landscapes of Southeastern Brazil. Forest Ecology and Management 282 (2012) 185–195 | Scopus/<br>Web of Science |
| 16 | 2012 | Cáceres NC, Casella J, dos Santos Goulart C. Variação espacial e sazonal atropelamentos de mamíferos no bioma cerrado, rodovia BR 262, Sudoeste do Brasil. Mastozool. neotrop. vol.19 no.1 Mendoza | Scielo/<br>ResearchGate |
| 17 | 2013 | Jácomo ATM, Furtado MM, Kashivakura CK, Marinho-Filho J, Sollmann R, Tôrres NM, Silveira L. White-lipped peccary home-range size in a protected area and farmland in the central Brazilian grasslands. Journal of Mammalogy, 94 (1), pp. 137-145. | Scopus |
| 18 | 2013 | Zimbres B, Furtado MM, Jácomo ATA., Silveira L, Sollmann R, Tôrres NM, Machado RB, Marinho-Filho J. The impact of habitat fragmentation on the ecology of xenarthrans (Mammalia) in the Brazilian Cerrado Landscape Ecology, 28 (2), pp. 259-269. | Scopus |

| # | Year | Paper | Scientific base |
|---|---|---|---|
| 19 | 2013 | Diniz MF & Brito D. Threats to and viability of the giant anteater, *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae), in a protected Cerrado remnant encroached by urban expansion in central Brazil. Zoologia 30 (2): 151–156 | Scopus |
| 20 | 2013 | Morcatty TQ et al. Habitat loss and mammalian extinction patterns: are the reserves in the Quadrilátero Ferrífero, southeastern Brazil, effective in conserving mammals? Ecol Res (2013) 28: 935–947 | Scopus |
| 21 | 2014 | Do Passo Ramalho F, Miotto RA, Martins N, & Galetti PM. Maned wolf (Chrysocyon brachyurus) minimum population size and genetic diversity in a Cerrado protected area of southeastern Brazil revealed by fecal DNA analysis. Mammalia, 78 (4), pp. 465-472. | Scopus |
| 22 | 2014 | Vynne C, Booth RK, Wasser SK. Physiological implications of landscape use by free-ranging maned wolves (*Chrysocyon brachyurus*) in Brazil. Journal of Mammalogy, 95 (4), pp. 696-706. | Scopus |
| 23 | 2014 | Rocha RG, Ferreira E, Martins ICM, Costa LP, Fonseca C. Seasonally flooded steppingstones: Emerging diversity of small mammal assemblage in the Amazonia-Cerrado ecotone, central Brazil. Zoological Studies, 53 (1), pp. 1-10. | Scopus |
| 24 | 2014 | Zeilhofer P, Cezar A, Orre NM, Jacomo ATA, Silveira L. Jaguar Panthera onca Habitat Modeling in Landscapes Facing High Land-use Transformation Pressure—Findings from Mato Grosso, Brazil. Biotropica 46(1): 98–105 | Scopus |
| 25 | 2014 | Magioli M et al. Stable Isotope Evidence of Puma concolor (Felidae) Feeding Patterns in Agricultural Landscapes in Southeastern Brazil. Biotropica 46(4): 451–460 | Scopus |
| 26 | 2014 | Timo TPC et al. Effect of the plantation age on the use of Eucalyptus stands by medium to large-sized wild mammals in south-eastern Brazil. iForest (2015) 8: 108-113 | Scopus |
| 27 | 2015 | Hardt E, Borgomeo E, dos Santos RF, Pinto LFG, Metzger JP, Sparovek G. Does certification improve biodiversity conservation in Brazilian coffee farms? Forest Ecology and Management, 357, pp. 181-194. | Scopus/<br>Web of Science |
| 28 | 2015 | Diniz MF, Brito D. Protected areas effectiveness in maintaining viable giant anteater (*Myrmecophaga tridactyla*) populations in an agricultural frontier Natureza & Conservação, 13: 145-151 | Scopus |
| 29 | 2016 | Saranholi BH, Bergel MM, Ruffino PHP, Rodríguez CKG, Ramazzotto LA, de Freitas PD, Galetti PM. Roadkill hotspots in a protected area of Cerrado in Brazil: Planning actions to conservation. Revista MVZ Cordoba, 21 (2), pp. 5441-5448. | Scopus |
| 30 | 2016 | Kennedy CM, Sochi K, Evans JS, Kiesecker J. Optimizing land-use decision-making to sustain Brazilian agricultural profits, biodiversity and ecosystem services. Biological Conservation, 204, pp. 221-230 | Scopus/<br>Science Direct |
| 31 | 2016 | Magioli M et al. Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. Eur J Wildl Res (2016) 62:431–446 | Scopus/<br>Web of Science |
| 32 | 2016 | Paolino RM, Versiani NF, Pasqualotto N, Rodrigues TF, Krepschi VG, Chiarello AG. Buffer zone use by mammals in a Cerrado protected area. Biota Neotropica 16(2): e20140117, 2016 | Scielo |
| 33 | 2017 | Melo GL, Sponchiado J, Cáceres NC, Fahrig L. Testing the habitat amount hypothesis for South American small mammals. Biological Conservation, 209, pp. 304-314 | Scopus/<br>Science Direct |
| 34 | 2017 | Miranda JES, Umetsu RK, Melo FR, Melo FCSA, Pereira KF & Oliveira SR. Roadkill in Brazilian Cerrado Savanna: comparing five highways in Southwestern Goiás. Oecologia Australis 21(3): 337-349 | ResearchGate |
| 35 | 2017 | Rodrigues TF et al. Managed forest as habitat for gray brocket deer (Mazama gouazoubira) in agricultural landscapes of southeastern Brazil. Journal of Mammalogy, xx(x):1–9, 2017 | Scopus/<br>ResearchGate |
| 36 | 2017 | Brum TR; Santos-Filho M, Canale GR, Ignácio ARA. Effects of roads on the vertebrates diversity of the Indigenous Territory Paresi and its surrounding. Braz. J. Biol., ahead of print Epub June 12, 2017 | Scielo |
| 37 | 2018 | de Souza JC, da Silva RM, Gonçalves MPR, Jardim RJD, Markwith SH. Habitat use, ranching, and human-wildlife conflict within a fragmented landscape in the Pantanal, Brazil. Biological Conservation, 217, pp. 349-357. | Scopus/<br>ResearchGate/<br>Web Of Science |

**Table 4a**. Types of mammalian responses (by species per family) according to the land-use identified in the 37 articles published between 2002 and 2018 for Cerrado mammal species. * indicates that the same species of a given family shows two different responses to the land-use identified in the article.

| family | N° of Species this families in Cerrado (Paglia et al.2012) | N° of species this family (this study) | N° articles by family (this study) | Human Activities other than agriculture | | | | | | Agriculture & livestock + Forestry | | | | | | | | | | | | | | | | | | Native habitats and Connectivity | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Iron Mining | | | Roadkill & Urban area | | | Agriculture only | | | Livestock only | | | Forestry only | | | Agriculture and Livestock | | | Agriculture and Forestry | | | Agriculture, Livestock and Forestry | | | Corridor & Fragments | | |
| | | | | + | ϕ | - | + | ϕ | - | + | ϕ | - | + | ϕ | - | + | ϕ | - | + | ϕ | - | + | ϕ | - | + | ϕ | - | + | ϕ | - |
| Atelidae | 1 | 1 | 2 | | | | | | 1 | | | | | | | | | | | | 1 | | | | | | | | | |
| Callitrichidae | 2 | 1 | 4 | | | | | | 1 | | | 1 | | | | | | | | 1* | 1* | | | | | | | | | |
| Canidae | 4 | 4 | 22 | | 1 | 1 | | | 1 | | 1* | 1* | | 1* | 1* | | 1* | 1* | 1* | 1* | 1* | | | | | | 1 | | 1 | |
| Caviidae | 6 | 4 | 11 | | | | | | 1 | | 1* | 1* | | 1* | 1* | | | 1 | | 1* | 1* | | | | | | | | | |
| Cebidae | 2 | 2 | 3 | | | | | | 1 | | | | | | | | | | | | 1 | | | | | | | | | |
| Cervidae | 4 | 4 | 11 | | | | | | 1 | | 1* | 1* | | 1 | | | | | | | 1 | 1 | | | | | | | | |
| Cricetidae | 48 | 27 | 7 | | | | | | | | 1* | 1* | | 1* | 1* | 1 | | 1 | | | 1 | | | | | | | | | |
| Cuniculidae | 1 | 1 | 8 | | | 1 | | | 1 | | | 1 | | | | | | | | | 1 | | | | | | | | | |
| Dasypodidae | 8 | 7 | 18 | | | 1 | | | 1 | | 1* | 1* | | 1 | 1 | | 1* | 1* | | 1* | 1* | | | | | | | | 1 | |
| Dasyproctidae | 4 | 1 | 4 | | | | | | 1 | | | 1 | | 1 | | | | | | | 1 | | | | | | | | | |
| Didelphidae | 26 | 17 | 14 | | | | | | 1 | | 1* | 1* | | | 1 | 1 | 1* | 1* | 1 | | 1 | | | | | | | | | |
| Echimyidae | 13 | 5 | 4 | | | | | | | | | | | | 1 | | | | | | 1 | | | | | | | | | |
| Erethizontidae | 2 | 2 | 5 | | | | | | 1 | | | 1 | | | | | | | | | 1 | | | | | | | | | |
| Felidae | 7 | 7 | 21 | | | 1 | | | 1 | | 1* | 1* | | 1 | 1 | | 1* | 1* | | 1* | 1* | | | | | | | | | |
| Leporidae | 1 | 2 | 10 | | 1 | | | | 1 | | | 1 | | 1 | 1 | | | 1 | | 1* | 1* | | | | | | | | | |
| Mephitidae | 2 | 1 | 6 | | | | | | 1 | | | 1 | | | | | | 1 | | | 1 | | | | | | | | | |
| Muridae | | 1 | 3 | | | | | | 1 | | | | | | 1 | 1 | | | | | | | | | | | | | | |
| Mustelidae | 5 | 3 | 14 | | | | | | 1 | | | 1 | | 1* | 1* | | 1* | 1* | | | 1 | | | | | | | | | |
| Myrmecophagidae | 2 | 2 | 18 | | 1 | 1 | | | 1 | | | 1 | | 1* | 1* | | 1 | | | 1* | 1* | | | | | | | | 1 | |
| Procyonidae | 3 | 3 | 16 | | | 1 | | | 1 | | 1* | 1* | | 1* | 1* | | | 1 | | 1* | 1* | | | | | | | | | |
| Suidae | | 1 | 2 | | | | | | | | 1* | 1* | | | | | | | | | | | | | | | | | | |
| Tapiridae | 1 | 1 | 10 | | | 1 | | | 1 | | | 1 | | 1* | 1* | | | | | 1* | 1* | | | | | | | | | |
| Tayassuidae | 2 | 2 | 9 | | | 1 | | | 1 | | | 1 | | 1 | | | | 1 | | | 1 | | | | | | | | | |

**Table 4b.** Types of mammalian responses (by species per family) according to the land-use identified in the 37 articles published between 2002 and 2018 for Cerrado mammal species.

| family | N° of Species this families in Cerrado | N° of species this family in this study | N° articles by family | Human Activities other than agriculture | | Agriculture & Livestock + Forestry | | | | | | Native habitats and Connectivity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Iron Mining | Roadkill & Urban area | Agriculture only | Livestock only | Forestry only | Agriculture and Livestock | Agriculture and Forestry | Agriculture, Livestock and Forestry | Corridor & Fragments |
| Atelidae | 1 | 1 | 2 | | (-) | | | | (-) | | | |
| Callitrichidae | 2 | 1 | 4 | | (-) | (-) | | | ∅ (-) | | | |
| Canidae | 4 | 4 | 22 | ∅ (-) | 14(-) | 3(∅) 2(-) | 2(∅) 4(-) | 5(∅) (-) | (+) 4(∅) 4(-) | | (-) | ∅ |
| Caviidae | 6 | 4 | 11 | | 4(-) | ∅ 2(-) | ∅ 3(-) | (-) | ∅ 3(-) | | | |
| Cebidae | 2 | 2 | 3 | | 2(-) | | | | (-) | | | |
| Cervidae | 4 | 4 | 11 | | 3(-) | ∅ 4(-) | 2(∅) | | 7(-) | (+) | | |
| Cricetidae | 48 | 27 | 7 | | | ∅ 11(-) | ∅ 15(-) | 3(+) 2(-) | 19(-) | | | |
| Cuniculidae | 1 | 1 | 8 | (-) | 2(-) | 3(-) | | | 2(-) | | | |
| Dasypodidae | 8 | 7 | 18 | 2(-) | 10(-) | ∅ 6(-) | 2(∅) 2(-) | ∅ (-) | 4(∅) 7(-) | | | 5(∅) |
| Dasyproctidae | 4 | 1 | 4 | | (-) | (-) | ∅ | | (-) | | | |
| Didelphidae | 26 | 17 | 14 | | 6(-) | ∅ 7(-) | 13(-) | (+) ∅ (-) | (+) 15(-) | | | |
| Echimyidae | 13 | 5 | 4 | | | | 3(-) | | 4(-) | | | |
| Erethizonthidae | 2 | 2 | 5 | | 3(-) | (-) | | | (-) | | | |
| Felidae | 7 | 7 | 21 | 4(-) | 9(-) | 3(∅) 8(-) | 3(∅) 2(-) | 2(∅) 6(-) | 4(∅) 13(-) | | | |
| Leporidae | 1 | 2 | 10 | ∅ | 2(-) | 4(-) | 2(∅) (-) | (-) | ∅ (-) | | | |
| Mephitidae | 2 | 1 | 6 | | (-) | (-) | | 2(-) | (-) | | | |
| Muridae | 3 | 1 | 3 | | (-) | | (-) | (+) | | | | |
| Mustelidae | 5 | 3 | 14 | | 7(-) | 3(-) | ∅ (-) | 2(∅) (-) | 4(-) | | | |
| Myrmecophagidae | 2 | 2 | 18 | ∅ (-) | 10(-) | 4(-) | 2(∅) 2(-) | ∅ | ∅ 4(-) | | | 2(∅) |
| Procyonidae | 3 | 3 | 16 | (-) | 9(-) | ∅ 2(-) | 2(∅) 2(-) | 4(-) | ∅ 3(-) | | | |
| Suidae | 1 | 1 | 2 | | | ∅ (-) | | | | | | |
| Tapiridae | 1 | 1 | 10 | (-) | 3(-) | (-) | ∅ (-) | | ∅ 2(-) | | | |
| Tayassuidae | 2 | 2 | 9 | (-) | (-) | 2(-) | 2(∅) | (-) | 4(-) | | | |
| | **148** | **99** | | | | | | | | | | |

meaning: 14(-) 14 negative responses for the species of this family in this type of land use

| exotics | |
|---|---|
| Muridae | 2 genus in Brasil: *Mus* e *Rattus* |
| Leporidae | 2 genus in Brasil: *Lepus* (exotic) e *Sylvilagus* (native) |
| Suidae | 1 genus in Brasil |

# CHAPTER II

## Spatial extent of landscape effects on herbivorous mammals in one region of the Cerrado and Atlantic Forest hotspots

## Abstract

Studies have highlighted the importance of considering multiple spatial scales when investigating the effects of habitat change on species, since species may respond to a specific landscape attribute on a specific scale. Changing the size or extent of grain size can affect landscape metrics, including the number, area, and spatial pattern of different patch types, and can trigger changes in metrics that evaluate landscape composition and configuration. Different authors have shown that landscape metrics exhibited consistent and predictable patterns across a wide range of grain sizes, while others changed with grain size in a nonlinear fashion. In this study, I investigated how three landscape metrics (percentage of forest cover, patch density and edge density) affected the occurrence of four herbivore species (*Dasyprocta azarae, Pecari tajacu, Mazama gouazoubira* and *Tapirus terrestris*) in a region dominated by Cerrado and Atlantic Forest remnants. For this, I used a landscape dataset, extracting the metrics calculated based on Landsat images, characterizing changes in forest cover from 2000 to 2017. The level of forest cover considered in this study was 75% to calculate landscape metrics. Landscape metrics were measured considering each camera trap as central point to different buffers sizes (500, 750, 1000, 1500, 2000, 3000, 5000, 10000 and 20000 meters) using vegetation maps. Such buffer sizes are commonly used to evaluate the relationships between landscape variables and the occurrence of medium to large mammals. I chose two main groups of metrics to characterize the general landscape structure: configuration (patch density - PD and edge density - ED), and composition (percentage of forest cover - PcoForest). To detect the response of the species to each landscape metric, as well as along each buffer size, I performed occupancy modelling, based on the species detection information from the camera capture data. I observed three types of response curves for the three metrics selected: edge density, showed a constant power law relation with increasing buffer size, suggesting that these metrics could be predicted with high precision over a wide range of grain size; patch density, had a constant pow er law relation with increasing buffer size, but only after 750 m. Finally, the percentage of landscape which showed no size-based relations across buffer sizes. Average edge density metric model results showed the *Dasyprocta azarae* response was best explained at the 500 m level. However, the other three species selected for analysis did not exhibit any response to edge density over the buffer size range considered. A similar pattern of results was observed with the patch density metric. The two dietary generalist species, *Tapirus terrestris* and *Mazama gouazoubira,* showed responses to 750 m and 1,000 m buffers, respectively. From this perspective, our result indicated that the ideal buffer size should be 5,000 m for landscape metric patterns, since multi-scale analyses showed a full explanation of the landscape patterns by metrics at the 5,000 m level. However, when species occurrences were included, the result shows ~~an~~ interspecific variation in response scales for the

different landscape metrics. Thus, working at a larger scale to understand ecological and biological responses increasingly requires studies of processes operating at the landscape scale. Since the 1980s the importance of scale has been recognized in ecology, and today, for landscape ecology, the scale focuses on interpretations of the complex interactions of natural and man-made systems. The results gained are important to increase knowledge of reactions of different metrics in the Cerrado.

## Resumo

Estudos têm destacado a importância de considerar múltiplas escalas espaciais ao investigar os efeitos da mudança de habitat em espécies, uma vez que as espécies podem responder a um atributo de paisagem específico em uma escala específica. A alteração do tamanho ou extensão dos grãos pode afetar as métricas de paisagem, incluindo o número, a área e o padrão espacial de diferentes tipos de patch, e pode desencadear mudanças nas métricas que avaliam a composição e configuração da paisagem. Diferentes autores vêm mostrando que as métricas de paisagem exibiram padrões consistentes e previsíveis em uma ampla faixa de tamanhos de grãos, enquanto outras foram alteradas com o tamanho de grão de uma forma não linear. Nesse estudo, investiguei como três métricas de paisagem (porcentagem de cobertura florestal, densidade de manchas e densidade de bordas) afetaram a ocorrência de quatro espécies de herbívoros (*Dasyprocta azarae*, *Pecari tajacu*, *Mazama gouazoubira* e *Tapirus terrestris*) em uma região de domínio predominante de Cerrado e remanescentes de Mata Atlântica. Para isso, foi utilizado um conjunto de dados da paisagem extraindo as métricas calculadas com base em imagens Landsat, caracterizando a extensão da floresta e as mudanças de 2000 a 2017. O nível de cobertura florestal utilizado neste estudo foi de 75% para calcular as métricas de paisagem. Foram medidas as métricas paisagísticas considerando cada armadilha fotográfica usando mapas da vegetação e diferentes tamanhos de buffers (500, 750, 1000, 1500, 2000, 3000, 5000, 10000 and 20000 metros), com\azumente usados para avaliar as relações entre as variáveis da paisagem e a ocorrência de mamíferos de médio a grande porte. Dois grupos principais de métricas foram escolhidos para caracterizar a estrutura geral da paisagem: configuração (densidade do patch – PD e densidade de borda - ED), e composição (porcentagem de cobertura florestal - PcoForest). Para detectar a resposta da espécie em cada métrica de paisagem, bem como ao longo de cada tamanho de buffer, foi extraída a modelagem de ocupação, com base nas informações de detecção de espécies dos dados de captura de câmera. Observei três tipos de curvas de resposta para as três métricas selecionadas: *densidade de borda*, mostrou uma relação de lei de potência constante com o aumento do tamanho do buffer, sugerindo que essas métricas poderiam ser previstas em uma ampla faixa de tamanho de grão com alta precisão; *densidade do patch*, revelou uma relação de lei de força constante com o aumento do buffer, mas somente após 750 m. E, por fim, o *percentual de paisagem* o qual mostrou relações de dimensionamento sem lei ao longo do tamanho do buffer. O resultado do modelo médio de métrica de densidade de borda revelou que a resposta de *Dasyprocta azarae* foi melhor explicada em 500 m. No entanto, as outras três espécies selecionadas na análise não exibiram qualquer resposta à densidade de bordas ao longo do intervalo de tamanho de buffer considerado. Um padrão semelhante de resultado foi observado com a métrica de densidade do patch. As duas espécies

generalistas em dieta, *Tapirus terrestris* e *Mazama gouazoubira*, apresentaram respostas para buffers de 750 m e de 1.000 m, respectivamente. Sob essa perspectiva, o resultado delineou que o tamanho ideal do buffer deve ser de 5.000 m para padrões de métricas da paisagem, uma vez que as análises em multi-escala mostraram uma explicação completa da paisagem pelas métricas de 5.000 m. Mas quando as ocorrências da espécie foram incluídas, o resultado mostra uma variação interespecífica das escalas de resposta para as diferentes métricas da paisagem. No entanto, fora da análise, foi possível refinar a resposta da escala ecológica de nossas espécies em escala local e abaixo de 1.000 m. Assim, trabalhar em uma escala maior para entender as respostas ecológicas e biológicas exigem cada vez mais a exploração dos processos que acontecem na escala da paisagem. Desde a década de 80 a importância da escala foi reconhecida na ecologia, e atualmente, para a ecologia da paisagem a escala se concentra nas interpretações sobre as interações complexas dos sistemas naturais e antrópicos. Os resultados são importantes para adquirir conhecimento sobre a reação de diferentes métricas no cenário da região de estudo.

## Introduction

Identifying the spatial scale at which biodiversity responds to landscape changes, as such as heterogeneity or structural fragmentation, has become a major challenge for landscape ecology and ecological and conservation sciences (Fahrig et al. 2011, Redon et al. 2014, Miguet et al. 2016, 2017). Studies have highlighted the importance of considering multiple spatial scales when investigating effects of habitat change on species, as theys might respond to a specific landscape attribute at a particular scale (Holland et al. 2004, Lyra-Jorge et al. 2009, Bogoni et al. 2017). In the context of biodiversity erosion triggered by human activities that shape land-use and land cover changes, knowing the scale at which biodiversity is affected by landscape attributes should help decision-makers design management plans to effectively maintain and restore biodiversity and its supporting natural habitats.

Multiscale analysis is commonly used by landscape ecologists to select the spatial scale at which studies should be carried out (*e.g.* Brennan et al. 2002, Holland et al. 2004, Holland & Yuang 2016, Melo et al. 2017, Huais 2018). Although different methods have been proposed in the literature, thegeneral approach is to run statistical analysis (correlation, models, regression and non-parametric) to test for the effects of landscape features on species attributes (*e.g.* richness, abundance, composition) at a set of different spatial scales and to extract their goodness of fit through an appropriate criterion index (*e.g.* correlation coefficient, $R^2$, AIC). The aim is then to plot spatial scales (*e.g.* buffer size) on the x-axis and goodness of fit on the y-axis. Identifying the maximum or minimum criterion index values on the y-axis, it is possible to determine the most appropriate spatial scale at which responses of species to habitat changes should be studied (i.e. the scale effect, Jackson & Fahrig 2012). This is sometimes challenging because of the: 1) lack of knowledge to allow identification of the suitable metrics to investigate biodiversity dynamics and those of grain size or extent, 2) statistical constraints from spatial autocorrelation in the date set, and 3) matters relating to landscape configuration (Villard & Metzger 2014).

sChanging grain size or extent might affect landscape metrics including the number, area, and spatial pattern of different patch types (Saura & Martinez-Millan 2001, Wu et al. 2000) and may trigger changes in metrics used to assess landscape composition (*e.g.*, diversity of patch types) and configuration (*e.g.*, spatial arrangement of different patch types) (Wu et al. 2002). Indeed, Wu et al. (2000) tested two sets of methods including direct and indirect multiscale approaches to quantify multiple-scale characteristics of landscapes. In their study, these authors showed that landscape metrics (including the number of patches, patch density, total edge, edge density, mean patch size, and patch size coefficient of variation), exhibited consistent, predictable patterns over a wide range of grain sizes, whereas others (including patch diversity, contagion, landscape fractal dimension) changed with grain size in a nonlinear way. Accordingly, then from a structural landscape pattern standpoint (*i.e.* the scale effect in landscape pattern), we might expect that a landscape is appropriately described when landscape metrics capture landscape composition and configuration (*i.e.* that any changes in grain size or extent will trigger many changes in landscape heterogeneity assessed by landscape metrics). In other words, one way to look at a landscape is by examining structural connectivity, namely, looking at landscape structures regardless of any biological or behavioral attributes of organisms interacting with them (Tischendorf & Fahrig 2000; Kindlmann & Burel 2008).

From an ecological standpoint, the spatial scale should be defined from the ecological mechanisms that are explored, and the scale at which they are expected to operate based on the perception of the organisms. However, studies that generate quantitative predictions on the scale at which species should respond to landscape attributes are rare (Jackson & Fahrig 2012). Huais (2018) argued that ecologists do not usually know *a priori* the spatial scale at which a new study should be examined, mainly due to a lack of a full understanding of the biological responses of the species involved (Jackson & Fahrig 2015). Although this statement might be true for a wide variety of taxa, this is debatable in others. Indeed, several studies, from the individual to metacommunity level, have clarified the link between spatial scales and the ecological responses of species that are investigated (Levin 1992, Saab 1999, Crawley & Harral 2001, Chase & Leibold 2002, Leibold et al. 2004, Rahbek 2005, Gabriel et al. 2010, Delsol et al. 2018). For instance, scale effects have been particularly well studied in habitat selection (Fortin et al. 2008) and movement (Fryxell et al. 2008) by large mammalian herbivores. Mayor et al. (2009) have reported spatial (and temporal) scales at which ecological and behavioural mechanisms underlying habitat selection in large mammalian herbivores should be investigated. Analysing the activities of animals at a fine scale (*i.e.* 1-100m) allows to investigate feeding site and patch selection, at a local scale (100m-10km), habitat selection and home range at a broader and, at the regional scale (>10 km), migration and (meta)population dynamics (Johnson 1980, Danell et al. 2006). Moreover, body size of species should also be considered when selecting study spatial scale (see Thornton & Fletcher 2014 for a meta-analysis in birds showing that body size is positively related to the characteristic scale of response to landscapes). Thus, a central objective of this chapter is to identify the optimal spatial extent within which to measure the environmental variable under study considering both the landscape structural perspective as well as the ecological one which considers the responses of the organisms.

The aim of this study was to investigate how three landscape metrics (percentage of forest cover, patch density and edge density) affinmaect the occurrence of four species of mammalian herbivores Azara's agouti (*Dasyprocta azarae*), Collared peccary (*Pecari tajacu*), Gray brocket deer (*Mazama gouazoubira*), and South American tapir (*Tapirus terrestris*) (see Table 5 for their ecological traits) in a tropical region characterized by mosaics of Cerrado and Atlantic Forest hotspots. Empirical studies suggest that the scale of effect of the landscape on a biological response can depend on which landscape variable is measured (*e.g.* McGarigal & McComb 1995, Holland et al. 2004, Boscolo & Metzger 2009, Schuster et al. 2013). Here I focused on these three metrics because they represent compositional and configurational facets of the landscape, influence species distribution of many biological groups and could be used at varying scales (Lidicker Jr 1999, Bastian et al. 2006, Bennett et al. 2006, Lu et al. 2013, Lowicki 2017). We used two approaches to investigate the scale effect. First from a structural landscape standpoint, we investigated the variation of these three-landscape metrics with different buffer sizes to detect the spatial scale that most effectively captured landscape heterogeneity. This spatial scale should be determined when the heterogeneity of landscape composition and configuration does not change with buffer size, and in this context, we expect a relatively large buffer size (several kilometers). Second, from an ecological perspective, we evaluated the effect of these three-landscape metrics on the occurrence of the studied species at different scales.

Based on Miguet et al. (2016)'s framework, I predicted that the scale of effect should be larger for larger-bodied species because such forms tend to be more mobile than smaller-bodied species (Bowman et al. 2002; Bowman 2003; Brouwers and Newton 2009). In this case, I expected that for agouti scale of effect would be smaller than for larger-bodied species, such as tapir. I also evaluated if the scale of effect is smaller for landscape variables that most strongly influence breeding and/or foraging success than for landscape variables that most strongly influence dispersal success. Doing this, I expect that the percentage of forest cover would show a scale effect smaller than the configurational metrics (patch density and edge density) for all species.

**Table 5.** Traits of studied herbivore mammal species on the Bodoquena Plateau, Mato Grosso do Sul, Brazil.

| Herbivore species | | Adult body mass (kg) | Diet | Habitat use | Home range (ha) | Dispersion capacity (m) | References |
|---|---|---|---|---|---|---|---|
| *Dasyprocta azarae* |  | 2.9 | Specialist (Fruit) | Forest/edges | 1.34 - 2.45 | 100 - 500 | Paglia et al. 2012, Eisenberg & Redford 1999, Henry 1999, Aliaga-Rossel et al. 2008, Jansen et al. 2012 |
| *Pecari tajacu* |  | 22 | Specialist (Fruit) | Forest/edges | 24 - 800 | 500 - 1000 | Bodmer 1991, Emmons & Feer 1997, Altricher & Boaglio 2004, Desbiez et al. 2010, Paglia et al. 2012, Galetti et al. 2015, Sowls 1984, Keuroghlian et al 2004, Fragoso 1994, Judas & Henry 1999, Pires et al. 2018 |
| *Mazama gouazoubira* |  | 21 | Generalist (Mixed feeder) | Forest/ Open area | 2.7 - 348 | 750 - 1000 | Leeuwenberg et al. 1999, Marques & Santos-Junior 2003, Santos Júnior 2005, Duarte et al. 2012, Pires et al. 2018 |
| *Tapirus terrestris* |  | 225 | Generalist (Mixed feeder) | Forest/ Open area | 0.1 - 100 | > 3000 | Bodmer 1989, Emmons & Feer 1997, Medici et al. 2007, Galetti et al. 2001, Paglia et al. 2012, Pires et al. 2018 |

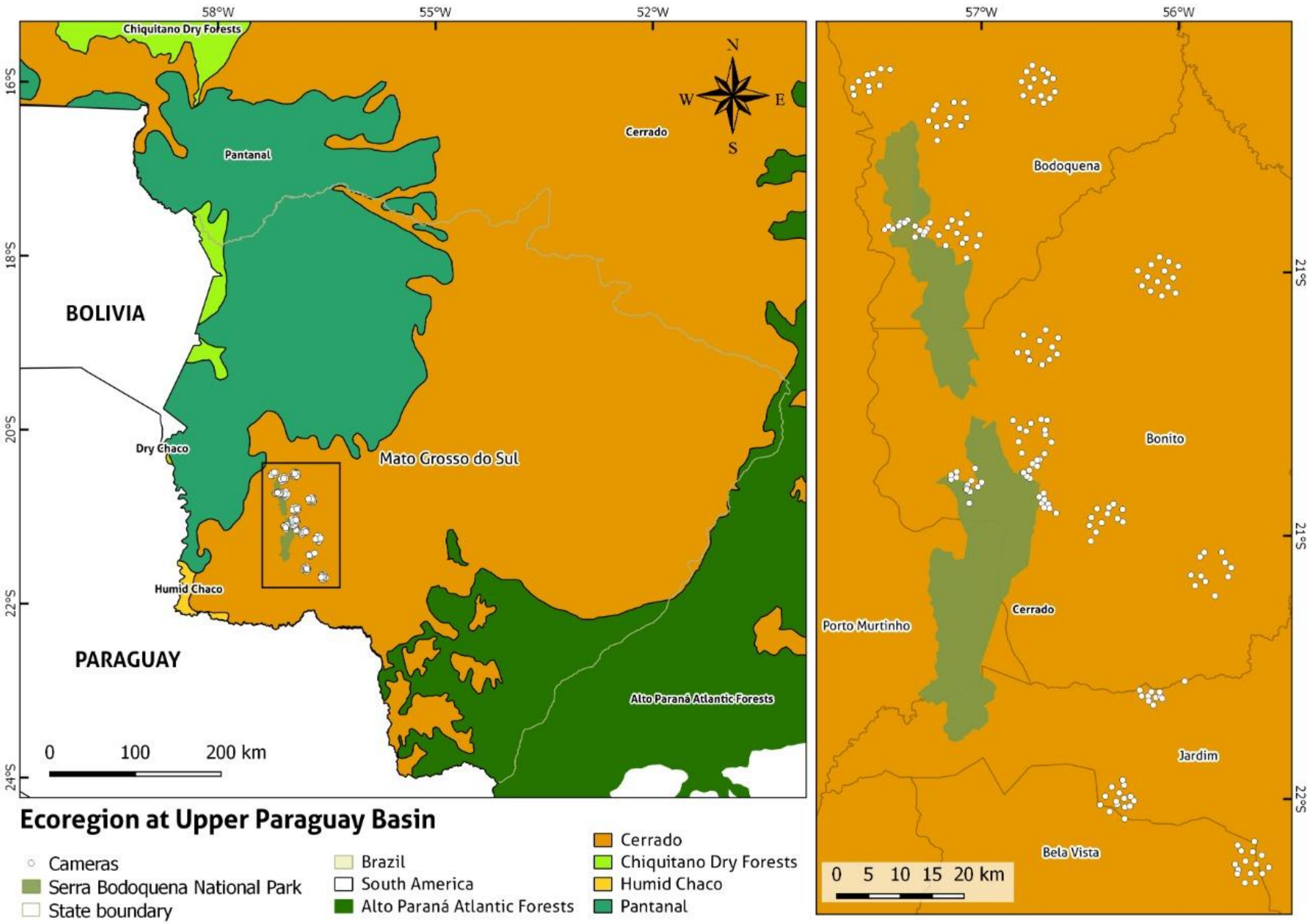

**Figure 5**. Map of study region, in Mato Grosso do Sul, state of the Brazil, show the geographic location and distribution of Brazilian ecoregion in the area and the geographic extent and distribution of the active camera traps in the study region in Bodoquena Plateau with a gradient of forest cover.

## Methods

### *Study system and species data*

The data presented in this paper came from a subset of a savanna monitoring networks in Bodoquena Plateau region (20°25'29.28" to 21°44'19.72" S and 56°52'24.46"56° to 17'23.36" W), CAPES-COFECUB Project. The plateau is located in Mato Grosso do Sul State, southern Brazil (Figure 5). The region is characterized by a mountain chain (altitude 450-800m), a tropical climate (20 to 22°C) with some variation along the plateau from tropical climate in the northern part to tropical humid in the southern part and annual rainfall (1300-1700 mm). The landscape of the region is composed of two main vegetation formation s: the Cerrado (Brazilian savanna) and the Atlantic Forest domains, mainly in the region inside 'Parque Nacional da Serra da Bodoquena (PNSB)'. This area represents an important conservation unit because it is an ecological corridor for biodiversity between the plateau and the BAP plain.

The species data set used in this paper was extracted from camera trap images sampled from the 193 survey site Bodoquena Plateau monitoring network. At each site, a camera trap was deployed for 25 consecutive days, between June 2016 to December 2017. The camera trap network was deployed across the landscape gradient (Figure 6b). Each camera trap was positioned following an standardized protocol to collect data on multiple mammal species: at all 18 sites were installed 193 randomized camera traps; so, for each site, we deployed a set of 10 to 15 cameras trap randomized inside of each site, with the exact number reflecting the percent of forest cover at each site, (*i.e.*, the greater the percentage of forest cover, the more cameras deployed). Camera traps were positioned 40 cm above the ground on the nearest tree to a computer-generated random point, at an angle of approximately 10° relative to the ground. Cameras were set to take a series of three shots when triggered. Camera trap delays to detect passing animal were set at an interval of 3 secs. At the end of the sampling period, SD cards were removed from the cameras and images were analysed by visual observations by the researcher using Wild.ID software (https://github.com/ConservationInternational/Wild.ID). Four herbivore mammal species representing a range of ecological strategies within the regional herbivorous mammal community were used in this paper (see Table 4).

*Landscape data*

Landscape metrics were computed based on the Global Forest Change land cover maps (Hansen et al. 2013). These maps are global products derived from time-series analysis of Landsat images (with a 30 m spatial resolution) showing forest extent and changes from 2000 to 2017. More specifically we used the “2000 Percent Tree Cover” product, which corresponds to the proportion of trees per output grid cell, *i.e.* the canopy closure for all vegetation greater than 5 m in height. In order to update this product, we used the “Forest loss year” product to remove all deforested areas between 2001 and 2017 from the forest class, tree cover was set to 0 for deforested areas. Based on this updated tree cover map, we then produced five binary forests vs. non-forest maps for the year 2017 by applying different thresholds of Percent Tree Cover (0, 5, 25, 50, and 75%). This step was important to compute landscape metrics for different definitions of forests, since we considered that not all mammal species evolve similarly in forested landscapes, with variations of home range, due to varying capacity for displacement, or food demand, for species more demanding in terms of plant composition (Royo & Carson 2005, Young et al. 2013, Chamaillé-Jammes et al. 2016, Ferreguetti et al. 2017, Zimbres et al. 2018).

Finally, to be able to to study a wide range of indicators of spatial extent landscape effects on the animal as suggested by Miguet et al. (2016), we measured landscaped metrics at each camera trap using maps of the vegetation and a series of buffer sizes commonly used to assess the relationships between landscape variables and the occurrence of medium- to large-size mammals (*i.e.* 500, 750, 1 000, 1 500, 2 000, 3 000, 5 000, 10 000 and 20 000 m). This design includes the different scales defined at a fine multiscale level in order to cover different potential indicator of species response at a local and regional scale (Johnson 19820, Danell et al. 2006), especially the relationship between mobility and spatial scale (*i.e.* local movements and dispersal movements related to smaller scales and dispersal movements related to larger scales, Miguet et al. 2016). I decided to exclude the two smallest buffer sizes (*i.e.* 100, 250m) from the final analysis because these buffer sizes would provide information from a small number of pixels, which would have the effect of overestimating or underestimating the species response to the scale (Strahler et al. 1986, Woodcock et al. 1987, Miguet et al. 2016). Metrics were calculated using the ClassStat function from SDMTools package using R software. The ClassStat function computes class statistics based on statistics calculated by FRAGSTATS (McGarigal & Marks 1995). To describe the landscape characteristics, we chose two main groups of metrics to characterise the overall landscape structure: configuration (Patch density - PD, edge density - ED) and composition (Percent of forest cover - PcoForest) metrics (Table 6). Given the number and variety of available metrics in Fragstats, it was our intent to suggest a suite of metrics that measured different aspects of habitat loss and fragmentation and that, when taken together, could provide a comprehensive assessment of habitat loss and fragmentation in a specific landscape. All selected study metrics had a correlation between them of less than 70%. According to Hair et al. (1998), correlations below 0.80 are necessary to avoid multicollinearity problems.

**Table 6**. Landscape metrics significantly related to scale and selected for this study.

| Metric name | Abbreviation | Meaning/ Description in Fragstat | Type of landscape structure |
|---|---|---|---|
| Percent of forest cover | PcoForest | The proportion of the buffer covered by forest | Composition |
| Patch density | PD | Number of patches per hectare | Configuration |
| Edge density | ED | Sum of the length of all patch edges divided by the total area of the buffer | Configuration |

*Data Analysis*

To detect closely spaced study sites and potentially overlapping sites across different landscape measures, we used the Focus computer program (www.carleton.ca/lands-ecol/; Holland et al. 2004).

Using the FOCUS-2.0 program, Plot-Buffer related sampling was conducted using 10.000 iterations to select the best combination for spatially independent points. Based on the retrials, Focus-2.0 randomly selected 169 combinations of 20 independent camera sites from our study sites. I chose to conduct our analysis using the same number of camera points and the same combinations for all analysis at each scale, because the purpose of the study was to understand the response of landscape metrics and the interaction of species- landscape metrics at different scales. To capture the response of each landscape metric across the different scales, for each metric we selected the average from the 20 camera sites at each buffer size for all possible combinations between them. Then, the 169 points for each buffer size were plotted to establish the curve showing response of the landscape metric to the given buffer size (Figure 6a, 6b, 6c and 6d). For each metric we plotted the mean and standard deviation at each buffer size, as well as the metric variance as suggested by Wu et al. (2000) to get a better description of the multi-scale or hierarchical structures of the landscape.

To detect the species response across each landscape metric, as well as along each buffer size, we extracted occupancy values, based on species detection information from the camera-trapping data (Figure 6e). Occupancy models use species detection data from camera trap surveys and assumes that occupancy probabilities do not change during the study period. Thus, for each species, we built a site detection matrix based on the pool of combinations from 20 camera sites. Thus, for each site, a value was allocated based on the presence or absence of the focal species during the survey, with 1 representing the detection or presence of the species at a given site, and 0 describing the non-detection or absence of the species at a given site. A mean for the 20 sites per species and cameras combinations was selected to define probability of species occurrence, through the landscape and during the survey. This study assumed that there are no false detections, but the absence of detection of these species could indicate that the camera site is truly unoccupied or that it is occupied, but that the species was absent during the survey. An occupancy matrix was consrructed in R (version 3.3.2) using the package "unmarked" (version 0.12-2). For each species, we extracted a model for detection probability of each combination between cameras, using the three-landscape metrics for each buffer sizes. Model selection was based on Akaike's Information Criterion (AIC). We then analysed the landscape metric independence associated with species occurrence by ranking these models using the mean of their AIC values. Were used a model-averaging approach when more than one plausible model (*i.e.*, Δ AICc <2) was identified, or when the evidence ratio in support of the “best” model was low.

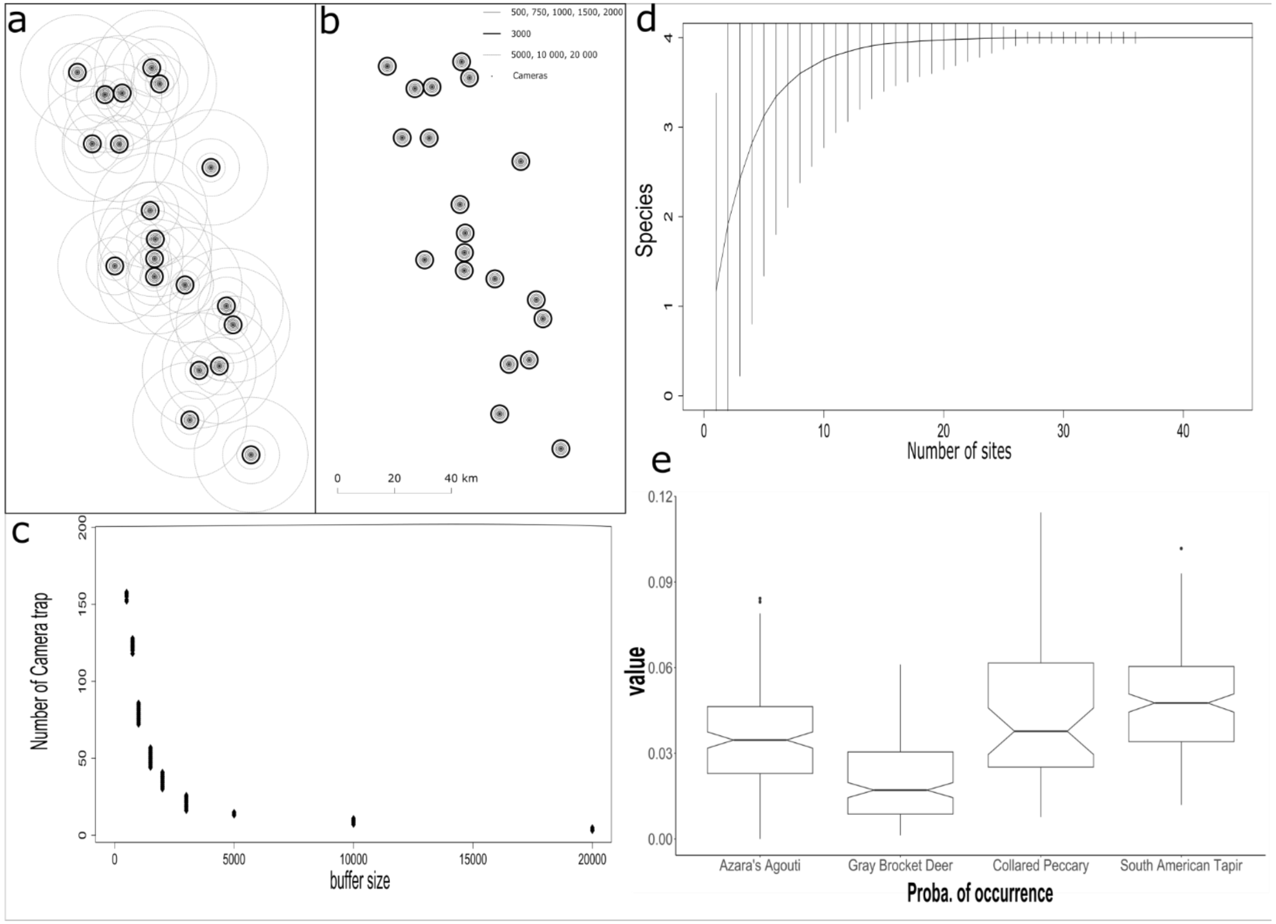

**Figure 6**. Design of the multi-scale study. a) Spatial location of 20 spatially independent sites using all buffer size selected showing potential overlapping; b) At the same spatial location indicating that predictor variables are fully independent at the small scale (3.000 m); c) Relationship between the spatial scale (buffer size in meters) and the number of fully independent sites selected by FOCUS-2.0 required to maintain a non-overlapping predictor variable; d) Species accumulation curve based on the 4 herbivore mammals selected and the standard deviation produced by 1 000 random reorderings; e) Estimated mean occurrence probability for the four selected species from 20 sites, with errors bars representing range of occurrence probabilities among the combination of 20 sites for each species.

## Results

### *Sensitivity of change –detection on landscape metric response across buffer sizes*

Accuracy along the percentage of tree-cover threshold varied widely across the range of landscape metrics selected in this study (Figure 7). Sensitivity varied across the selected landscape metric but did not indicate a loss of response omission to buffer size. For the three tested metrics, there were no obvious effects for the percentage of tree cover on the trends in metric response to buffer size. The two-configuration metrics tended to display a similar curve patterns when the threshold of tree-cover exceeded 50 % (Figures 7a and 7b). However, for the composition metric, the tree-cover threshold tends to influence on the shape of the curves (Figure 7c). Indeed, the shape of the curve when the buffer size is < 1500m, tends to vary depending on the percentage of tree-cover threshold. Thus, the different curves suggest that the best tree-cover threshold to define forest in this landscape is c* equal to 75%. Accordingly, this value will be used throughout the rest of the paper.

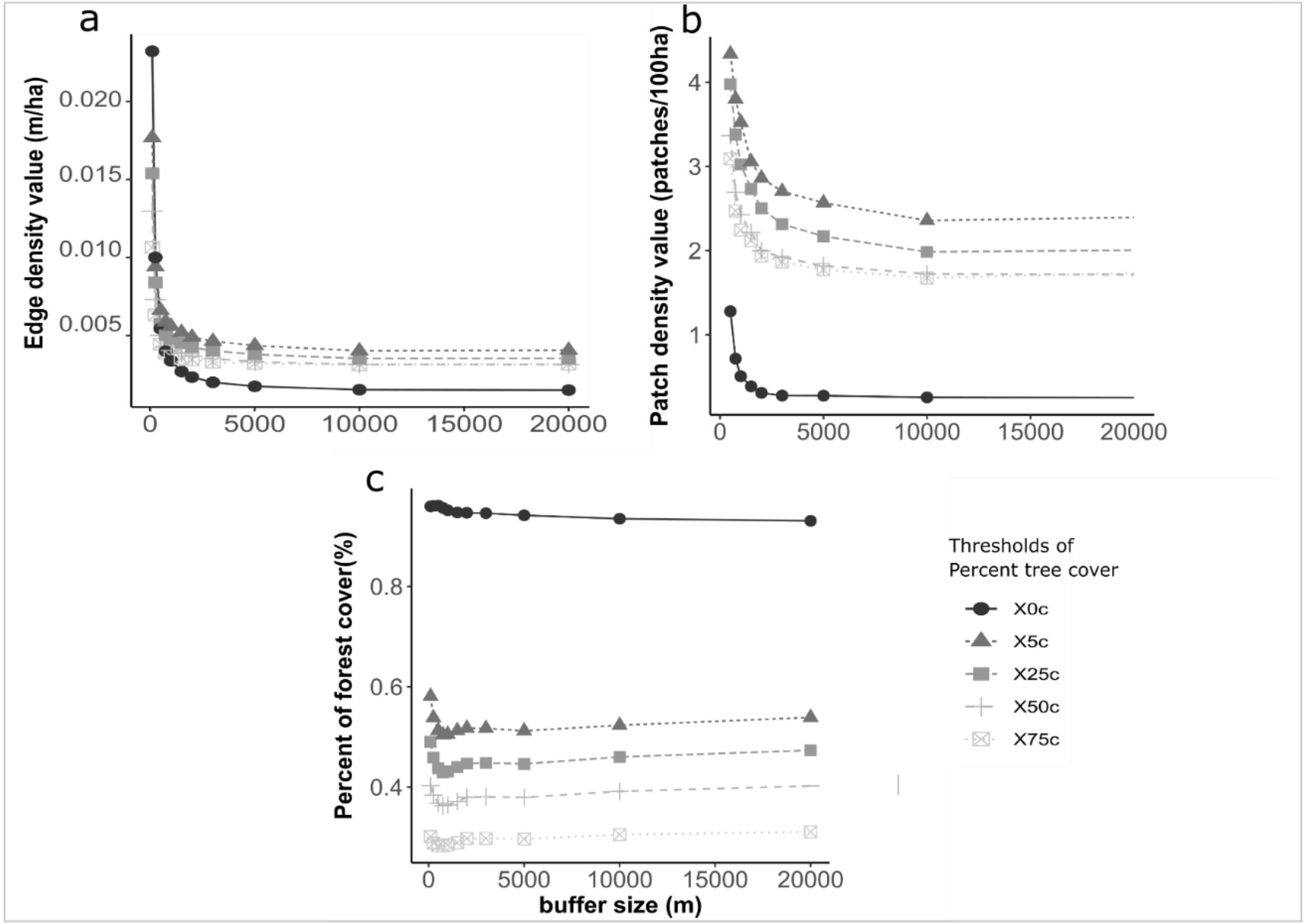

**Figure 7**. Relationship between buffer size and the percent of tree cover sensitivity for different landscape metrics. a) Edge density; b) Patch density; and c) Percent of forest cover (where x0c = 0% forest cover, x5c = 5%, etc).

*Effect of changing buffer size on landscape metrics*

We found three types of response curves for the selected three metrics - *Edge density (1)* showed a constant power law relationship with increasing buffer size, suggesting that these metrics could be predicted with high accuracy over a wide range of grain sizes. The metric displayed a decreasing scaling relation with greater aggregation patterns and decreased monotonically with increasing spatial scale. The ED curve (Figure 8a) was concave and tended to stabilise after the inflexion point at 750 m as the variance curve of ED, but the variance curve seemed to increase after 5,000 m (Figure 8d).

*Patch density (2)* revealed also a constant power-law relationship with increasing buffer size, but only after 750m (Figure 8b). The curve was concave between 500 and 750m, before becoming convex and positive with increasing buffer size. The pattern of Patch density with buffer size was determined significantly by patch heterogeneity acrossthe landscape, as suggested by the PD variance curve (Figure 8e).

*Percent of forest cover (3)* showed no-law scaling relations across the range of buffer sizes. PcoForest metric curve displayed a stable and unchanged curve with buffer size increase, but with a small-amplitude fluctuation with no discernible regularity (Figure 8c). The parameter variance curve, except for the variance at 1,000m and 5,000m due to the location of Serra da Bodoquena National Park (PNSB), suggested a homogeneity in forest cover proportion within the study landscape (Figure 8f).

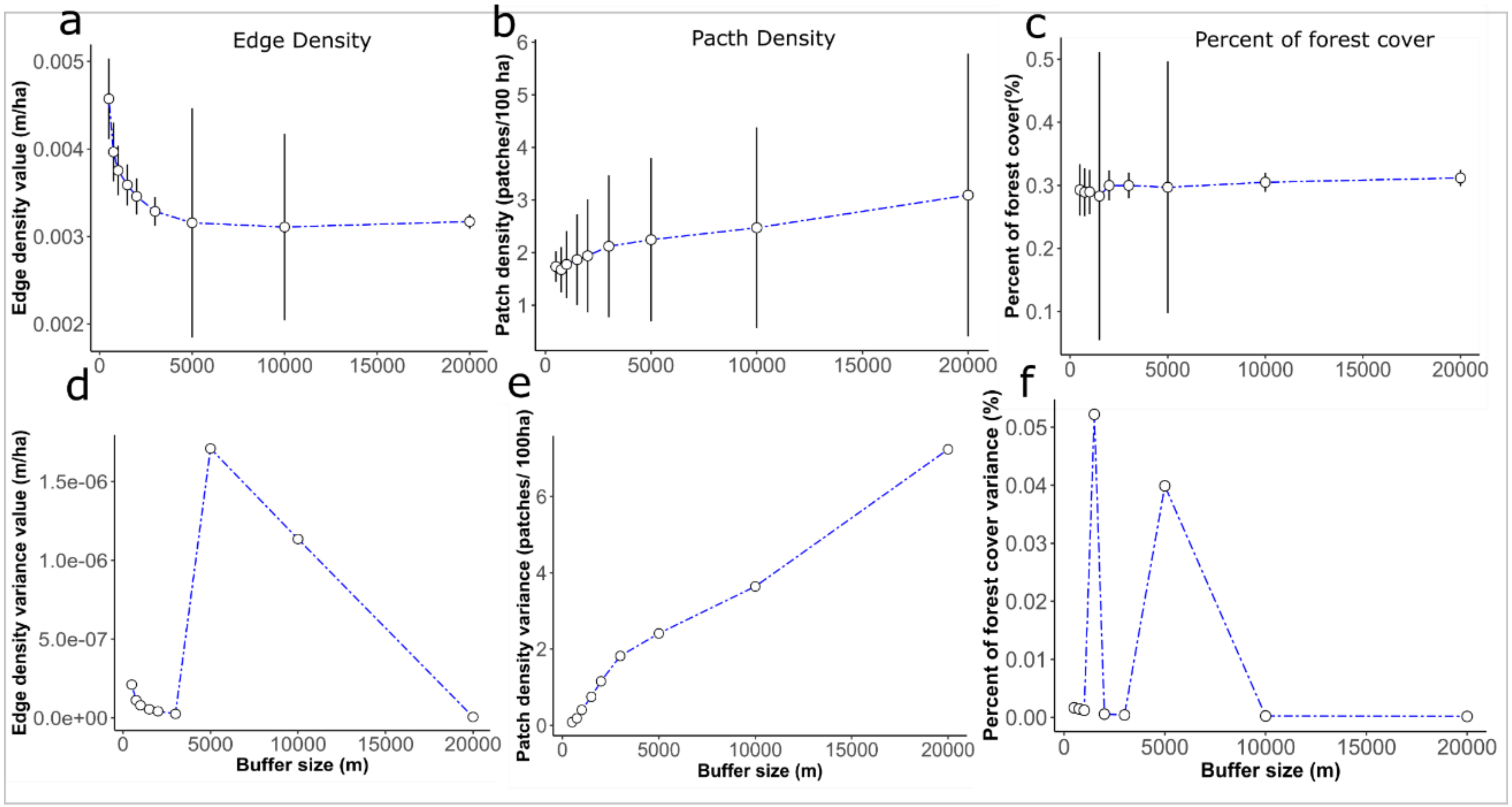

**Figure 8**. Change in three landscapes metrics patterns and their variance with buffer size (a, d) edge density (b, e) patch density (c, f) percentage of forest cover. The value averages were obtained using values from all 193 sites.

### *Landscape metric effects on selected species*

Overall, for the combination of 20 sites, there was an probability of detecting the selected species if the site was occupied (Figure 9a and 9b) in the Cerrado ecosystem. The result from the averaged edge density metric model showed that the response by Azara's Agouti (*Dasyprocta azarae*) was best explained at 500 m (ΔAIC < 2, Figure 9a). However, the other three species selected for the analysis (Figure 9b, 9c, 9d) exhibited no response to edge density across the considered buffer size range. A similar result pattern was found for the patch density metric (Figure 10), where only Azara's Agouti appeared to respond to this landscape metric at 500 m (ΔAIC < 2). Conversely, three of the four species appeared to respond to forest cover percentage. Although models of PcoForest for each species displayed different buffer size responses (Figure 11), the relevant buffer size based on ΔAIC was 500 m for Azara's Agouti (Figure 11a). In the two mixed feeders, the buffer size was 750 m for the South American Tapir, and 1,000 m for the Gray Brocket Deer (Table 7).

**Table 7.** Scale of species responses to landscape metrics (in meters) based on AICc values.

| Landscape metric | Azara's Agouti | Gray Brocket Deer | Collared peccary | South American Tapir |
|---|---:|---:|---:|---:|
| Edge density | 500 | *No response* | *No response* | *No response* |
| Patch Density | 500 | *No response* | *No response* | *No response* |
| Percent of forest cover | 500 | 1,000 | *No response* | 750 |

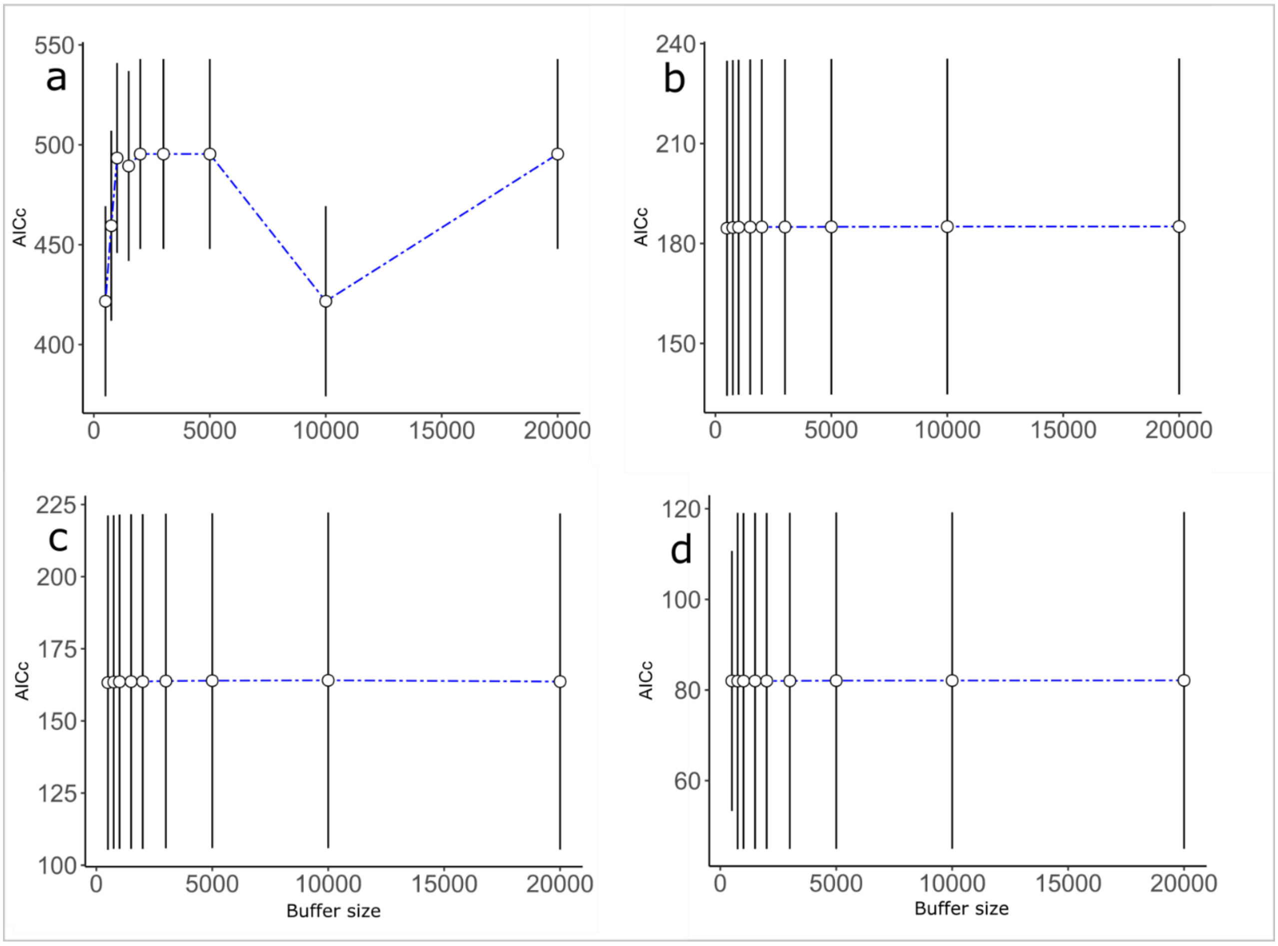

**Figure 9**. Species response to the Edge Density metric across the buffer size range. a) Azara's Agouti (*Dasyprocta azarae*); b) South American Tapir (*Tapirus terrestris*); c) Collared peccary (*Pecari tajacu*); d) Gray Brocket Deer (*Mazama gouazoubira*).

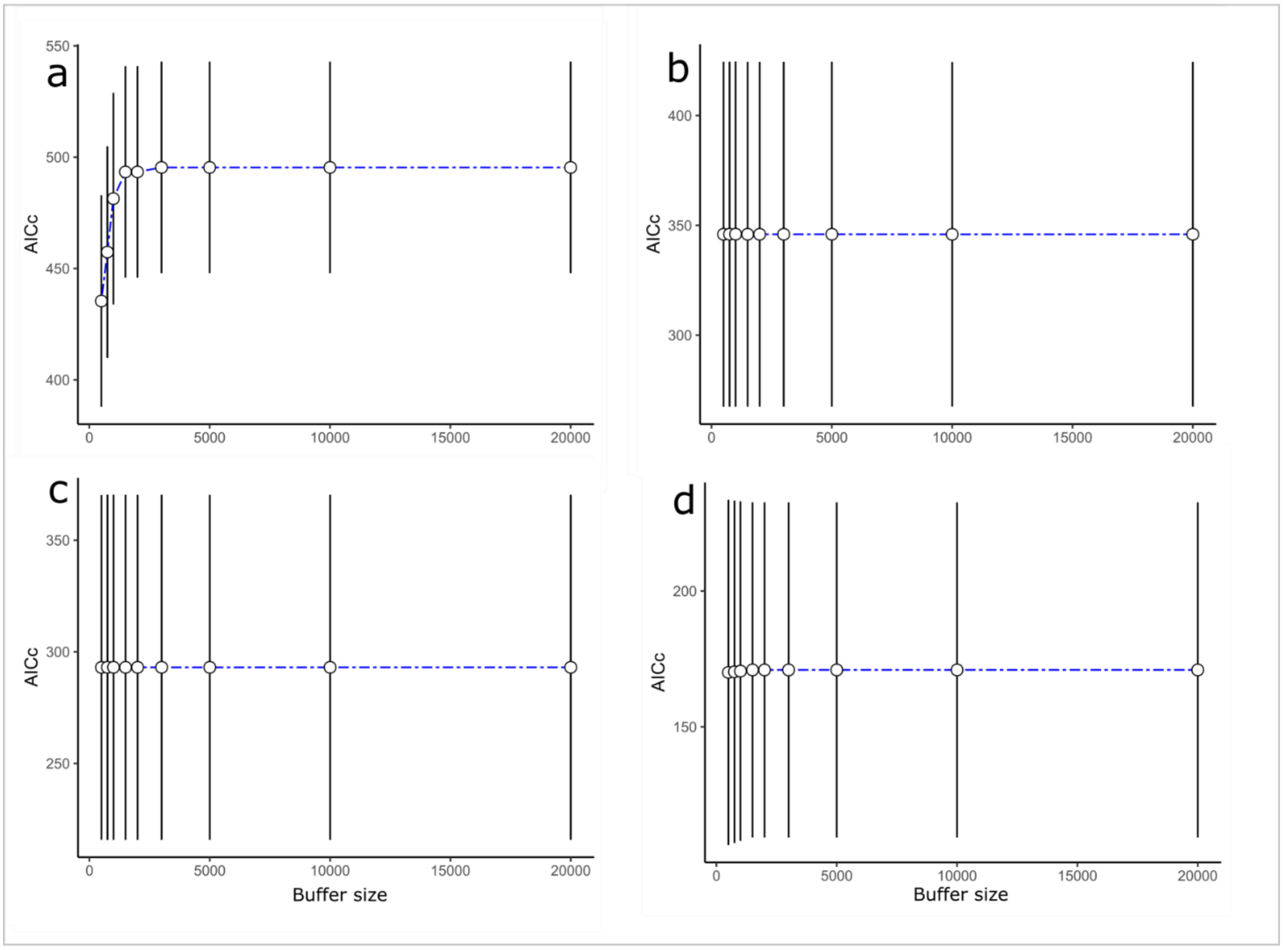

**Figure 10**. Species response to the Patch Density metric across the buffer size range. a) Azara's Agouti (*Dasyprocta azarae*); b) South American Tapir (*Tapirus terrestris*); c) Collared peccary (*Pecari tajacu*); d) Gray Brocket Deer (*Mazama gouazoubira*).

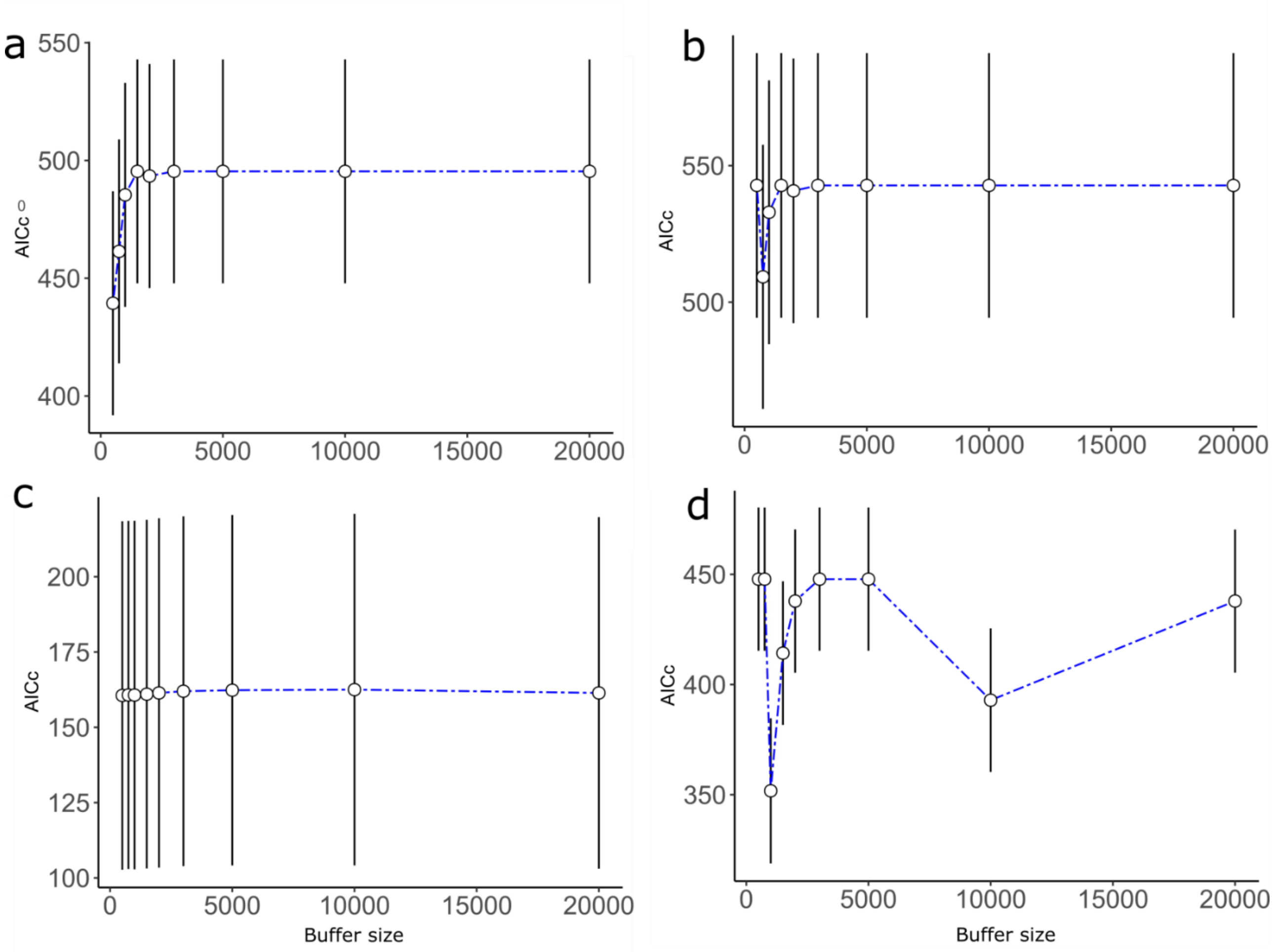

**Figure 11**. Species response to the Percentage of Forest Cover metric across the buffer size range. a) Azara's Agouti (*Dasyprocta azarae*); b) South American Tapir (*Tapirus terrestris*); c) Collared peccary (*Pecari tajacu*); d) Gray Brocket Deer (*Mazama gouazoubira*).

## Discussion

Landscape management and research would be easier if the scale of effect did not have to be estimated empirically in a multi-scale study based on species responses but could be predicted *a priori* based only on landscape structural approaches. For this perspective, the result outlined that such an 'optimum' buffer size should be 5,000 m for the Bodoquena Plateau. Despite the divergence of landscape metric responses observed across increasing buffer size, the landscape pattern was fully described after metric stabilisation at 5,000 m. Indeed, no useful information was provided above this buffer size that could increase configuration and composition metric assessment.

From a structural landscape analysis perspective, the three metrics, describing different landscape facets, displayed eclectic responses across the buffer size gradient. Their responses diverged from patterns reported elsewhere in the literature (Wu et al. 2002). Edge and patch density, in a Cerrado landscape, have displayed both different types of response curves to changing spatial scales, while following a simple scaling relationship (*i.e.* a decreasing power function for Edge density and an increasing power function in the case of Patch density, see Figure 7). Thus, in the case of Cerrado, results showed that the responses of some landscape metrics to changing scales, previously considered as metrics behaving erratically, could provide a predictable response. Thus, metric responses provided evidence of variation of the general response patterns of a specific landscape metric. One interesting finding highlighted the fact that the configuration metrics in our analysis were the only ones to explain a response to the scale extent, and this can help in understanding how landscape change processes occur and how responses are influenced according to the level of local fragmentation, so assisting landscape planning actions.

On the other hand, the composition metric in our study showed a quite stable response across the spatial range, which is consistent with the description of savanna landscapes, characteristically heterogeneous and different *phytophysiognomy* (Eiten 1972, 1993, Klink & Machado 2005). This result could have also been influenced by the precision of the pixel threshold we used to define forest (*i.e.* 75%). A smaller value might have provided different responses. However, the composition variable illustrated the importance of tree presence in the Cerrado, characterizing here that variation in tree cover have different phytophysiognomies on this Domain, as noted by Goodland (1971).

Our results also show that patch density variation increases with buffer size, suggesting substantial fragmentation of forest fragments in the Cerrado in correlation with increased scale extension. This result is also present in the edge density response variance which, at 5,000 m, is unusually large, suggesting substantial variation in the size and shape of the fragments, with a higher concentration of small forest areas or a significant amount of edges for the larger areas. This observation may be related to the presence of the 'Serra da Bodoquena National Park (PNSB) protected area, which occurs within in the study region and has, within its limits, a higher concentration of forest fragments. The presence of the Park is also observed in the PcoForest variance curve, which shows two peaks of high variability in percent forest at 1,000 m and 5,000 m. Such values are explained by the proximity to a large forest, such as Cerradão (a type of forest formation with high tree density), here the PNSB Protected Area.

Despite the important patterns detected by our landscape structural analysis, a key question emerges: *Should we use the scale 5,000 m as a unit to study mammals and plan for their conservation in this region?* The main practical message from our findings is that the 5,000 m scale extracted from a pure landscape structural approach could not provide a best scale to investigate ecological responses of the chosen study species to the selected landscape metrics. This has consequences for conservation planning because most initiatives involving ecological zoning, and biodiversity land-use prioritization use as planning units' landscapes larger than 1000 m.

As expected, species response varied depending on landscape metrics and scales. Only three of the four species displayed a response to at least one of landscape metrics considered. Interestingly, all the best spatial scales for the species responses were local (Johnson 1980, Danell et al. 2006, Jackson and Fahrig 2015), unlike our expectations and below the 5,000 m recorded with the landscape structural approach. Considering the species individually, as expected, the small herbivorous mammal, Azara's agouti (*Dasyprocta azarae*), had its best spatial scale at 500 m, for all metrics, conforming that landscape structure influences various aspects of a species biology. In contrast, and as expected, the two generalist species (*Mazama gouazoubira* and *Tapirus terrestris*) only showed a scale effect for forest cover percentage at > 750 m.

Collared peccary (*Pecari tajacu*) was the only species not to demonstrate any scale of response to our selected metrics. This result is interesting and unexpected from considerations of the life history of the species. Indeed, this species has specific traits, including diet and habitat preferences, that would suggest that environmental changes such as loss of native forest cover would be associated with extinction drivers for the species. The lack of scale responses by collared peccary to our configuration and composition metrics, descriptors mainly related the forest matrix, could indicate that the species may have found new conditions (*i.e.* food items, food patch) for survival in the adjacent matrix with agricultural and livestock. Another possible explanation might be related to vegetation gradient used to define forest cover in the study (*i.e.* threshold of percent of tree cover of 75%). In fact, collared peccary may have a different perception of vegetation cover from Cerrado, due to its diet, which is focussed largly on fruits and seeds (Barreto et al. 1997, Flores et al. 2013, Galetti et al. 2015). This species can find its food around singe trees or tree clusters and, therefore, may not have the same perception of forest as we used for our analysis. A lower threshold, with the analysis including a revised tree cover vegetation index (*e.g.* EVI) to define the percentage of forest at the pixel level could provide a more accurate estimate of the species response to the landscape metric (Miguet et al. 2016).

As we expected, however, Grey Brocket and the South American tapir, both generalist in terms of their diet and habitat, showed greatest flexibility in terms of landscape metrics (Medici et al. 2007, Bueno et al. 2013, Hilbert et al. 2013, Ferreguetti et al. 2015, 2017b). In addition, both these species have large home ranges (see Table 4), and therefore are likely to have higher metabolic demands, and 'energy requirements'. Consequently, the distribution of their key resources will occur at scales available in larger landscapes. (Schoener 1968, Peter 1983, Holling 1992, Bowman et al 2002, Boscolo & Metzger 2009, Brouwers & Newton 2009). So, our results for the forest cover gradient of Cerrado and Atlantic Forest suggest that the response of the species is related to their body size and home range, as has been shown for other species of herbivores (Wilmshurst et al. 2000, Laca et al. 2010, Fisher et al. 2011).

Diet and habitat use seem to be more related to landscape metrics than to scaling-response patterns. In this study, a difference in the response scale was observed for generalist species which did not show any response to the configuration metrics, while one of the specialist species, *Dasyprocta azarae,* displayed a finer scale response to the metrics. According to Wang et al. (2013), these two-configuration metrics can be considered as good fragmentation measurement tools. For example, the lower response scale for specialist feeders is expected because such species require stable resource availability and so will be more affected if such feeding resources are reduced by fragmentation (Miguet et al. 2016). Additionally, a species' mobility capacity will be a determining factor when accessing new sites of resource availability. A similar functional difference was also found for habitat use characteristics with more specialist users (Forest/edges), such as *Dasyprocta azarae*, showing smaller of response scales than than generalist users (Forest /Open area), such as *Mazama gouazoubira*, for the composition metric. In fact, gray deer and the South American tapir live in open mixed habitats near the forest and therefore would be expected to show a low sensitivity to landscape change (Ghiarello 1999, Dotta & Verdade 2007) compared to Azara's agouti (*Dasyprocta azarae*), which is more of a forest habitat specialist (Fleury & Galetti 2004). Thus, the observed relation between percentage of forest cover, species habitat preference and their response scales highlighted the importance of species ecological requirement in defining the scale at which they responded to forest cover levels: at a smaller local scale for specialist *vs.* larger local scale for generalist species (Miguet et al.2016). A similar pattern was detected for carnivorous species in Brazil, where the percentage of Cerradão impacted generalist carnivorous persistence less (Melo et al. 2010). Indeed, habitat generalists may have better dispersal ability than habitat specialists and so display a larger scale response (Melo et al. 2010, see Miguet et al. 2016). However, this may be linked to landscape configuration and heterogeneity characteristics, via changes in species foraging behaviour.

The results reported here have important implications for biodiversity conservation in the region. While the use of information from large scales (*e.g.* > 5,000 m) may facilitate the process of regional planning by representing the structure of the landscape dynamics in the Bodoquena Plateau, as we shown, this scale does not account for important landscape variables for the herbivore mammals. So, if an initiative has the aim of conserving multiple mammal species, it is important to approach this challenge using multiscale and hierarchical conservation planning that will enable prioritization of the locations with the greatest conservation need where the greatest conservation benefit can be accomplished most efficiently (see Wiens & Bachelet 2009, Hay & Marceau 2011). Such hierarchical nesting of conservation plans, for example, should allow assessment of how the conservation actions taken at the Bodoquena Plateau will help meet specific goals for each species set at a specific scale. Accordingly, conservation strategies for the Bodoquena Plateau could be usefully and effectively informed by our findings. For example, instead of using multiple scales chosen arbitrarily, a conservation plans for mammals in this region could be focused on landscape information at the 500 m, 1,000 m, and 5,000 m scales, as these seem to match the perceptions and responses of species present, but which have very different environmental requirements, including the scale appropriate for representing the structural landscape pattern of the region.

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# CHAPTER III

## Idiosyncrasies of herbivore mammal responses to land-use changes in a region increasingly affected by agribusiness in the Cerrado hotspot

## Abstract

Of almost 4000 species of terrestrial mammalian herbivores on our planet, 74 species are large herbivores (> 100 kg), of which more than half are listed as threatened while the remainder have decreasing populations. This loss is a cause of increasing concern and not only represents a loss of a species but can also have impacts on the whole ecosystem of which the species are part. Herbivores influence the ecosystem in a multitude of ways. While their most obvious role is as fruit dispersers, they act also as ecological engineers in the creation and physical modification of the structure of the habitats, influencing trophic guild structures and participating in top-down and bottom-up processes. Additionally, they exercise effects on other animals, including in their role as the prey of carnivorous. Here, we ask whether herbivore mammal species composition and species occupancy probability are influenced by land-use changes in a region of Cerrado and Atlantic forest vegetational natural ecosystems. For this, were evaluated the response of herbivores within a native vegetation loss gradient in a land-use change context, with a matrix of agriculture (soybean and corn). Were evaluated small, medium and large-sized species – one of the first studies to sample this size range in the same area in the Cerrado domain – cujos dados come from the subset of global savanna monitoring networks in Bodoquena Plateau region (20°25’29.28” to 21°44’19.72” S and 56°52’24.46”56° to 17’23.36” W), with the project ‘*PELD Planalto da Bodoquena*. We recorded a total of 23 species of small, medium and large herbivore mammals with cameras trap and live traps. The pattern of occupancy as a function of the percent of forest cover in the landscape within the 5,000 m buffers was highly species dependent. Six species responded to percentage of forest cover, and one to patch density. Here, only White-lipped Peccary (*Tayassu pecari*) which is habitat and diet specialist, South American Red Brocket (*Mazama americana*) which is forest dependent, and Gray Brocket Deer (*Mazama gouazoubira*) which is not forest dependent responded positively to forest cover percentage. We associated this response with the diet of these species, primarily their dependence on native fruits and herbs. Possibly, for dietary herbivorous species, we note that a threshold below 30% of the forest may indicate significant loss of individuals in our study area. The Feral pig (*Sus scrofa*) had a negative response, preferring open areas. The same was observed for Capybara (*Hydrochoerus hydrochaeris*), a species adapted to open areas and associated with water bodies and for Punaré (*Thrichomys fosteri*), a species that uses forest but occurs in open edge vegetation in the Cerrado and other Domains. The lack of a clear response by herbivore mammals to the land cover may not be uniform but reflect species-

specific responses to a suite of different processes. Firstly, it is possible that the studied environmental gradients were not strong enough to elicit clear responses from the chosen groups. Secondly, source-sink dynamics has been suggested as an important mechanism by which resilience is expressed at the population level by mammal species in fragmented landscapes in Brazil.  Third, the presence of different species along the disturbance gradient may indicate low overall level of hunting pressure. Fourthly, extinction debt may occur in the region: land-use changes in Bodoquena is a recent phenomenon. In terms of conservation and management, a big question that emerges from our results and those of other recent studies is: how could we optimize the conservation of a community where most species respond in idiosyncratic ways to land-use changes? We recommend different strategies and complementary methods to prioritize the conservation of herbivorous mammals in our study area.

## Resumo

Entre as espécies de herbívoros terrestres mamíferos do nosso planeta, 74 espécies são consideradas grandes herbívoros (> 100 kg), dos quais mais da metade estão listados como ameaçados, enquanto o restante tem populações decrescentes. Essa perda é uma causa de preocupação crescente e não representa não só a perda de uma espécie, mas também pode ter impactos em todo o ecossistema do qual as espécies fazem parte. Os herbívoros influenciam o ecossistema como dispersores, na criação e modificação física da estrutura dos habitats, e pode influenciar as estruturas de guildas tróficas nos processos top-down e button-up. Aqui, perguntamos se a composição de espécies de mamíferos herbívoros e a probabilidade de ocupação das espécies são influenciadas pelas mudanças no uso da terra em uma região de ecossistemas de Cerrado e remanescentes de Mata Atlântica. Para isso, avaliamos a resposta de herbívoros dentro de um gradiente de perda de vegetação nativa em um contexto de mudança no uso da terra, com uma matriz de agricultura (soja e milho). Foram avaliadas espécies de pequeno, médio e grande porte - o primeiro estudo a amostrar essa faixa de tamanho na mesma área de estudo, que constitui a região do Planalto da Bodoquena (20 ° 25'29.28 ”a 21 ° 44'19.72” S e 56 ° 52'24.46 ”56 ° a 17'23.36” W), viabilizado pelo projeto 'PELD Planalto da Bodoquena’. Registramos um total de 23 espécies de pequenos, médios e grandes mamíferos herbívoros com armadilhas fotográficas e armadilhas de captura (Tomahawk e Sherman). O padrão de ocupação em função do percentual de cobertura florestal na paisagem dentro dos 5000 m foi altamente dependente das espécies. Seis espécies responderam ao percentual de cobertura florestal e uma à densidade de cobertura. Aqui, apenas a Queixada (*Tayassu pecari*), especialista em habitat e dieta, o Veado Mateiro (*Mazama americana*), que é dependente da floresta, e o Veado Catingueiro (*Mazama gouazoubira*), que depende da floresta, mas também utiliza áreas abertas, responderam positivamente à maior porcentagem de cobertura florestal. Associamos essa resposta à dieta dessas espécies, principalmente à dependência de frutas e ervas nativas. Possivelmente, para espécies herbívoras da dieta, observamos que um limiar abaixo de 30% da floresta pode indicar perda significativa de indivíduos em nossa área de estudo. O Porco selvagem (*Sus scrofa*) teve uma resposta negativa, preferindo áreas abertas. Esse padrão também é observado para a Capivara (*Hydrochoerus hydrochaeris*), espécie adaptada a áreas abertas e associada a corpos d'água e o Punaré (*Thrichomys fosteri*), uma espécie de pequeno mamífero que utiliza floresta, e ocorre em vegetação de borda aberta no Cerrado e em outros biomas. A falta de uma resposta clara dos mamíferos herbívoros à cobertura da terra pode não ser

uniforme, mas reflete respostas específicas da espécie a um conjunto de processos diferentes. Em primeiro lugar, é possível que os gradientes ambientais estudados não tenham sido suficientemente fortes para obter respostas claras dos grupos escolhidos. Em segundo lugar, a dinâmica fonte-coletor tem sido sugerida como um importante mecanismo pelo qual a resiliência é expressa em nível populacional por espécies de mamíferos em paisagens fragmentadas no Brasil. Terceiro, a presença de diferentes espécies ao longo do gradiente de perturbação pode indicar baixo nível geral de pressão de caça. Em quarto lugar, a dívida de extinção pode ocorrer na região: as mudanças no uso da terra em Bodoquena são um fenômeno recente. Em termos de conservação e manejo, uma grande questão que surge de nossos resultados e de outros estudos recentes é: como podemos otimizar a conservação de uma comunidade onde a maioria das espécies responde de maneira idiossincrática às mudanças no uso da terra? Recomendamos diferentes estratégias e métodos complementares para priorizar a conservação de mamíferos herbívoros em nossa área de estudo.

## Introduction

Human global environmental actions in recent years are driving species extinction rates at an intensity that greatly outpaces those of the past (Chapin et al. 1998, Ceballos & Ehrlich 2002, Hooper et al. 2012, Pimm et al. 2014). Of the almost 4000 species of terrestrial mammalian herbivores on the planet, 74 species are considered to be large herbivores, of which more than half are listed as threatened while the remainder have decreasing populations (Ripple et al. 2015). Iconic animals such as African elephants (*Loxodonta africana*), common hippopotamus (*Hippopotamus amphibius*) and black rhinoceros (*Diceros bicornis*), plus the last large mammal in Neotropical region, the lowland tapir (*Tapirus terrestris*), are among these threatened herbivores (Hamsen & Galetti 2009, Medici 2010, Keuroghlian et al. 2014, Ferreguetti et al. 2017). This loss is a cause of increasing concern and not only represents a loss of a species but can also have impacts on the whole ecosystem of which the species are part. Herbivores influence the ecosystem in a multitude of ways. While their most obvious role is as seed dispersers (Bodmer 1991, Keuroghlian & Eaton 2009, Nagy-Reis et al. 2017), they act also as ecological engineers in the creation and physical modification of the structure of the habitats, influencing trophic guild structures and participating in top-down and bottom-up processes (Fritz et al., 2002, Hopcraft et al. 2009, Smit & Putman 2011). Additionally, affect other animals (Foster et al. 2014), including their role as prey of carnivorous (Hopcraft et al. 2009, Cavalcanti et al. 2010, Azevedo et al. 2016).

Nearly all threatened mammal species occur in developing countries, where major threats include land-use change, hunting, and resource depletion by livestock and agriculture (Cullen Jr et al. 2001, Zimbres et al. 2012, Morcatty et al. 2013, Keenan et al. 2015, Ripple et al. 2015, Arvor et al. 2017). In South America, most studies on how land-use change affects herbivore mammals have been done in forest systems, such as Amazon, Atlantic forest and Pantanal (*e.g.* Pardini et al. 2010, Jácomo et al. 2013, Galetti et al. 2015, Rodrigues et al.

2017). In addition, there has been a strong tendency to focus on large and medium-sized species (Di Marco et al. 2017).

Including information about little-studied but highly important groups is at the heart of conservation strategies. Improvement requires overcoming various knowledge shortfalls, including how small, medium and large-sized herbivores respond to land-use changes in landscapes characterized by mosaics of native vegetation, such as those where savannas (Cerrado) and Atlantic forest coexist. Cerrado and Atlantic Forest are biodiversity hotspots, and together harbour more than 50% of the endemic species in Brazil (Myers et al. 2000, Paglia et al. 2012). Estimates indicate that approximately half of the original Brazilian savanna coverage has been transformed into planted pastures, annual crops and other forms of anthropic land-use (Klink & Machado 2005, PPCerrado 2014, Beuchle et al. 2015, Stan et al. 2015, Strassburg et al. 2017), affecting resources, such as the water and soil cycles (Hunke et al. 2015, Spera et al. 2016, Nobrega et al. 2017). The marked expansion of agrobusiness activity has contributed substantially to the large-scale landscape changes in Brazilian ecosystems (Castro et al. 2012, Grecchi et al. 2014, Moraes et al. 2017, Strassburg et al. 2017). The Atlantic forest has suffered a dramatic loss, with less 12% of the original vegetation now remaining all over Brazil (Ribeiro et al. 2009).

One of the most prominent land-use changes affecting mammals in Brazil is the replacement of native vegetation by exotic pastures (*e.g. Brachiaria* spp.), plantation monocultures (*e.g. Eucalyptus* spp.), and crops (*e.g. Glycine mas* – soy, and *Zea mays* - corn). Because numerous species of herbivores depends on native vegetation and landscape heterogeneity for food and shelter, transformations of native vegetation extent, configuration and composition have frequently been shown to alter the structure and functioning of mammalian communities (Lyra-Jorge et al. 2008, Cáceres et al. 2010, Villéger et al. 2010, Zimbres et al. 2012, Zeilhofer et al. 2014, Fahrig 2017, Hannibal et al., 2018).

In a community, the consequences of landscape changes may impact different herbivore species in different ways. Species responses may vary according to the degree to which a taxon depends on forest conditions and functional significance of the landscape. In landscapes characterized by mosaics of vegetation types of different phytophysiognomies (*e.g.* forests, savannas and grasslands), herbivore assemblages will contain species that differ in their dependence on native closed-canopy vegetation, especially for forests. In general, studies have shown that for the Cerrado ecosystem, a number of mammalian species can survive even in environments with high levels of disturbance, and with differences in dependence on forest cover, with negative and positive correlations between patch size and species richness (Cáceres et al. 2010, Santos-Filho et al., 2012, Bernardo & Melo, 2013, Magioli et al., 2016, Regolin et al. 2017, Hannibal et al. 2018). Additionally, the capacity of Cerrado-inhabiting species to exploit areas of open vegetation, allows them to use intermediate matrix vegetation forms as a source of supplementary resources, as well as a means of transit within the landscape (Lange et al. 2012, Driscoll et al. 2013, Brady et al. 2014, Borges-Matos et al. 2016). For example, Borges-Matos et al. (2016) studied the composition of a non-volant small-mammal assemblage in an Amazonia-Cerrado transition region and did not find significant relationship between patch size or connectivity, but a strong and significant relationship to matrix type. They considered the matrix to be the most important landscape variable in determining small-mammal community composition in that landscape.

In the case of the Atlantic Forest it seems to be different, as the size and isolation of the spots seem to be the most important elements of the landscape (see Vieira et al 2009). In other ecosystems, there is a growing body of evidence that matrix heterogeneity is important for small mammal composition and that matrix size and distribution may influence species distribution and use (Borges-Matos et al. 2016).

Historical factors can also account for the links between anthropogenic environmental gradients and the responses of herbivores in mosaic landscapes. Brown (1997) and Melo et al. (2019) suggested that some animal groups do not respond to the processes of forest fragmentation in the Atlantic Forest, Cerrado, or Amazonia, because they have experienced historical processes of forest contraction and expansion and that these have generated more resilient communities, which in consequence are less sensitive to habitat fragmentation. In syntheses, except with some specific cases of high dependence of forest cover, *e.g.* primates (Chapman & Onderdonk 1998), the responses of herbivores seem to be strongly context dependent. This is clearly a situation which demands focused studies that consider aspects of land-use configuration and composition, together with land-use management practices (Fahrig 2017), and their influence on environment.

In this article, we ask whether herbivore mammal species composition and species occupancy probability are influenced by land-use changes in a region of natural vegetative ecosystems with predominance of the Cerrado and remnants of the Atlantic Forest. For this, we evaluated the response of herbivores within a gradient of native vegetation loss in a land-use change context with a matrix of agriculture (soybean and corn), and pasture. We evaluated small, medium and large-sized species – the first of its kind in sampling this size range in the same area. Based on the habitat amount hypothesis (Fahrig 2013, Melo et al. 2017), we expect that species that depend on specific forest-based resources (*e.g.* frugivores *Pecari tajacu, Tayassu pecari Dasyprocta azarae*) will be more susceptible to forest loss. However, we expect that this relationship will not be linear because in landscapes with intermediate levels of forest and agriculture, frugivores could benefit from resources from both systems. For generalist species, such as tapirs (*Tapirus terrestris*), we expect that the loss of forest will have a positive or neutral effect depending on the matrix, since they should potentially gain food and other opportunities from the changes created by agriculture. For grazers, such as *Mazama* sp. (deer) and *Hydrochoerus hydrochaeris* (capybara), we expect forest loss to have a positive effect, because forest loss increases herbaceous species that provide food resources for these species. We also mentioned that human-modified environments tend to have a lower density of predators - so mortality is reduced, surveillance may be lower, more open habitats can be used and less nutritious foraging can be used, with no time-limited costs for the need to avoid predators because they are always on the move. Moreover, we expect that the agriculture-dominated landscape would result in a general decrease in the occupation of most herbivore mammals because species will have more difficulty in permeating extensive agricultural areas and may suffer from indirect impacts such as pesticides or direct ones such as vulnerability to predation and conflicts with humans, plus road kill and hunting and collection for pets and for sale.

## Methods

### *Study area*

The data presented in this paper come from the subset of global savanna monitoring networks in Bodoquena Plateau region (20°25’29.28” to 21°44’19.72” S and 56°52’24.46”56° to 17’23.36” W), with the project ‘*PELD Planalto da Bodoquena: rede de interações em longo prazo’*, Mato Grosso do Sul State, southern Brazil (Figure 12). The region is characterized by a mountain range (altitude 450-800m), a tropical climate (20 to 22°C), with some variation from tropical climate in the northern part; to tropical humid in the southern part. Annual rainfall is 1300-1700 mm. The landscape of the region is composed by two main areas, Cerrado (Brazilian savanna) and the Atlantic Forest biomes. Overall, region represents an important conservation area, which acts as an ecological corridor.

To categorize the landscapes where field samples were collected, we first divided the entire region into areas of 5,000 hectares (see methodology in Tables 1SM and 2SM, and

Figure 1SM until 7SM), and from the locations thus available, selected 15 landscapes to represent the changes in land-use cover and configuration. These landscapes cover the entire vegetation cover gradient (from 9 to 91%) and are distributed across the entire study region (Figure 12 and see Figures 1SM until 6SM, and Table 1SM, for complete information).

### *Scale and landscape metrics*

Given that the study area lies within a region of great landscape complexity and structure, we used 5,000 m buffers that contained all relevant information to describe our landscape pattern. In such buffers, we analysed all species occupancy along gradients of native vegetation loss (*see Chapter 2*). Using the ClassStat function, in which class statistics are calculated by Fragstats (McGarigal & Marks, 1995), we computed the metrics using the SDMTools implementation package in R software. To describe the landscape characteristics, we chose two main groups of metrics, composition and configuration, that have been used in many studies aiming to measure aspects of landscape pattern (Neel et al. 2004, Lustig et al. 2015, Frank & Walz 2017, Lowicki 2017, Zhang et al. 2018). For configuration we used patch density (PD), and edge density (ED), and for composition we used percent of forest cover (FC), percent of agriculture (Agr), and percent of pasture (Past). We used a Pearson's correlation matrix to examine correlations between all selected metrics.

### *Camera and Live traps to sampling herbivore mammals*

From February 2016 to December 2017, the species data set used in this paper was sampled from 15 sites, along the landscape gradient of 4,720 km² (Figure 12). In total we placed 193 camera traps and 88 transect lines, totalizing 4,576 live traps. For each site, we deployed a set of at least 10 to 15 cameras trap and of 208 to 312 live traps per night. The randomization of cameras and transects containing live traps considered the percent of forest cover at each site (*i.e.*, more cameras and transects in region sites with higher forest percentage). Camera traps were deployed for 25 consecutive days on average and were positioned 40 cm above the ground on the nearest tree of a computer-generated random point, at an angle of approximately 10° to have a maximum view on the ground. Cameras were set to take a series of three shots when triggered and we do not use bait to attract.

For small mammal sampling, we installed 26 stations per transect, containing 26 live-trap Tomahawk ™ (70 X 35 x 40 cm, 45 X 20 X 20 cm and 30 x 17.5 x 15.5 cm) on the soil, and 26 Sherman (30 X 8 X 9 cm) in the vegetation up to a height of 1.5m (Belant & Windels 2007, Caceres et al. 2011a). Along the transect traps were separated by distances of approximately 20 m (dictated by trapping site availability). Live traps were baited with slices fruits and a mixture of oats, peanut butter and banana. At each site, the sample effort was 56 live traps/transect for three consecutive nights, with six transects per site, totalling a sampling effort of 1008 traps/site. We considered this effort comparable with other studies (Jones et al., 1996, Vieira & Palma 2005, Holland & Bennett 2007, Hannibal & Godoi 2015).

### *Data Analysis*

We investigated the influence of landscape structure on the occupancy probability of herbivore mammals through single-season occupancy models (MacKenzie et al., 2003). The data from camera and live traps were used to calculate the detection/non-detection of 23 target species of herbivore mammals. We modelled the occupancy probability for each species using three non-correlated variables extracted from sampling sites (Table 6SM). The sampling units were 10 to 15 camera traps, associated with 312 live traps inside in six transects at each of the 15 sites. Our best-fit models were selected using the Akaike Information Criterion (AIC) (Akaike 1973), adjusted for small sample size (AICc), and all models with a ΔAICc value < 2 were considered to be equivalent and finally, we used Akaike weight to understand the relative importance of model selected was the best of all those available (Hurvich & Tsai 1989, Burham & Anderson 2002). All parameter estimates and standard errors are reported from the 'best-fit' model with the lowest AICc. The models included the landscape as random variable to take resampling into account. We compared models with a stepwise-backward approach, testing the influence of the removed variable with an analysis of variance (ANOVA) between models. If the p-value was significant, then the tested variable had an effect on occupancy and stayed in the final model. We tested the goodness of fit of the model and the normality of the residuals by graphical observation. Finally, we used an RDA (redundancy analysis) to confirm whether species composition was explained by landscape metrics. Selection of variables was made using the 'forward selection' method and the best variable was selected. We conducted all analyses using RStudio version 1.1.456 and R 3.4.4. For calculating the occupancy analysis, we used the package "unmarked" (Fiske and Chandler 2011).

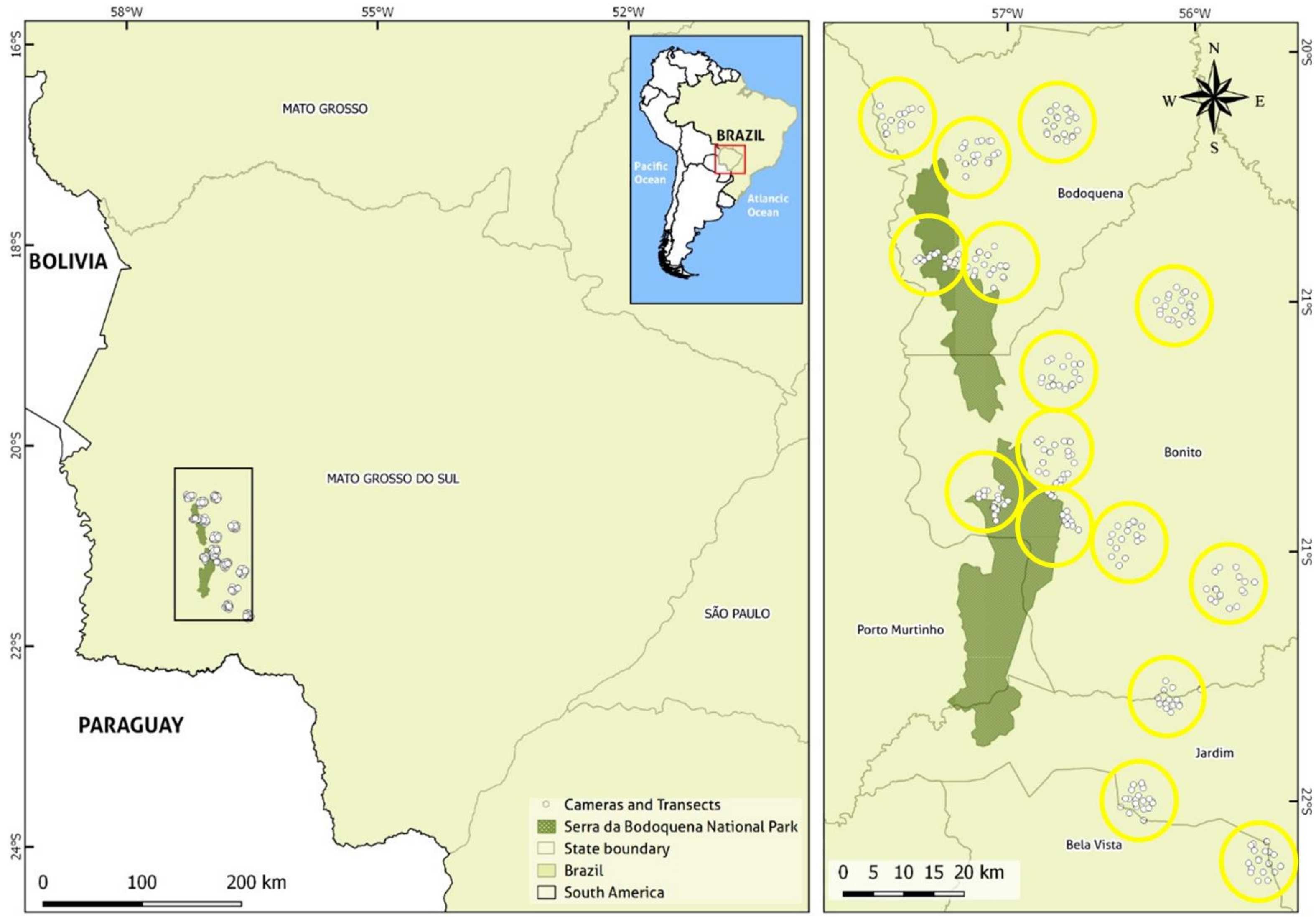

**Figure 12**. Study region in Bodoquena Plateau, Mato Grosso do Sul State, with 15 sites (yellow buffers with 5000 m) where were a set of camera traps and live traps were located (see methods for details).

## Results

### *Herbivore mammals: patterns of occupancy and landscape structure*

Summing all 15 sample sites across the gradient for all study periods, we achieved a total effort of 5,228 camera traps across 407 days and obtained a total of 16,276 photos of herbivore mammals, plus 185 captures of small mammals in 13,728 live traps from the 88 transects (see details in Table 2SM). We recorded a combined total of 23 species of small, medium and large herbivore mammals, with the cameras and live traps (Table 2SM). Species richness varied along the gradient and did not increase with the amount of native vegetation cover (Figure 13*;* Figure 7SM).

The pattern of occupancy as a function of the forest cover percent in the landscape within the 5000 m buffers was highly species dependent. Six species responded to forest cover percentage, and one to patch density (Table 8). Only *Tayassu pecari* which is forest dependent and have diet specialist, *i.e.* a frugivorous specie, *Mazama americana* which is forest dependent, and *Mazama gouazoubira* which is forest dependent and use also open areas (Figure 14) responded positively to forest cover percentage. As expected, *Sus scrofa* have a negative response, preferring open areas. The same is observed for *Hydrochoerus hydrochaeris*, a species adapted to open areas and associated with water bodies (Alho et al. 2011), and for *Thrichomys fosteri*, a species that uses forest but occurs in open edge vegetation in the Cerrado and other biomes (dos Reis & Pessoa 2004). All other species failed to show significant responses.

The RDA demonstrated a relationship between species composition and the landscape metrics ($R^2$ = 0,47; $P < 0.002$) (Figure 15). The percentage of forest cover was the best variable selected and explained by axis 1 of the RDA ($R^2 = 0.395$). This axis showed the association of *Tayassu pecari, Mazama americana* and *Mazama gouazoubira* with forest landscapes. The small mammal, *Micoureus constantiae*, a species generally restricted to moist, humid forests or gallery forests (Vieira 2006, Cáceres et al. 2007, Cáceres et al. 2008, Hannibal and Cáceres 2010, Hannibal and Neves-Godoi 2015, Smith & Owen 2016), also showed some association with level of forest cover. On the other hand, the RDA 2 axis showed *Oligoryzomys fornesi, Monodelphis domestica, Rhipidomys macrurus, Sus scrofa* and *Hydrochoerus hydrochaeris* as mainly occupying more degraded landscapes.

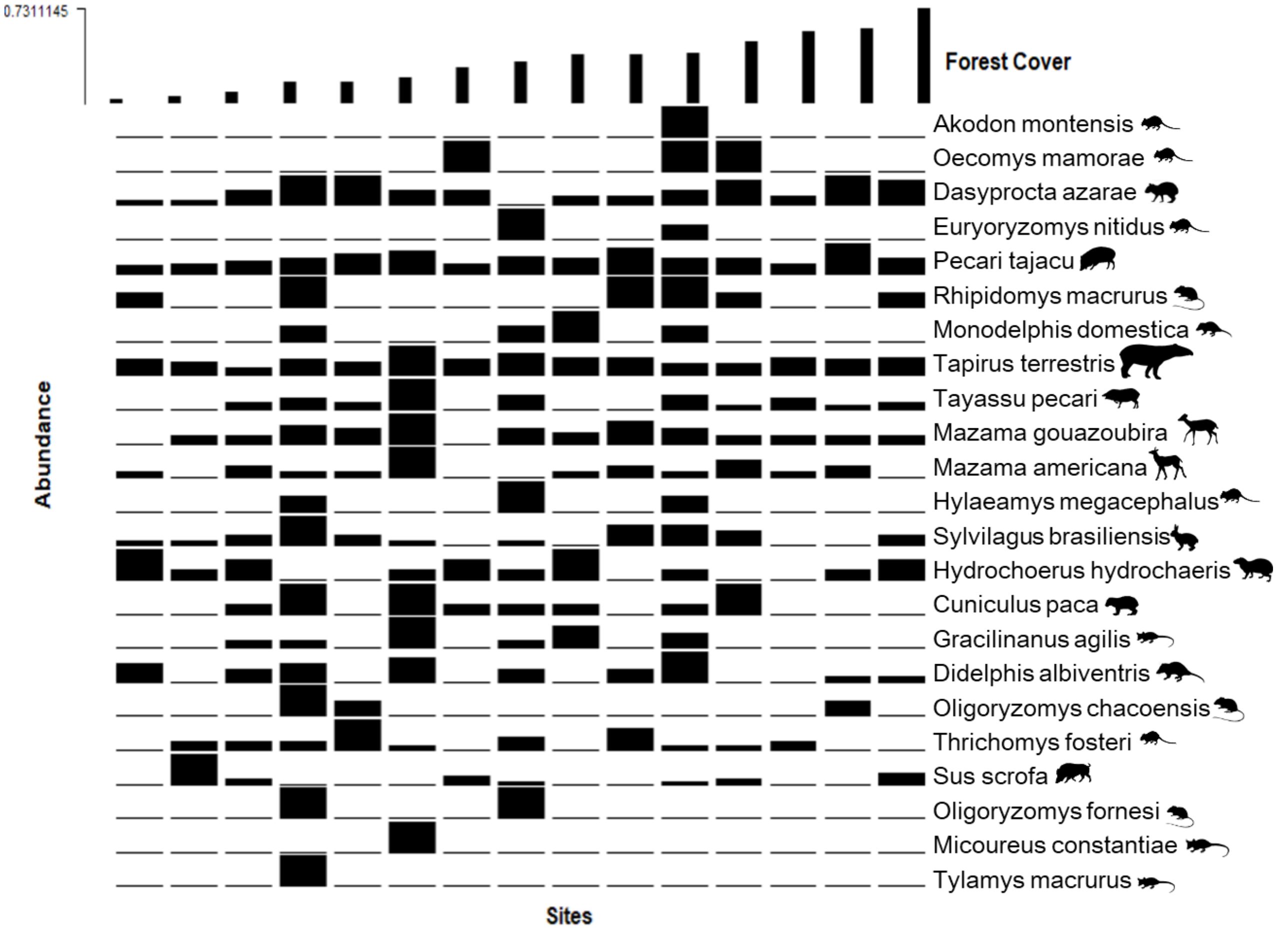

**Figure 13**. Direct ordination showing the number of records for each species (from cameras and live traps) along the forest cover gradient on the Bodoquena Plateau.

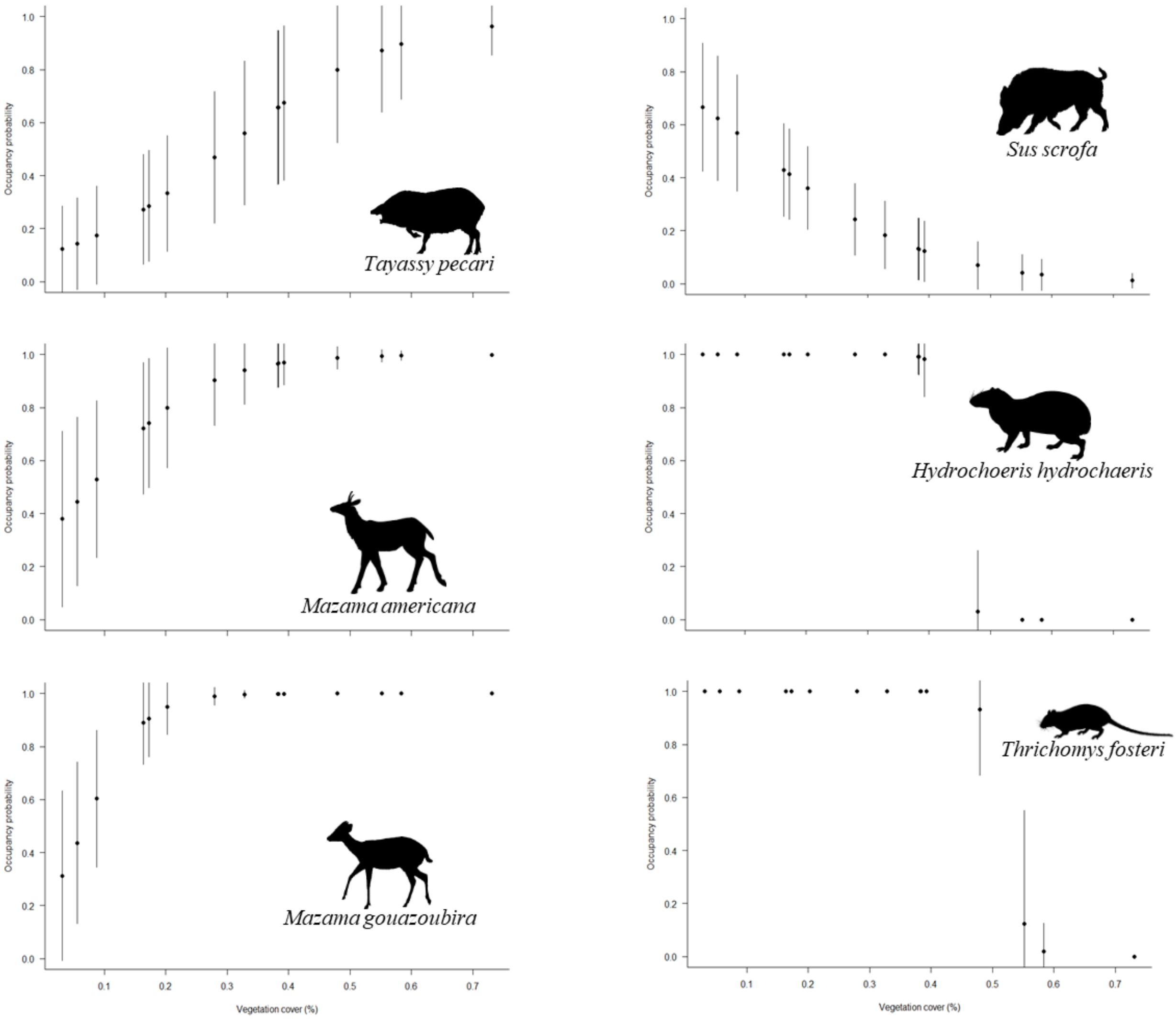

**Figure 14**. Occupancy probability responses of herbivore mammals associated with proportion of forest cover along the gradient using a 5,000 m buffer.

**Table 8**. Occupancy models for species of herbivore mammals in a landscape scale (5 km) along a gradient of native vegetation loss in Cerrado region, Brazil. Data estimated from sampling between February 2016 and December 2018. Legend: FC = % forest cover; PD = Patch density; Agr = Agriculture. Model of occupancy (Ψ ), k = number of parameters in the model, AIC = Akaike Information Criterium, ΔAICc = Akaike information criterion for small samples, Akaike weight = model weight.

| Family | Species | Model | *k* | AIC | ΔAICc | Akaike weight | *Method* |
|---|---|---|---|---|---|---|---|
| *Tayassuidae* | *Tayassu pecari* | Ψ(FC) p(occupancy) | 3 | 74.09 | 0.00 | 0.534 | Camera trap |
| *Tayassuidae* | *Pecari tajacu* | Ψ(.) p(occupancy) | 2 | 209.27 | 0.00 | 0.48 | Camera trap |
| *Cervidae* | *Mazama americana* | Ψ(FC) p(occupancy) | 3 | 117.36 | 0.00 | 0.44 | Camera trap |
| *Cervidae* | *Mazama gouazoubira* | Ψ(FC) p(occupancy) | 3 | 167.02 | 0.00 | 0.697 | Camera trap |
| *Suidae* | *Sus scrofa* | Ψ(FC) p(occupancy) | 3 | 73.40 | 0.00 | 0.577 | Camera trap |
| *Caviidae* | *Hydrochoerus hydrochaeris* | Ψ(FC) p(occupancy) | 3 | 68.37 | 0.00 | 0.788 | Camera trap |
| *Dasyproctidae* | *Dasyprocta azarae* | Ψ(.) p(occupancy) | 2 | 171.57 | 0.00 | 0.47 | Camera trap |
| *Leporidae* | *Sylvilagus brasiliensis* | Ψ(Agr) p(occupancy) | 3 | 119.02 (did not converge) | 0.00 | 0.532 | Camera trap |
| *Cuniculidae* | *Cuniculus paca* | Ψ(.) p(occupancy) | 2 | 79.21 | 0.00 | 0.47 | Camera trap |
| *Tapiridae* | *Tapirus terrestris* | Ψ(.) p(occupancy) | 2 | 210.99 | 0.00 | 0.48 | Camera trap |
| *Didelphidae* | *Monodelphis domestica* | Ψ(FC) p(occupancy) | 3 | 41.41 (did not converge) | 0.00 | 0.38 | Live trap |
| *Didelphidae* | *Didelphis albiventris* | Ψ(PD) p(occupancy) | 3 | 72.33 | 0.00 | 0.50 | Live trap |
| *Didelphidae* | *Didelphis albiventris* | Ψ(Agr) p(occupancy) | 3 | 73.95 (did not converge) | 0.00 | 0.882 | Camera trap |
| *Didelphidae* | *Gracilinanus agilis* | Ψ(.) p(occupancy) | 2 | 53.58 | 0.00 | 0.44 | Live trap |
| *Didelphidae* | *Micoureus constantie* | Ψ(.) p(occupancy) | 2 | 18.74 | 0.000 | 0.36 | Live trap |
| *Didelphidae* | *Thylamys macrurus* | Ψ(.) p(occupancy) | 2 | 14.94 | 0.00 | 0.34 | Live trap |
| *Echimyidae* | *Thrichomys fosteri* | Ψ(FC) p(occupancy) | 3 | 65.07 | 0.00 | 0.52 | Camera trap |
| *Echimyidae* | *Thrichomys fosteri* | Ψ(.) p(occupancy) | 2 | 97.40 | 0.00 | 0.38 | Live trap |
| *Cricetidae* | *Hylaeamys megacephalus* | Ψ(Agr) p(occupancy) | 3 | 33.92 (did not converge) | 0.00 | 0.523 | Live trap |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| *Cricetidae* | *Rhipidomys macrurus* | Ψ(Agr) p(occupancy) | 3 | 59.35 (did not converge) | 0.00 | 0.52 | Live trap |
| *Cricetidae* | *Oligoryzomys fornesi* | Ψ(.) p(occupancy) | 2 | 35.25 | 0.00 | 0.47 | Live trap |
| *Cricetidae* | *Akodon montensis* | Ψ(.) p(occupancy) | 2 | 14.94 | 0.00 | 0.40 | Live trap |
| *Cricetidae* | *Oecomys mamorae* | Ψ(.) p(occupancy) | 2 | 14.94 | 0.00 | 0.40 | Live trap |
| *Cricetidae* | *Euryoryzomys nitidus* | Ψ(.) p(occupancy) | 2 | 28.11 | 0.00 | 0.44 | Live trap |
| *Cricetidae* | *Oligoryzomys chacoensis* | Ψ(.) p(occupancy) | 2 | 35.25 | 0.00 | 0.47 | Live trap |

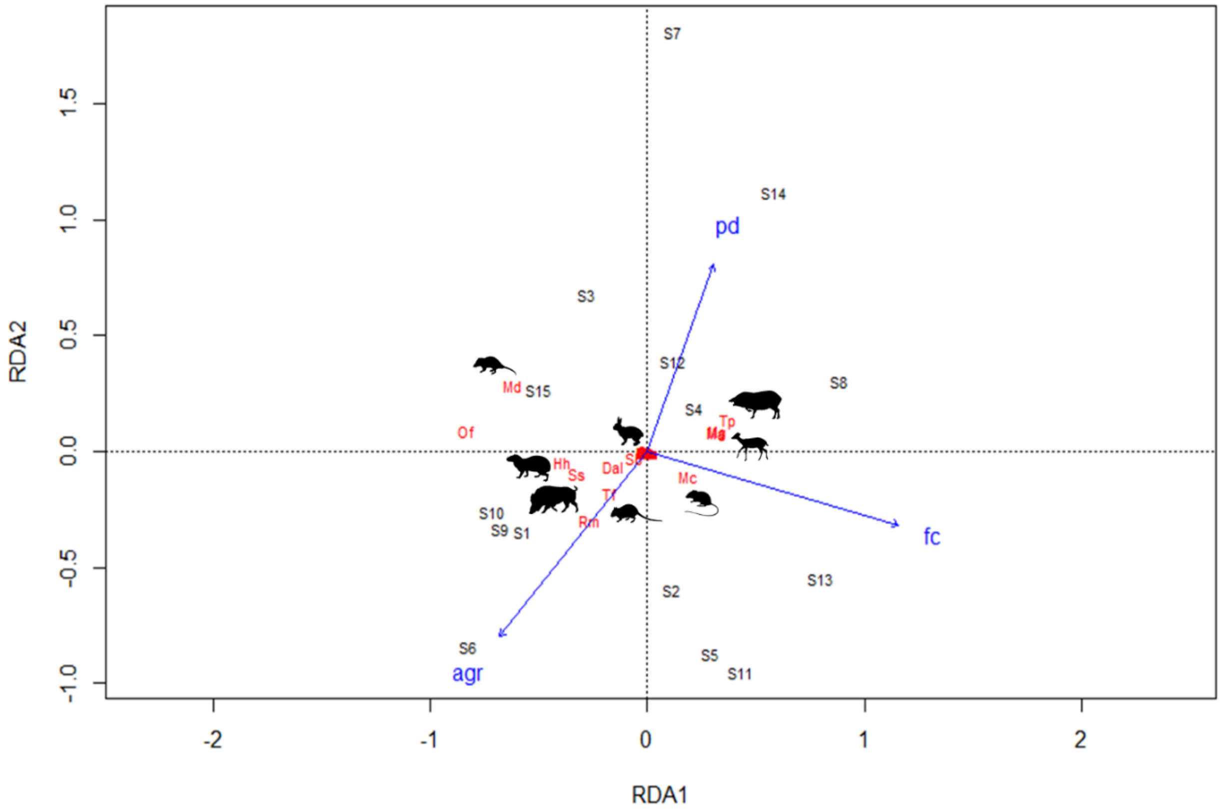

**Figure 15**. Redundancy analysis diagram of herbivore mammal occupancy and landscape metrics, (fc= percentage of forest cover; pd= patch density; agr= percentage of agriculture). Species legend: Md = *Monodelphis domestica; Of = Oligoryzomys fornesi; Hh = Hydrochoerus hydrochaeris; Ss = Sus scrofa; Tf = Thrichomys fosteri; Rm = Rhipidomys macrurus; Dal = Didelphis albiventris; Sb = Sylvilagus brasiliensis; Mc = Micoureus constantie; Tp = Tayassu pecari; Mg = Mazama Gouazoubira; Ma = Mazama americana;* Landscape metric legend: pd = patch density; fc = forest cover (%); agr = agriculture (%); S1 – S15 = sites in study area.

## Discussion

The results add to an increasing number of studies that have shown idiosyncrasies in mammal species responses to land-use change in Neotropical regions (*e.g.* Lyra-Jorge et al. 2009, Magioli et al. 2016, Zimbres et al 2018). Studies have shown that the responses of mammal species to habitat loss and agriculture vary widely across landscapes (Jácomo et al. 2013, Paolino et al. 2016, Ferreguetti et al. 2018), and they do not reflect any general pattern in relation to morphological traits and phylogeny (Zimbres et al 2018). As most species in our study did not respond to the forest gradient, we believe that herbivores in mosaic landscapes are more associated with specific landscape characteristics, such as resource availability and management practices, rather than the extent of forest in general. However, we identified that some species, as such *Tayassu pecari* and *Mazama americana* show clear forest dependency, making them part of a group that is more sensitive to habitat loss and land-use change (Chollet et al. 2012, Keuroghlian et al. 2014, Ferreguetti et al. 2015, Nagy-Reis et al. 2017).

The lack of a common pattern in species responses to land-use changes has been attributed to the high variability in ecological requirements and tolerances of some but not all species (Pardini et al. 2017, Melo et al. 2018). For example, peccaries and deer are more dependent on plant composition due to their diet than capybara that feed on grasses for the most part in terms of spatial and temporal use of the landscape (Desbiez et al. 2009, Keuroghlian et al. 2009, Keuroghlian & Eaton 2009, Flores et al. 2013, Nagy-Reis et al. 2017).

The lack of a clear response by most species of herbivore mammals' species to the land cover gradient may not be uniform but reflect species-specific responses to a suite of different processes. Firstly, it is possible that the studied environmental gradients were not strong enough to elicit clear responses from chosen groups. Studies have revealed circumstances where the landscape structure was highly dynamic or the amount of habitat in the landscape was above a certain level, and landscape configuration seems to have little or no effect on the distribution of organisms (Fahrig 1992, 1998). In addition, some authors have pointed out that ecological responses to the process of fragmentation can result in positive and negative effects on the species

(Fahrig et al. 2017, Fletcher et al. 2018, Fahrig et al. 2019). Secondly, source-sink dynamics has been suggested as an important mechanism by which resilience is expressed at the population level by mammal species in fragmented landscapes in Brazil (*e.g.* Bogoni et al. 2017). These processes probably explain part of the variation in our data, especially because most landscapes on the Bodoquena Plateau are characterized by mosaics of native vegetation, including one National Park, embedded between pasture and/or agricultural areas. All parts of this could function as a source area and thus potentially maintain functional connectivity, so decreasing the biodiversity loss. Additionally, this region is particularly rich in hydrological resources, including clear water limestone-bed springs (Pott et al. 2014), and their associated riparian zones, which form a key regional resource that contributes to the presence of mammals and other groups, resulting in a high local and regional biodiversity (Cáceres et al. 2007, Casatti et al. 2010, Cordeiro et al. 2014, Tencatt et al. 2014, Souza & Guillermo-Ferreira 2015, Koroiva et al. 2017).

Third, the presence of different species along the disturbance gradient may indicate the low overall level of hunting pressure. Although subsistence hunting has not been shown to occur in the region, we recognized that fact that the entire region is dominated by a large number of private landholdings, from small to large, plus rural settlements and three urban centers, so that a wide variety of anthropic natural resource use forms may exist. However, the level of disturbance by local urban centers, which presents small and distant cities is still low when compared to other studied sites. If we consider the perception of terrestrial mammal species, this factor may be an even low level of disturbance. Consequently, we need more information about hunting in the region before being able to infer its role in shaping regional mammal diversity with any degree of accuracy. Fourthly, extinction debt may occur in the region: land-use changes in Bodoquena is a recent phenomenon (Roque et al. 2016). In less than 40 years the land has experienced a drastic change, from low intensity grazing and cattle ranching to large-scale agricultural production. In recent years, government programs have stimulated local development through agricultural expansion, and Bonito is one of the current foci of soy production (Aprosoja-MS Projeto MEA 2017, Silva & Pivello 2009, Pott et al. 2014). Therefore, species with long generation times, such as *Tapirus terrestris*, may currently occur through the entire gradient, but their population may not be viable in the long term.

Small mammals have been suggested to be sensitive to native vegetation loss and habitat quality changes in Cerrado (Cáceres et al. 2011, Carmignotto et al. 2014, Melo et al. 2017, Hannibal et al. 2018), Atlantic (Pardini 2004, Pardini et al. 2005) and Amazon forests (Santos-Filho et al. 2012, Palmeirin et al. 2018), particularly the forest specialist species. This study shows that small mammals did not respond to a gradient of forest loss at either the 5 km or 500 m scales. It is possible, that the arguments we raised above are also valid for the small mammals. The lack of clear response could also be an artefact of the relatively low sampling effort at the local scale by our study compared to previous ones (Bovendorp et al. 2018). Moreover, species detection probability, which is dependent on the sampling method used (Lyra-Jorge et al., 2008), can affect the results by increasing in beta diversity induced by pseudo-absences (Ghisan & Thuiller 2005, Grahan et al. 2007, Zeilhofer et al. 2014). Other potential reasons for our difficulties in finding clear patterns for small mammals could be related to their low abundance in the area, probably due to interaction with medium- and large-bodied mammals still living in much of the Bodoquena Plateau landscape. In summary, with the current small mammal data at our disposal we cannot draw clear conclusions concerning the effect of land-use change on this group.

Native mammals tend to occupy native vegetation, whereas invasive species tend to use all areas, including forest, open areas and even non-native vegetation (matrix). *Sus scrofa*, which is the only invasive mammalian herbivore species in the study region, showed a negative relationship with the percentage of forest cover, preferring open areas (Galetti et al. 2015, Pedrosa et al. 2015). We also found two exceptions with native species: *Thrichomys fosteri* a rodent that prefers Cerrado vegetal formations (Bonvicino & Lacher 2008, D'Elia & Myers 2013), and *Hydrochoerus hydrochaeris* a species that is dependent on water and which is highly tolerant of open habitats (Alho & Rondon 1987, Zimbres et al. 2018).

Although, there is no clear common response associated with the studied traits, (*e.g.* body size), we found that forest specialist species such as *Tayassu pecari* and *Mazama americana* showed a positive relationship with forest cover. We associated this response with the diet of these species, primarily their dependence on native fruits and herbs (Gayot et al. 2004, Beck 2006, Keuroghlian & Eaton 2008, Galetti et al. 2015), since these resources are in our study area (*e.g. Mauritia flexuosa*, *Annona coriacea*, *Duguetia furfuracea*, *Diopyros hispida*, *Andira humilis*, *Xylopia aromatica* and *Guadua paniculata*), and are present mainly in remnants of native vegetation (Galetti & Aleixo 1998, Pott et al. 2006, 2014).

For such herbivore species, *Tayassu pecari* and *Mazama americana*, we noticed that the suggested threshold below 30% of forest (Andren 1994, Banks-Leite et al. 2014), indicates significant loss of individuals in our study area. Species specialists are more sensitive to landscape changes because in a connectivity loss scenario such species are restricted in their dispersal capacity, due to factors such as limitations in locomotion and consequent increases in the degree of isolation (Bowman et al. 2002, Püttker et al. 2013).

### Implications for conservation

In terms of conservation and management, a big question that emerges from our results and those of other recent studies (Gardner et al. 2009, Banks-Leite et al. 2014, Ferreguetti et al. 2017, Zimbres et al. 2018) is: how could we optimize the conservation of a community where most species respond in idiosyncratic ways to land-use changes? We recommend different and complementary strategies for herbivore mammals in our study area.

First, our work adds evidence that, for forest specialist species, the top priority for their effective conservation should be the maintenance of the greatest possible coverage of native vegetation. The exact coverage level is debated for different groups and regions (see Roque et al. 2017, Melo et al. 2018). However, many authors have suggested that at least 30% of native cover should be kept (Andren 1994, Pardini et al. 2010, Estavillo et al. 2013, Banks-Leite et al. 2014, Ochoa-Quintero et al. 2015, Melo et al. 2018). In our study, species specialized for forest habitats and frugivory, *Tayassu pecari*, *Mazama americana* and *M. gouazoubira* showed sensitivity when habitat loss reached around "20 to 40" %. Therefore, we suggest maintaining native areas in Bodoquena Plateau above 30% of native vegetation and the complementing with restoration in those areas currently at less than 30% to increase connectivity. In the River Paraguay Basin Plateau, however, the priority is different. There, we suggest focusing on restoration because the proportion of anthropogenic areas, mostly pasture and agriculture, is already over 60% (Roque et al. 2016).

In some systems, the key dynamic is one where dispersal and colonization maintain local diversity at a much higher level than the productivity of the locality alone could support (Economo 2011). This could be the case in our study area. Even in landscapes with low amounts of native vegetation we could find mammals, such as *Tapirus terrestris, Pecari tajacu and Dasyprocta azarae*, the latter present in our area of study only in riparian zones or edges of the fragments, and more 14 species, including small mammals, that did not respond to native vegetation loss in this scale of 5,000 m. However, their presence in such landscapes may be related to landscape connectivity which homogenizes the local community, reducing the perceived conservation value of areas native vegetation (whether legally protected to otherwise) (Economo 2011, Fahrig et al. 2011). Even though they may, in fact, be key due to their role as sources in a local sink-source population dynamic for such species. In this sense, it is necessary to understand how species use the areas and how each performs its different ecological functions. For example, because the matrix influences patch quality and connectivity differently for different species, a number of species are able to use areas on the boundaries between the remnant forest and the surrounding habitat matrix (Bender et al. 2003, Brady et al. 2011, Laurance et al. 2011, Lange et al. 2012, Borges-Matos et al. 2016).

On the western portion part of the plateau, the forest and fragments of other native vegetation in the 'Serra da Bodoquena National Park' and 'Kadiwéu Indigenous Land' form an area of great environmental complexity and high forest cover. This probably acts has a mass effect and acts as a source for the regional source-sink dynamic, and so plays an important role in maintaining mammal communities in Cerrado landscapes, where many species are able to cross open areas. In such circumstances, heterogeneity and permeable landscapes are critical for influencing species with such differentiated functional traits. Therefore, for the region under consideration, we suggest that management policies that attempt to maximize heterogeneity and connectivity (including habitat quality) as well as focusing on biodiversity representation, are the key to the effective long-term maintenance of mammal communities on the Bodoquena Plateau.

Reconciling the requirements of conservation and agricultural production is the biggest land-management challenge in the Cerrado. Mato Grosso do Sul is one of the Brazilian states where more than 50% of the vegetation has been converted into other land-uses (Silva et al., 2011, PPCerrado 2015, Roque et al., 2016). Considering that the agricultural land area is predicted to increase over the next few years (Foley et al., 2011), the Bodoquena Plateau becomes a priority for sound environmental planning (Roque et al., 2016). The challenge is to implement conservation strategies that can maximize biodiversity via agricultural practices that have low deforestation rates and favor recovery of degraded areas, linking conservation and restoration actions with high quality agricultural production. In the absence of natural habitat, herbivore mammals will use marginal habitat, and is therefore of key importance that the mosaic landscape is maintained, and that the focus that guides decisions for habitat patch conservation is one that ensures that connectivity persists in a changing environment with increasing fragmentation of native habitat patches (Magioli et al. 2016).

Restoration projects in degraded areas, and the preservation of riverine areas connecting watercourses environments at the local and regional levels also are key conservation elements. Effectively implemented such practical measures can improve the structure of the traditional agricultural landscape and allow biodiversity conservation to proceed in an integrated manner. Increasing our understanding of the habitat use and behavior of herbivore mammal species in landscapes undergoing anthropogenic changes may help create regulations and more comprehensive conservation legislation to generate information on species at the national level, especially in high vulnerability areas. Conservation actions are particularly necessary regionally because large mammals can be driven to local extinctions by habitat conversion or other factors, such as by unregulated hunting. Incorporation of environmentally friendly technologies, that limit agrochemical uses and reduce soil contamination are vital for keeping mammal dispersion and survival rates in such landscapes.

Finally, conflicts with native fauna may arise through landowners due to the damage that some herbivorous mammals can cause to crops (Jácomo et al., 2013). In this case, payment schemes for ecosystem services, including mammalian maintenance, would be strategic. This could be especially appropriate for sentinel species such as diet and habitat use specialists who, due to their sensitivity to habitat loss, provide high returns under this scheme. To improve our understanding of changes in herbivore mammal communities to the point where realistic scenarios involving wildlife decline can be reliably predicted, requires larger numbers of replicated studies that examine particular aspects, for example, the behavioral and functional diversity of individual species, and to compare the ecology of wildlife in biological communities with and without anthropic activities. Local policies, based on ecological research with technologies such as satellite monitoring, and data from CAR (Cadastro Ambiental Rural, a register aiming to assist the Brazilian Public Administration in the process of environmental regularization of rural properties and possessions) need to become the base for environmental planning and conservation in the region.

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## Supplementary Material

Landscape sampling design for project ‘PELD Planalto da Bodoquena: redes de interações ecológicas’

*Study area definition*

To define the landscapes where field samples will be collected, we first divided the entire region in hexagons of 5000 ha. (hereafter landscapes). Using the information about altitude we defined as the entire study area only those landscapes located above 150 meters of altitude (360 landscapes). By using the information from the GEOMS 2007 we differentiated three main land-use cover types (‘Floresta estacional decidual’, ‘áreas de tensão ecológica’ and ‘vegetação ciliar’) in all landscapes in the region (Figure 1SM).

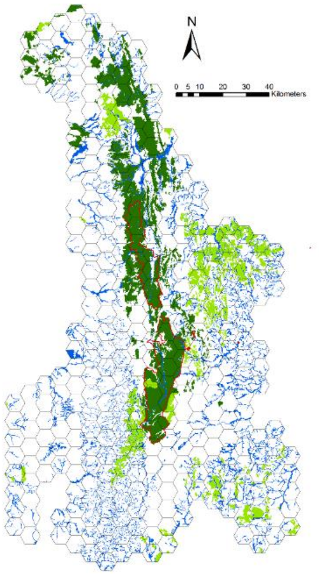

**Figure 1SM**. Total number of landscapes (360) above 150 mt., and the three land-use cover types: ‘Floresta Estacional Decidual’- dark green, ‘Áreas de tensão ecológica’- light green and ‘Mata ciliar’- blue.

By using the combined information from these three vegetation types we performed an analysis of the total remaining vegetation and some configuration measurements of the remaining vegetation within the 360-landscape analysed. To perform this analysis, we transformed the shape files into raster files and processed the information using Fragstagts (Figure 2sm a-c).

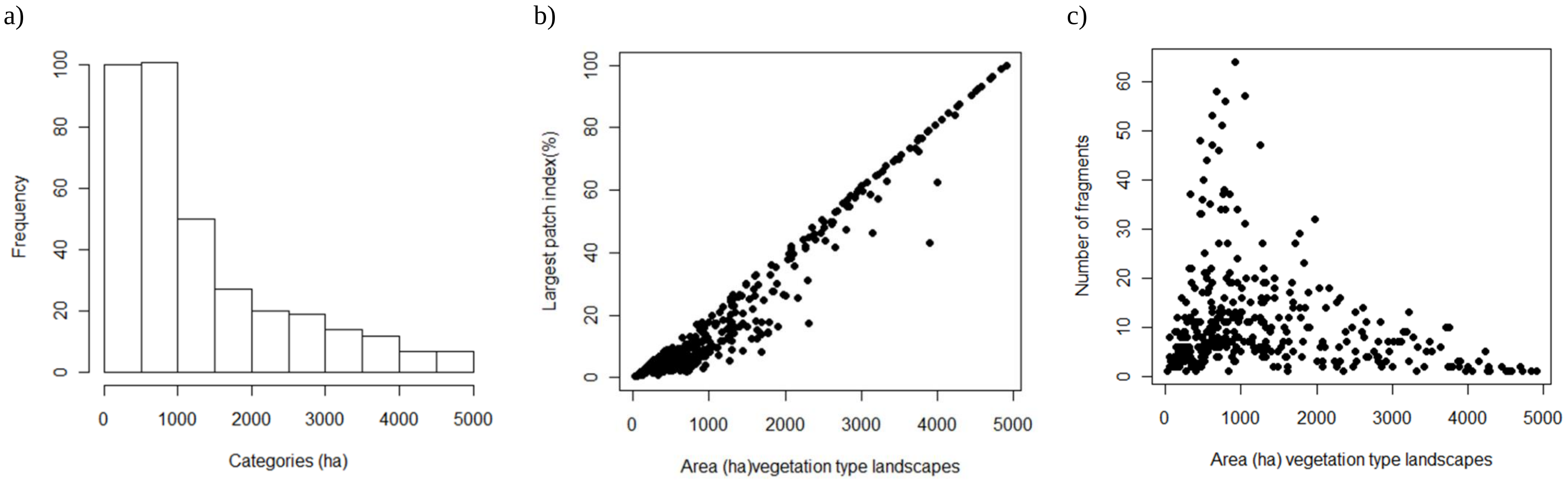

**Figure 2SM**. Frequency of landscapes according to total remaining vegetation (a), largest patch index and total remaining vegetation (ha) (b), variation in the number of fragments and total remaining vegetation (c).

Using this information, we selected 20 out of 360 landscapes available representing the changes in land-use cover and configuration. Those landscapes cover the entire gradient of remaining vegetation cover (from 3 to 98% remaining vegetation cover) (Figure 3SM) and are distributed across the entire area (Figure 4SM).

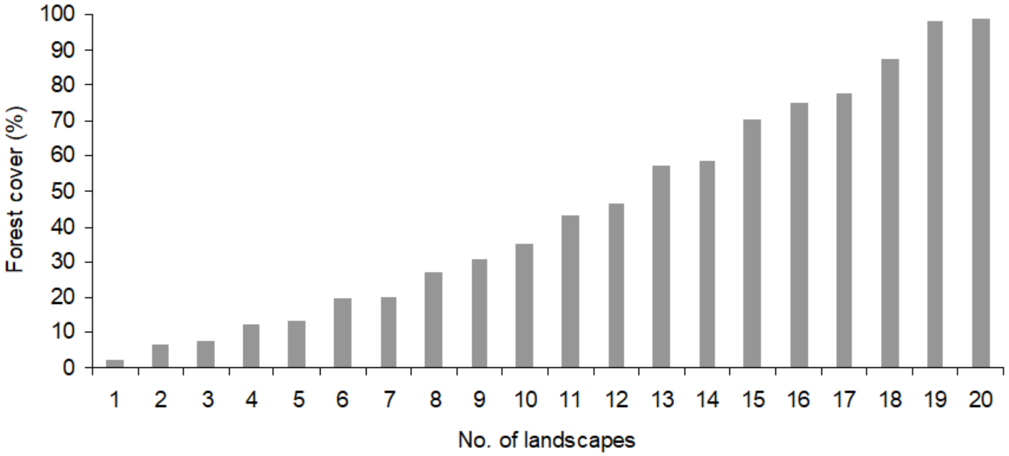

**Figure 3SM**. Total remaining vegetation cover (%) and number of landscapes selected.

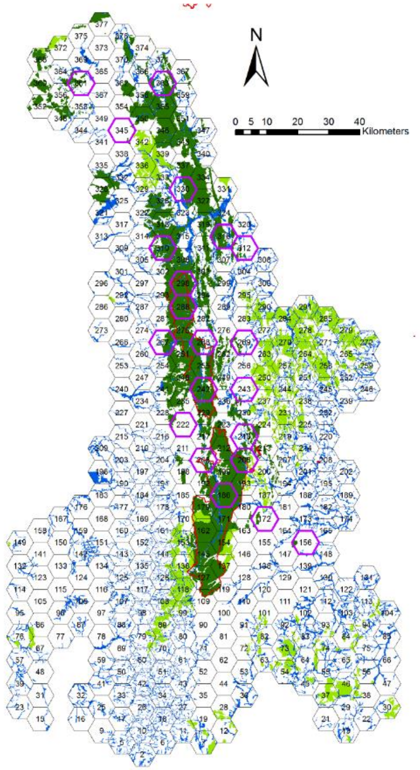

**Figure 4SM**. Location of the selected landscapes (lilac borders) across the whole region.

The selected landscapes keep a similar pattern of changes in forest configuration across the entire land-use change cover (Figure 5SM a-b).

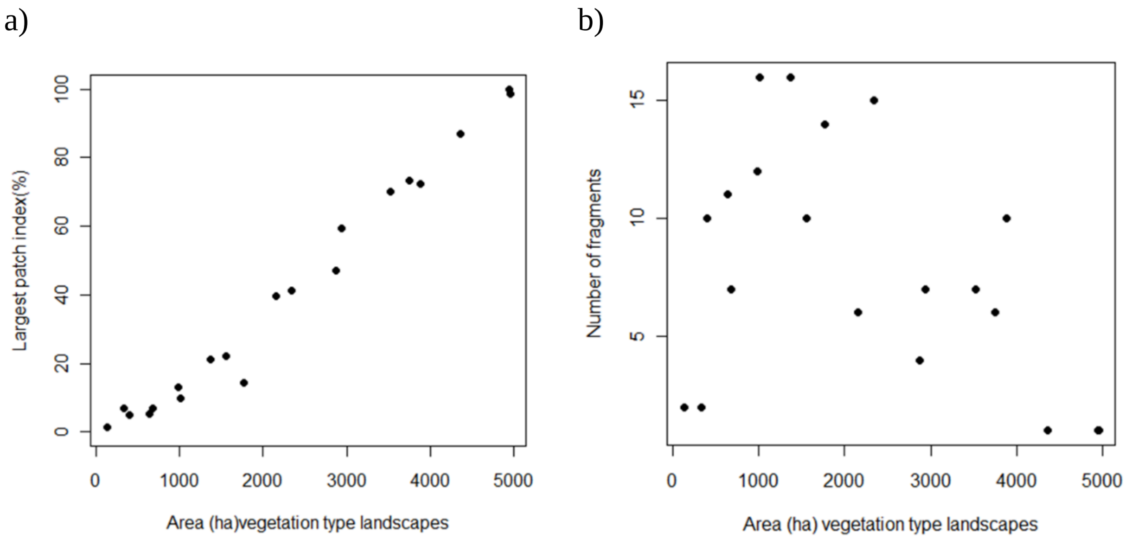

**Figure 5SM**. Largest patch index and total remaining vegetation (ha) and a., and variation in the number of fragments and total remaining vegetation b. of the selected landscapes (20).

In addition, the selected landscapes are expected to maintain certain proportionality in terms of the focal land-use cover (Floresta estacional decidual), and also with the riparian vegetation (riparian vegetation) (Figure 6SM a-b).

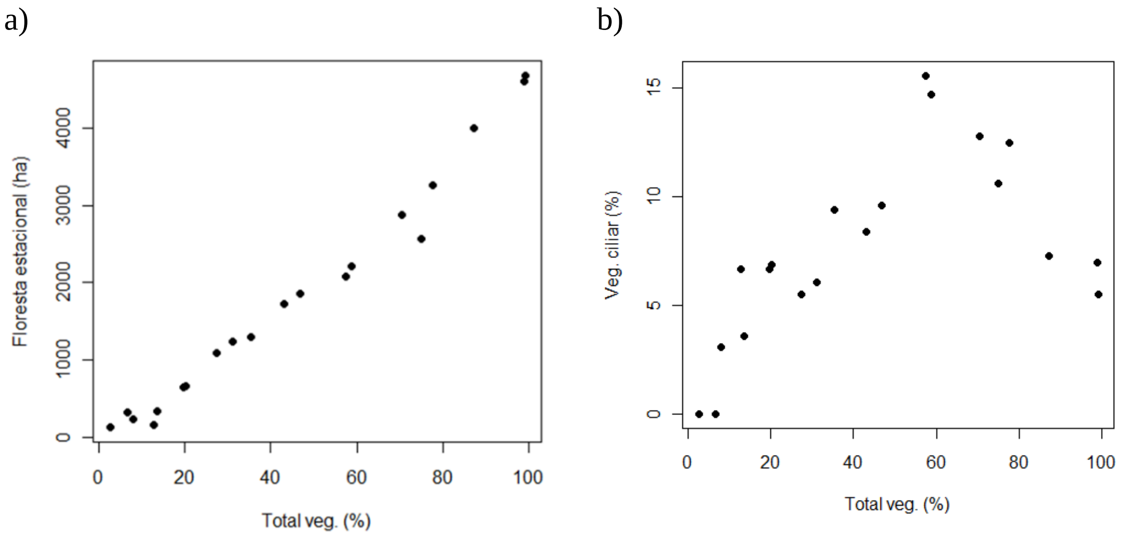

**Figure 6SM**. Floresta estacional and total remaining vegetation cover (%) a. and relationship between riparian vegetation and total remaining vegetation within the selected landscapes.

**TABLE 1SM**. Landscape information: Sampling sites along the gradient of forest cover. Period of data collection : February/2016 until December/2017.

| Region code | Municipality | Central point (21K UTM) | | Period | Vegetation type | Land Area (buffer in meters) |
|---|---|---|---|---|---|---|
| | | Longitude | Latitude | | | |
| SITE1 | Bonito | 551223.82 | 7658444.45 | rain | Cerrado/Atlantic Forest | 5000 |
| SITE2 | Bonito | 539530.31 | 7672137.86 | rain/dry | Cerrado/Atlantic Forest | 5000 |
| SITE3 | Bonito | 539271.78 | 7687287.30 | dry | Cerrado/Atlantic Forest | 5000 |
| SITE4 | Bonito/Bodoquena | 559300.37 | 7699070.62 | dry | Cerrado/Atlantic Forest | 5000 |
| SITE5 | Bonito | 526943.51 | 7664527.84 | rain | Cerrado/Atlantic Forest | 5000 |
| SITE6 | Jardim | 572663.05 | 7600074.98 | rain | Cerrado | 5000 |
| SITE7 | Bodoquena | 539990.28 | 7731819.76 | rain | Cerrado/Atlantic Forest | 5000 |
| SITE8 | Bodoquena | 513421.31 | 7732409.54 | rain | Cerrado/Atlantic Forest | 5000 |
| SITE9 | Jardim | 559399.23 | 7630415.41 | dry | Cerrado | 5000 |
| SITE10 | Jardim | 552579.10 | 7611259.05 | dry | Cerrado | 5000 |
| SITE11 | Bonito | 539924.02 | 7663168.06 | dry | Cerrado/Atlantic Forest | 5000 |
| SITE12 | Bonito/Bodoquena | 528642.94 | 7706281.15 | dry | Cerrado/Atlantic Forest | 5000 |
| SITE13 | Bonito | 520056.34 | 7707121.59 | dry | Cerrado/Atlantic Forest | 5000 |
| SITE14 | Bodoquena | 526589.88 | 7725607.40 | rain | Cerrado/Atlantic Forest | 5000 |
| SITE15 | Bonito | 567393.83 | 7649459.07 | rain | Cerrado | 5000 |

**TABLE 2SM.** Methods and sampling effort for collected herbivore mammal community information in 15 sites along of gradient of the native vegetation loss.

| **Region code** | **Method** | **#camera trap points** | **# days CT per site** | **sampling effort (CT points * days CT per site)** | **data cameras** | **period** | **Method** | **#live traps * #tst** | **# nights LT per site** | **sampling effort (LT*tst*night per site)** | **data transects** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE 3 | Camera-trap | 13 | 18 | 234 | Jun-16 | dry | Live-trap | 52*6 | 3 | 936 | Apr-16 |
| SITE 2 | Camera-trap | 13 | 21 | 273 | Jul-16 | rain/dry | Live-trap | 52*6 | 3 | 936 | Mar-16 |
| SITE 5 | Camera-trap | 14 | 35 | 490 | Nov-16 | rain | Live-trap | 52*6 | 3 | 936 | Oct-16 |
| SITE 6 | Camera-trap | 15 | 26 | 390 | Dec-16 | rain | Live-trap | 52*6 | 3 | 936 | Nov-16 |
| SITE 7 | Camera-trap | 15 | 21 | 315 | Jan-17 | rain | Live-trap | 52*6 | 3 | 936 | Jan-17 |
| SITE 1 | Camera-trap | 12 | 24 | 288 | Feb-17 | rain | Live-trap | 52*4* | 3 | 624 | Feb-16 |
| SITE 8 | Camera-trap | 10 | 34 | 340 | Mar-17 | rain | Live-trap | 52*6 | 3 | 936 | Feb-17 |
| SITE 4 | Camera-trap | 14 | 26 | 364 | Apr-17 | dry | Live-trap | 52*6 | 3 | 936 | May-16 |
| SITE 9 | Camera-trap | 11 | 27 | 297 | May-17 | dry | Live-trap | 52*6 | 3 | 936 | Apr-17 |
| SITE 10 | Camera-trap | 15 | 37 | 555 | May-17 | dry | Live-trap | 52*6 | 3 | 936 | May-17 |
| SITE 12 | Camera-trap | 12 | 27 | 324 | Jul-17 | dry | Live-trap | 52*6 | 3 | 936 | Aug-17 |
| SITE 11 | Camera-trap | 15 | 27 | 405 | Aug-17 | dry | Live-trap | 52*6 | 3 | 936 | Jul-17 |
| SITE 13 | Camera-trap | 12 | 29 | 348 | Sep-17 | dry | Live-trap | 52*6 | 3 | 936 | Aug-17 |
| SITE 14 | Camera-trap | 11 | 31 | 341 | Oct-17 | rain | Live-trap | 52*6 | 3 | 936 | Oct-17 |
| SITE 15 | Camera-trap | 11 | 24 | 264 | Nov-17 | rain | Live-trap | 52*6 | 3 | 936 | Nov-17 |

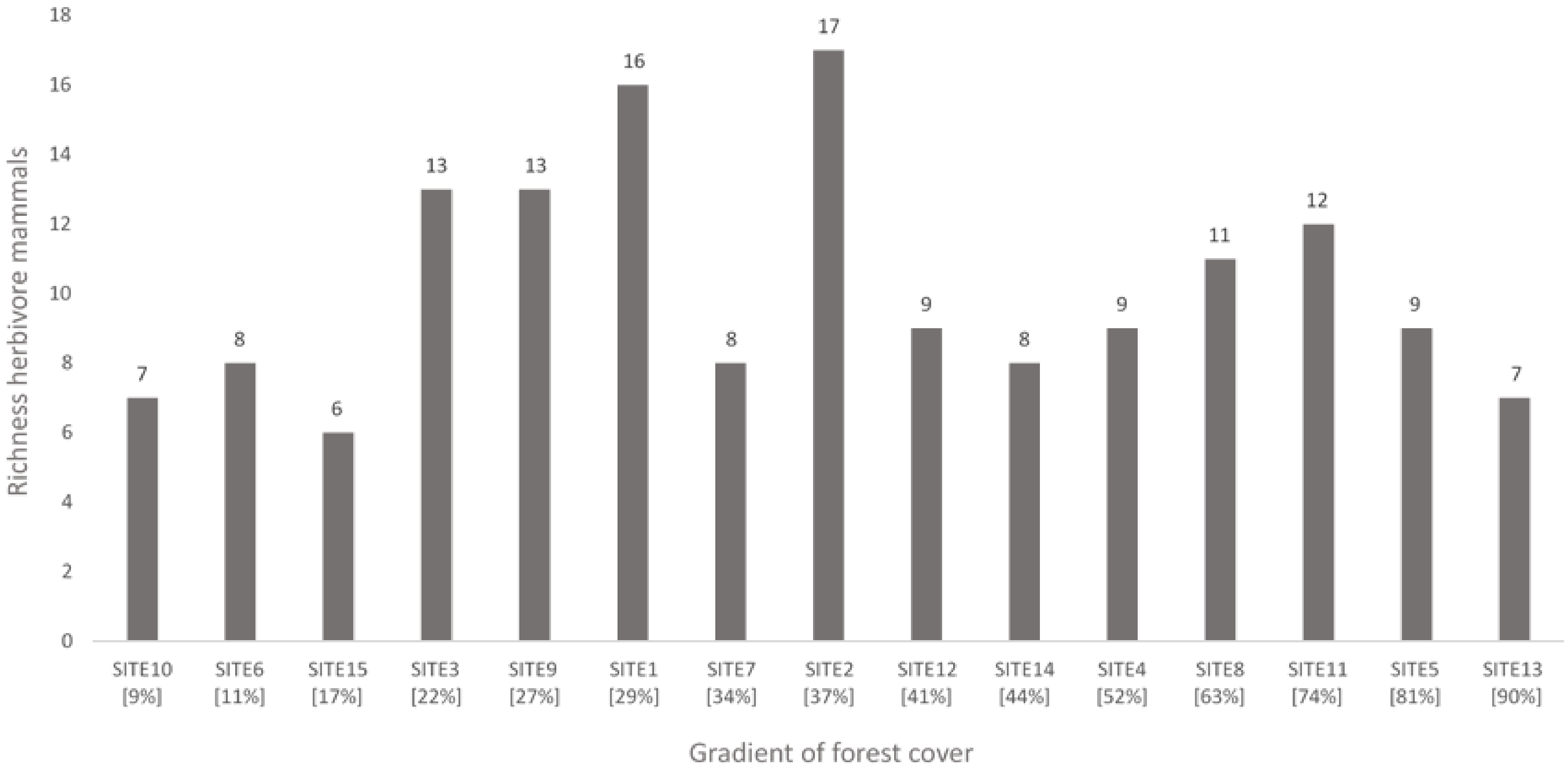

**Figure 7SM**. Richness of herbivore mammals by sampling sites along the forest cover gradient (%) between February 2016 and December 2017 in Bodoquena Plateau, MS.

## GENERAL COMMENTS

Although there is an increasing number of studies on mammal communities in the Cerrado and Atlantic Forest hotspots, my thesis calls attention to important ecological knowledge gaps in terms of understanding the effects of land-use changes on herbivores mammals. In this sense, the thesis fills part of these gaps for the Bodoquena Plateau, particularly on the responses of the herbivores to the loss of native vegetation at multiple scales.

Studies on some species of herbivorous mammals have been developed in the Bodoquena Plateau in the last decades, such as the ‘Projeto Queixadas’ (https://www.facebook.com/peccary.pecari) and the ‘Programa de Monitoramento da Biodiversidade do Parque Nacional da Serra da Bodoquena (ICMBio)’. However, my thesis is the first systematic study on community responses along a gradient of native vegetation loss in public and private areas.

Based on a database with more than 300,000 photos of animals in camera traps and data from live traps for small mammals from 15 landscapes, I showed that mammal species responses idiosyncratically to land-use change in the Bodoquena Plateau. These responses of mammal species along the gradient of native vegetation loss and agriculture vary widely across landscapes, and they do not reflect any general pattern in relation to morphological traits or phylogenetic. As most species in my study did not respond to the forest gradient, I believe that herbivores in mosaic landscapes are more associated with specific landscape characteristics, such as resource availability and management practices, rather than the extent of forest in general. However, we identified that some species, as such *Tayassu pecari* and *Mazama americana* show clear forest dependency, making them part of a group that is more sensitive to habitat loss and land-use change. Recognize these points can be essential to our understanding of how and which species are signalizing in landscapes with increase the land-use threats.

As outcomes of my thesis, I highlight some complementary databases: one on small mammals collected in live traps, which gather biological information such as hairs, ectoparasites, and biometric data, and another with native plants which are mammalian feeding sources. I believe that these datasets will allow future about the effects of land use changes on ecological networks involving mammals.

Reconciling the requirements of conservation and agricultural production is the biggest land-management challenge in the Cerrado biome. Mato Grosso do Sul is one of the Brazilian states where more than 50% of the vegetation of the Cerrado biome has been converted to other land-uses. Considering that the agricultural land area is predicted to increase over the next few years, Bodoquena Plateau becomes a priority for sound environmental planning. The challenge is to implement conservation strategies that can maximize biodiversity via agricultural practices that have low deforestation rates and favor recovery of degraded areas, linking conservation and restoration actions with high-quality agricultural production. In the absence of natural habitat, herbivore mammals will use marginal habitat, and is therefore of key importance that the mosaic landscape is maintained, and that the focus that guides decisions for habitat patch conservation is one that ensures that connectivity persists in a changing environment with increasing fragmentation of native habitat patches.

It is important to recognize some caveats. For example, the sampling design doesn’t allow me to figure out the effect of fragmentation from the native vegetation loss on herbivores mammals. Moreover, my study is limited in terms of temporal dynamics. As suggested in the chapters, major research questions remain to be addressed to further understand how anthropogenic systems influence mammal ecological dynamics, and reversely. We also suggest that engaging in a social-ecological perspective will help address these questions. In this way, monitoring the mammal populations including aspects about your functional diversity combined with landscape properties in Bodoquena plateau should be a top priority of the Long-Term Ecological Program of the region.

I believe that my work in this thesis opens new aspects for understanding the impacts of land-use changes on biodiversity in a region marked by a different vegetal formation of the Cerrado and remnants of Atlantic Forest embraced in a matrix of agricultural systems. However, there are still large knowledge gaps to better inform conservation and management strategies and to create sustainable landscapes at different scales.

## Appendix I

Example camera trap images and live trap of Bodoquena Plateau herbivore mammal species (2016 and 2017).

*Dasyprocta azarae* with acuri fruit (*Attalea phalerata*) - (image take in the private area, Bodoquena, MS)

*Cuniculus paca* – (image take in the Boca da Onça Ecotour, Bodoquena, MS)

*Mazama gouazoubira* – (image take in the Novo Horizonte Farm, Bonito, MS)

*Mazama americana* – (image take in the private Farm, Bonito, MS) (correct date: July 2016)

*Pecari tajacu* group - (image take in the Novo Horizonte Farm, Bonito, MS)

*Tayassu pecary* – (image take in the Parque Nacional da Serra da Bodoquena, Bodoquena, MS)

*Tapirus terrestris* – mother and baby (image take in the Novo Horizonte Farm, Bonito, MS)

*Sylvilagus brasiliensis* – (image take in the private Farm, Bonito, MS) (correct date: July 2016)

*Thrichomys fosteri* – mother and baby (captured in live trap in the Santo Antônio Farm, Jardim, MS)

*Thrichomys fosteri* and *Didelphis albiventris* (captured in live traps in the private areas, Bodoquena, MS)