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Effects of habitat loss and fragmentation on small mammals in a tropical South-American Savanna: an ecological and functional approach

Geruza Leal Melo

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Advisor: Dr. Nilton Carlos Cáceres

Examination board

Dr. Thomas Püettker

[Universidade de São Paulo]

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[University of Vermont]

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General abstract

The habitat loss and fragmentation are the main current threats to biodiversity. Many studies have been conducted in order to investigate the species response to changes in their habitat. Despite the expansion of knowledge in the area, many questions have not been answered yet, considering the divergence in the results among different studies or the emergence of new theories and hypotheses. Among them, the applicability of the island biogeography theory in terrestrial systems, the extinction and fragmentation thresholds hypotheses, the habitat amount hypothesis and alterations in the functional and phylogenetic structure of metacommunities in fragmented landscapes still bring relevant questions. The Cerrado is considered a hotspot for biodiversity conservation, however few studies have been conducted in the region to investigate the fragmentation effect in the fauna, despite the rapid conversion of its natural areas in anthropic land covers in recent decades. My main goal in this thesis is to investigate the effect of fragmentation and habitat loss in small mammals of Cerrado, by considering different approaches. Through an extensive sampling effort in 54 patches inserted in landscapes with variations in the habitat amount, I evaluated the response of rodents and marsupials to patch size and isolatation, as well as the woodland amount in the landscape. More specifically, I evaluated: 1- the effect of patch size in six 22,500 ha landscapes with different levels of remaining vegetation cover (10, 30 and 50% of habitat amount). 2 - I tested the habitat amount hypothesis in local landscapes (buffers with 250 to 6000 m radius) using subsets of the sample points in order to control the variation in patch size, isolation and habitat amount in the landscape. 3 - I evaluated the effect of habitat loss and fragmentation considering a functional and a phylogenetic perspective. Overall, my results showed that the habitat amount in the landscape is the most important factor to predict species richness; in turn, patch size has a secondary role. The generalist species abundance increased both in landscapes with less vegetation cover as well as in smaller patches. My results corroborate the habitat amount hypothesis, i.e. in general, after controlling for the habitat amount variation, patch size and isolation have no effect on the specialist species richness. However, I found a weak patch size effect in landscapes with intermediate habitat amount. Furthermore, patch size causes an alteration in the phylogenetic community structure, with marsupials being more abundant in smaller patches than rodents, whereas the latter are more common in larger ones. Regarding the functional community structure, the fragmentation gradient acts as an environmental filter for the species. Moreover, most preserved sites (in respect to both patch size and habitat amount) show greater functional diversity. This is the first study with an extensive sampling effort in the Cerrado evaluating the fragmentation effect, with replicates not only at the patch-level, but also at the landscape-level. These findings will be useful for future decisions on landscapes management in this very diverse and unique region.

Key-words: Didelphimorphia, fragmentation threshold, habitat cover, phylogenetic signal, savanna, species-area relationship, Rodentia.

Resumo geral

A fragmentação e perda de habitat são as principais ameaças atuais a biodiversidade. Muitos estudos têm sido realizados com o intuito de investigar a resposta das espécies as alterações em seu habitat. Com a expansão do conhecimento na área, muitas questões ainda continuam sendo debatidas, seja pela divergência de resultados entre diferentes estudos ou pelo surgimento de novas teorias e hipóteses. Entre elas, a aplicabilidade da teoria de biogeografia de ilhas em áreas terrestres fragmentadas, limiares de extinção e fragmentação, hipótese do "habitat amount" e alterações na estrutura funcional e filogenética de metacomunidades em paisagens fragmentadas são questões ainda pertinentes. O Cerrado é considerado um "hotspot" para conservação da biodiversidade, porém poucos estudos têm sido conduzidos na região para avaliar o efeito da fragmentação sobre sua fauna, a despeito da rápida conversão de suas áreas naturais em áreas antropizadas nas últimas décadas. Nesta tese meu objetivo principal foi investigar a resposta de pequenos mamíferos do Cerrado à fragmentação e perda de habitat sob diferentes enfoques. Por meio de um extenso esforço de captura em 54 fragmentos florestais e em paisagens com variações na quantidade de cobertura vegetal, avaliei a resposta de roedores e marsupiais em relação à fragmentação (tamanho e isolamento do fragmento e quantidade de vegetação na paisagem). Mais especificamente, foram avaliados: 1- o efeito do tamanho do fragmento em paisagens de 22.500 ha com diferentes níveis de cobertura vegetal remanescente (10, 30 e 50%). 2 – testei a hipótese do "habitat amount" em paisagens locais (buffers de 250 a 6000 m de raio) utilizando subconjuntos dos pontos amostrais de forma a controlar a variação entre tamanho e isolamento do fragmento e quantidade de vegetação na paisagem. 3 - Avaliei como as comunidades respondem à fragmentação em uma perspectiva funcional e filogenética. De forma geral, meus resultados mostraram que a quantidade de vegetação na paisagem é o fator mais importante para predizer a riqueza de espécies, o tamanho do fragmento por sua vez teve um papel secundário. Já a abundância de espécies generalistas aumenta tanto em paisagens com menor quantidade de vegetação quanto em fragmentos menores. Meus dados corroboraram a hipótese do "habitat amount", ou seja, de forma geral quando controlei a variação na quantidade de vegetação na paisagem, o tamanho do fragmento e isolamento deixaram de ter efeito sobre a riqueza de espécies especialistas. Porém, encontrei relação com o tamanho de fragmento em paisagens com níveis intermediários de fragmentação. Ainda, a estrutura filogenética das comunidades sofreu alteração em relação ao tamanho de fragmento, sendo que em fragmentos menores marsupiais são mais abundantes que roedores, enquanto que os últimos são mais comuns em fragmentos maiores. Em relação à estrutura funcional das comunidades, o gradiente de fragmentação funcionou como filtro ambiental para as espécies. Por outro lado, locais mais preservados (em relação tanto ao tamanho do fragmento quanto à quantidade de vegetação) apresentaram maior diversidade funcional. Este é o primeiro estudo com esforço amostral substancial no Cerrado avaliando o efeito da fragmentação, com réplicas não só a nível de fragmento, mas também a nível de paisagem. Estes resultados evidenciam que a perda de habitat, e secundariamente a fragmentação, resultam em alterações substanciais nas comunidades de pequenos mamíferos sob diversos enfoques. Há alterações na riqueza, abundância, composição de espécies e estrutura funcional e filogenética em relação ao gradiente de fragmentação e perda de habitat. Estes resultados deverão auxiliar os tomadores de decisão sobre medidas de conservação nesta região tão diversa e única.

Palavras-chave: Didelphimorphia, limiar de fragmentação, quantidade de habitat, relação espécie-área, Rodentia, sinal filogenético.

General introduction

We are facing a biodiversity crisis because the extinction ratio nowadays is larger than expected to occur normally (Dirzo & Raven 2003). Scientists have alerted that we are walking towards the Earth's six mass extinction (Barnosky et al. 2011, Ceballos et al. 2015). In fact, 75% of amphibians, mammals, and birds are predicted to go extinct within 240-540 years (Barnosky et al. 2011). Behind this increase in extinction rates are the humans' activities that modify the earth surface in an incredibly fast speed.

The main threats to wildlife species are habitat loss, climate change, overexploitation, pollution, and species invasions (e.g. Wilcove et al. 1998, Brook et al. 2008, Pereira et al. 2012). Among this threats, habitat loss and fragmentation are the major factors responsible for the currently species extinction (Barnosky et al. 2011). The land cover change results in a combination of decreasing habitat available for the species and changes in the spatial configuration and quality of the remaining patches (Andrén 1994, Fahrig 2003).

The island biogeography theory (MacArthur & Wilson 1963) has inspired conservation and ecological studies (Laurance 2008, Fahrig 2013). It predicts that smaller and more isolated islands comprise less species richness than larger islands or similar-sized islands which are located closer to mainland. In this sense, scientists consider the patch area and isolation analogous to island area and isolation, and use these variables to predict the species richness in terrestrial systems of fragmented areas (e.g. Diamond 1975, Watling & Donnelly 2006, Magura et al. 2010). The extrapolation of the predictions of the island biogeography theory to non-natural fragmented terrestrial landscapes brought a lot of influence in management of these areas, for example, in reserves design (Diamond & May 1976). Although useful to predict general patterns, the theory has limitations when extrapolated to terrestrial systems (Haila 2002). The theory does not take into account the matrix composition, which can influence patch isolation (Gascon et al. 1999, Ricketts 2001, Prevedello & Vieira 2010). The more similar the matrix composition to the patches composition, the easier for the species to disperse between patches (Prevedello & Vieira 2010). Therefore, the matrix is not always analogous to the inhospitable water matrix (for terrestrial species) surrounding true island systems. In addition, the landscape context (e.g. habitat amount) can also affect the species-area relationship in forest patches (Andrén 1994, Pardini et al. 2010, Fahrig 2013).

Andrén (1994) showed in a review that the species-area relationship in fragmented areas is not linear. The patch size has a positive effect in species richness just in landscapes below a certain threshold (around 20-30% of habitat amount) of habitat loss in the landscape. He found that near this threshold some properties of the landscape, like the distance between patches, start increasing in an exponential way. Therefore, above the threshold, the patches are closer to each other, and even small patches can keep a high richness. However, below the threshold, the patches become isolated such an extent that landscape connection is lost and the species-area relationship takes root. The fragmentation threshold hypothesis was corroborated for some studies (e.g. Henein et al. 1998, Collingham & Huntley 2002) and not found in others (e.g. Parker & Mac Nally 2002).

Pardini et al. (2010) expanded the fragmentation threshold hypothesis showing that in landscapes with severe habitat loss (10% of habitat amount) the area is not a good predictor of species richness because regardless of patch size, just generalist species would remain in these landscapes. The idea that the fragmentation (or patch size) effects are more important in intermediate values of habitat amount has been considered in other studies as well (Banks-Leite et al. 2014, Villard & Metzger 2014). Therefore, to achieve representative results of ecological theories and liable to predictions applicable to conservation strategies, restoration and sustainable use, it is essential to consider landscapes with a wide range in habitat amount and not only those ones that still maintain high biodiversity (Cousins & Eriksson 2008, Cousins 2009).

However, recently Fahrig (2013) challenged the role of patch size and isolation to predict species richness in fragmented landscapes. She proposes the habitat amount hypothesis that predicts that species richness in patches with standardized sampling should increase with the total habitat amount in the "local landscape" of the sample. Therefore, the number of species in a sample is independent of the particular patch area in which the sample is located, except in the proportion that this patch area contributes to the habitat amount in the "local landscape" of the sample. The author used a series of arguments to defend this point of view, but summarizing she attributes the species-area relationship in patches with the sampling area effect. She observed that the species-area slopes in continuous and fragmented regions are similar, although the richness was lower in the fragmented regions (see Fahrig 2013 for a review). Therefore, she related this difference with the habitat amount surrounding the sample units. On the other hand, in island systems the species-area slope is steeper than the species-area slope in continuous habitat (Watling & Donnelly 2006). The habitat amount hypothesis has not been directly tested until now. However, some studies that compared the role of habitat loss and fragmentation in affect species richness show evidence that fragmentation effect, when not correlated with habitat loss, has no effect in species richness (see Fahrig 2003 for a review).

Another important point is that, not all species are negatively affected by habitat loss. While some species declines, others are not affected or even increase in altered landscapes (Stuart et al. 2004, Pardini et al. 2010). Identify what puts some species at risk is a major goal to conservation actions, since we can focus the limited resources to the most vulnerable species. Differences in the vulnerability to landscape change between species are probably related to species traits. Traits in this sense are related to any feature (morphological, physiological, behavioral, etc.) that can affect the fitness of a species (Violle et al. 2007).

To describe the communities based in their richness, abundance, or composition, does not allow to identify witch species traits are favored or excluded in face of a disturbance. The functional approach investigates how organisms are functionally structured in the communities, that is, which functional traits are selected or filtered in the presence of an environmental disturbance (Podgaiski et al. 2013). Therefore, to describe communities based on traits allows the identification of patterns of organization that can, to some extent, be extrapolated to communities with different species composition from those of the original research, which provides the generalization of knowledge required for conservation actions.

In general, the species community composition can be driven by neutral processes (e.g. dispersal limitation; Hubbell 2001) or by their niche based on habitat (e.g. environmental filters and biotic interactions; Cornwell & Ackerly 2009). From the niche perspective, the species communities' organization show two opposite trends. On the one hand, the action of environmental filters can generate an organization pattern with trait convergence, that limits the species present in the community to those more similar in certain traits (Keddy 1992). On the other hand, biotic interactions between species that compose a community can affect its structure, leading to species arrangements that can diverge more to each other in terms of the functional traits than expected if they were randomly distributed. Negative biotic interactions generate similarity limitation between species (Diamond 1975), a pattern that results in trait divergence (Wilson 1999).

In addition, the phenotypic characteristics of the species that composes an assembly are simultaneously the result of their evolutionary history and their ecological response to the current environment. Thus, it is expected that closer phylogenetically species share more phenotypic characteristics than with the more distant ones. This tendency for phylogenetic conservation in phenotypic traits of phylogenetically related species is called phylogenetic signal (Blomberg & Garland 2002).

Taking this in mind, we can ask if the fragmentation and habitat loss can act as an ecological filter acting not only at species richness, abundance and composition, but also at community functional and/or phylogenic structure. Although, the functional and phylogenetic patterns have been investigated in many different situations (e.g. Cianciaruso et al. 2013, Gianuca et al. 2013, Podgaiski et al. 2013), the role of habitat loss and patch size at a functional and phylogenetic perspective are just starting to be investigated (e.g. Brashares 2003, Magioli et al. 2015).

The Cerrado is a savannic biome that occupies a vast territory of Brazil and small portions of Paraguay and Bolivia. The region shows high vegetation heterogeneity with grassland, scrub-like savanna, woodlands, and gallery forest (Eiten 1982). This is considered a biodiversity hotspot, taking into account the high number of plant endemism and conversion of natural areas into anthropogenic land covers (Myers et al. 2000). Despite the eminent risk for its biodiversity, since 50% of the natural covers of the Cerrado have already been converted and about 80% is under some form of human use (Mittermeier et al. 1999, Machado et al. 2004, Klink & Machado 2005), little is known about the effect of habitat loss and fragmentation in the region.

The small mammals (rodents and marsupials) play an important role in ecosystems function through seed dispersal, seed predation, and resource for larger predators, among others (Pizo 1997, Grelle & Garcia 1999, Vieira & Izar 1999, Pimentel & Tabarelli 2004). They are also very diverse taxonomically and ecologically (Bergallo 1994, Reis et al. 2006) and have a rapid life cycle. Therefore, small mammals are a useful tool for studies in fragmented landscapes. We sampled small mammals in the Brazilian Cerrado to investigate how habitat loss and fragmentation affect the species richness, abundance, composition and functional and phylogenetic structure.

The thesis is structured in the following three chapters to investigate the role of patch size and habitat amount in the landscape considering different aspects of species communities:

In the **first chapter** we employed a model selection approach to evaluate how patch size, habitat amount in the landscape and their interaction explain the variation in the species response. We separate the species into habitat generalist and specialist as these groups can show opposite responses to the fragmentation process (Pardini et al. 2010). We sampled six landscapes with 10, 30 and 50% of habitat amount. Inside each landscape, we sampled seven to nine patches with different sizes. Considering that patch size and habitat amount are usually positively correlated, we choose patches in order to do not have a correlation between these predictors. Because small mammal species in a savanna region are better suited to naturally open areas than forest-dwelling species, we expected a relationship between species descriptors (alpha diversity) and patch size just in landscapes with less habitat amount (10% of cover), but the gamma diversity would still be high in all landscapes.

In the **second chapter**, we used a local-landscape approach to test the habitat amount hypothesis. We sampled 100 transects and measured: the habitat amount in the surrounding landscape, the patch size and the isolation (mean distance to the nearest three patches). More specifically, we tested the strength of effect of habitat amount in the landscape, patch size and isolation to predict the specialist small mammal richness. We used generalized linear models considering the predictors together and singly, using subsets of that data controlling for correlation between them. According to the habitat amount hypothesis, we expected that when we consider subsets of the data set controlling for the correlation between predictors, the habitat amount would have a positive effect in species richness, however, patch size and isolation would have no effect on species richness anymore.

In the **third chapter**, we considered the small mammals sampled in 54 woodland patches of different sizes and inserted in six landscapes with different habitat amount. We described the species based in traits that we believe are important to its adaptation to the environment. Then, we applied an approach based on the scaling up of phylogeny and traits information of each species to the community level weighted by species abundance. After, the community structure matrixes (based into their phylogeny and traits composition) were correlated with the patch size and habitat amount predictors in order to find trait convergence and/or divergence assembly pattern as well as an alteration in the phylogenetic community structure. As disturbance gradients can act as environmental filters (Podgaiski et al. 2013), we expected that trait-convergence assembly patterns would be more important in structuring communities than divergence patterns. On the other hand, we expect that in larger and/or less fragmented landscapes, trait-divergence assembly patterns will be more prevalente, because communities facing a smaller effect of environmental filters were being mainly structured by biotic interactions such as competition, which would limit the similarity between species communities.

Chapter 1 - The interacting effect of patch size and habitat amount on small-mammal communities in a Savanna region of South America

Abstract

The habitat amount and patch size have a positive effect in species richness in fragmented landscapes. However, some studies in forest areas showed that the relationship of patch size and species richness is not linear, depending on the habitat amount in the landscape. We sampled 49 patches in six landscapes with 10, 30 and 50% of habitat cover in a savanna region of South America. Employing an information criteria approach, we evaluated how the generalist and specialist small mammals respond to patch size and habitat amount in the landscape. Considering that small mammal species in this region are better suited to naturally open areas than forest-dwelling species, as the Cerrado ecoregion is composed by a mixture of open and forest vegetation types, we expected a relationship between species descriptors (richness, abundance and diversity) and patch size just in landscapes with less habitat amount (10% of cover), but the gamma diversity would still be high in all landscapes. Overall, our results show that there is a substantial decreased in the richness of small-mammal specialist species as woodland areas are replaced by exotic pastures in landscapes of the Cerrado. On the other hand, generalist species become more abundant in smaller patches and landscapes with less habitat amount. The lack of a patch-size effect is in accordance with the habitat amount hypothesis, which predicts that the habitat amount in the landscape is the main predictor of species richness. These results highlight the need to understand the long-term effect of fragmentation and habitat loss in the Cerrado since the region is being subjected to a continuous process of fragmentation in the recent decades.

Key-words: fragmentation threshold, habitat cover, savanna, species-area relationship.

Resumo

A quantidade de habitat e o tamanho do fragmento são preditoras importantes para riqueza de espécies em paisagens fragmentadas. Entretanto, alguns estudos em áreas florestais mostraram que a relação entre tamanho do fragmento e riqueza de espécies não é linear, variando de acordo com a quantidade de vegetação na paisagem. Nós amostramos 49 fragmentos inseridos em seis paisagens com 10, 30 e 50 % de cobertura vegetal natural em uma região de Cerrado. Empregando uma abordagem de seleção de modelos, avaliamos como espécies de pequenos mamíferos generalistas e especialistas respondem ao tamanho do fragmento e quantidade de vegetação na paisagem. Considerando que as espécies de pequenos mamíferos nesta região podem ser mais adaptadas a ambientes abertos do que espécies estritamente florestais, nós esperávamos uma resposta das espécies ao tamanho de fragmento apenas nas paisagens com menor quantidade de vegetação (10 % de cobertura vegetal), mas a diversidade gamma ainda seria alta em todas as paisagens. Surpreendentemente, exceto para a abundância de generalistas, a riqueza e diversidade não foram relacionadas ao tamanho do fragmento. Entretanto, a quantidade de vegetação na paisagem teve um efeito importante, com a riqueza de espécies especialistas declinando em paisagens com menor quantidade de habitat e espécies generalistas se tornando abundantes. A falta de relação espécie-área está de acordo com a hipótese do “habitat amount” que prevê que a quantidade de vegetação na paisagem seria a principal preditora da riqueza de espécies. Estes resultados enfatizam a necessidade de se compreender os efeitos da fragmentação no Cerrado já que esta região tem sofrido com o desmatamento nas últimas décadas e apenas uma pequena parcela do bioma encontra-se protegido na forma de unidades de conservação.

Palavras-chave: limiar de fragmentação, cobertura vegetal, savana, relação espécie-área.

Introduction

The habitat loss and fragmentation have been one of the biggest challenges for the biodiversity conservation (Fahrig 2003). Their negative effects are a result of a combination between the decrease in total habitat available for the species and changes in the spatial configuration and quality of the remaining patches (Andrén 1994, Fahrig 2003).

The island biogeography theory (MacArthur & Wilson 1967) was proposed to explain species richness on islands, but it is widely used to describe the habitat fragmentation effect in continental areas (Andrén 1994, Haila 2002). In this sense, the species-area relationship and extinction and colonization rates would be equivalent in terms of islands or habitat patches. However, different from islands, surrounded by an inhospitable environment, the patches in continental areas are separated by a matrix that can be used by the species with different frequency depending on its composition and the species present in the patches, i.e. its permeability is variable (Umetsu & Pardini 2007, Umetsu et al. 2008). In this case, the premise that the patches are isolated can be violated by generalist species that use different habitats in the landscape, including the matrix (Addicott et al. 1987). On the other hand, specialist species are more affected by fragmentation because their population can become completely isolated in the remaining patches (Pardini et al. 2010).

In addition to the patch area, the habitat amount in a given landscape also influences the species richness and composition present in the patches. Andrén (1994) proposed the existence of a fragmentation threshold around 30% of the remaining habitat amount in the landscape, below which an increase in habitat loss results in an exponential increase in the distance between patches to such an extent that the landscape connectivity is eroded. Thus, in landscapes with 30% or less amount of total habitat, species richness in patches would decrease more rapidly than expected by patch habitat loss only, because isolation of patches becomes an important factor influencing species richness in patches additional to habitat loss.

Pardini et al. (2010) tested the fragmentation threshold hypothesis in fragmented landscapes of the Atlantic Forest and proposed another conceptual model. It predicts that in landscapes with just 10% of habitat amount the area is not a good predictor of species richness because, regardless of patch size, just generalist species would remain in these landscapes. Therefore, to achieve representative results of ecological theories and liable to predictions applicable to conservation strategies, restoration and sustainable use, it is essential to consider landscapes with a wide range in habitat amount and not only those ones that still maintain high biodiversity (Cousins & Eriksson 2008, Cousins 2009).

Most of the knowledge about the impacts of habitat loss and fragmentation comes from studies conducted in essentially forest biomes (e.g. Malcolm 1997, Pardini 2004, Pardini et al. 2010). However, little is known about how populations and communities present in more heterogeneous and open biomes, such as the savanna formations, respond to the habitat loss and fragmentation process. The Cerrado is a rich and diversified physiognomy, with high plant beta diversity (Felfili et al. 2004). Its formations extend from open grassland to gallery forests. The plant heterogeneity between sites results in a highly diverse fauna, which gives the Cerrado the title of the richest savanna in the world and a biodiversity hotspot due to the high degree of plant endemism and threat level for the conversion of natural areas (Myers et al. 2000). Covering 22% of the Brazilian territory, in recent decades the Cerrado is suffering a rapid process of conversion of natural vegetation into agricultural and pasture areas. The loss of natural vegetation has already reached about 50 to 60% of its original area (Mittermeier et al. 1999, Machado et al. 2004, Klink & Machado 2005). Conservation strategies rely on information on how biodiversity is maintained and / or affected in remaining patches, in order this information assist in the conservation planning and restoration strategies.

Small non-flying mammals (rodents and marsupials) have a short life cycle and relatively small home range. Moreover, they are extremely diverse in taxonomic and ecological terms (Bergallo 1994, Reis et al. 2006). These traits place this group as an appropriate tool for ecological studies in fragmented landscapes.

Due to the lack of studies on habitat loss and fragmentation in savannas and the intense conversion of the natural areas of Cerrado in which the region is undergoing recently, our goal is to evaluate how patch size and habitat amount in the surrounding landscape interact and act on richness, abundance, diversity and composition of small mammal communities. We separated the species into two groups: generalist and specialist species as each group can respond to the habitat loss and fragmentation in different ways. We employ a model selection approach to evaluate how patch size, habitat amount in the landscape, and their interaction explain the variation in the data. We expect that due to the high heterogeneity between different phyto-physiognomies of the Cerrado, the fragmentation threshold would be below 30% of remaining habitat amount in the landscape. Thus, the effects of patch size will be evident only in landscapes with less habitat amount since the Cerrado species are better suited to naturally open areas than forest-dwelling species. In this sense, only in landscapes with 10% of habitat amount the richness, abundance and diversity of species, especially the specialist ones, will be positively correlated with patch size, but the gamma diversity would still be maintained in the landscape as a whole. In landscapes with intermediate or high level of habitat amount (30% and 50% of habitat cover), the richness, abundance and diversity will be independent of patch size.

Material and methods

Study area

We sampled six landscapes of 22,500 ha each, between the coordinates 20º17’ to 21º15’S and 54º53’ to 56º31’W, with different percentages of habitat amount: two with 10, two with 30 and two with 50 % of habitat cover in the Cerrado of Mato Grosso do Sul, Brazil (Figure 1).

We choose seven to nive patches to sample small mammals inside each landscape. Although smaller patches are more common in landscapes with lower percentage of habitat amount and larger ones are mostly present in the landscapes with higher habitat amount, we sampled the greatest possible range on patch sizes in each landscape, in order to do not have difference in average patch size between landscapes (Appendix 1). In addition to the criterion of size, we were restricted to sample patches for which we obtained permission from the owners to access the area, as all landscapes are located inside private properties. The distance of each sampled patch to the nearest patch did not differ between landscapes as well (Appendix 2). In total, we sampled 49 patches: 18 in landscapes with 10% of habitat cover (nine patches in each of two landscapes), 16 in landscapes with 30% (eight patches in each) and 15 in landscapes with 50% (seven and eight patches in each).

The landscapes are similar in relation to topography and climate, but differ in the average distance between patches, which is higher in landscapes with less habitat amount (Appendix 3). To reduce the variation in species composition between areas, the maximum distance bettwen landscapes was ≈ 160 km and all of them are inserted in the same river basin. Thus, differences in species composition between landscapes should be primarily related to differences in the habitat fragmentation and not to differences in species distribution range between areas.

Woodland areas compose the main natural vegetation in the southern Cerrado (Silva et al. 2006); most of the open areas in this region are highly modified grazing lands composed by exotic species.We installed the transect lines just in woodland areas, since the gallery forest can have a particular fauna (Johnson et al. 1999) and were not present in all patches.

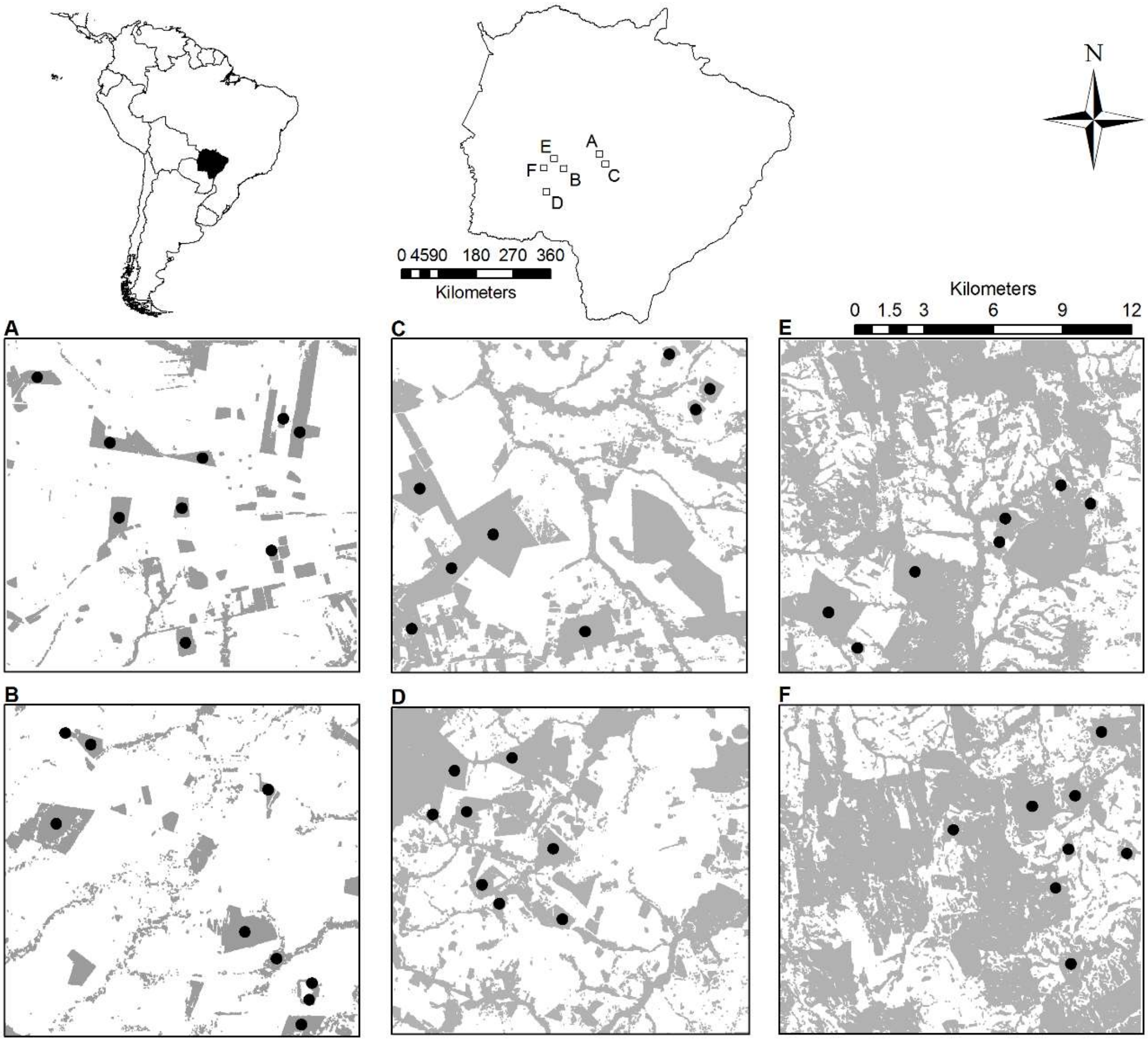


Figure 1. Landscapes with 10% (A and B), 30% (C and D) and 50% (E and F) of habitat amount indicating the distribution of the 49 woodland patches sampled in a Cerrado region of Mato Grosso do Sul, Brazil. In gray natural areas of woodland cover.

Landscape analysis

We classified recent TM/Landsat-7 images of south region of Cerrado using the GIS SPRING program (Camara et al. 1996). Using a supervised classification, we classified the study region into a binary habitat/nonhabitat map where habitat was defined as forest cover (woodland areas).

We use the normalized difference vegetation index (NDVI) to quantify the average density of vegetation in each patch. This index is based on the antagonistic behavior of the spectral reflectance measurements acquired in the visible (red) and near-infrared regions. The NDVI provides an estimation of vegetation density in each patch because it is highly correlated with vegetation parameters such as green-leaf biomass, green-leaf area, and absorbed photosynthetically active radiation (Curran 1982, Goward et al. 1985).

Data collection

Each patch received 20 live-traps distributed along two transect lines that were at least 300 meters distant from each other and at 50 m from the patch edge. In each transect ten live-traps were placed alternately on the ground (wire: 33 x 12 x 12 cm) and in the understory (Sherman: 30 x 9 x 7 cm) at 1.5 m height.

Four field phases of five or six consecutive nights each were conducted, two in the rainy season (February/March 2012 and November/December 2012) and two in the dry season (July/August 2012 and June/July 2013). The total sampling effort was 408 trap-nights in each patch and 19,992 trap-nights considering all patches.

We marked the small mammals captured with numbered ear-tags (Fish and small animal tag size 1, National Band and Tag, Newport, KY, USA) and released at the same point of capture. When identification in the field was not possible, we euthanized the individual for identification in the laboratory. Sampling techniques were approved by the Instituto Chico

Mendes de Conservação da Biodiversidade (ICMBio) (protocol 30808-2) and are in compliance with guidelines published by the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2011).

Data analyses

We classified the species in generalist and specialist species according to the following criteria: 1) publications indicating the species as sensitive to habitat loss/fragmentation; 2) restricted distribution range and 3) specificity regarding to habitat use (occurrence restricted to woodland areas) (Appendix 4).

We evaluated how the richness and abundance of generalist and specialist species respond to the fragmentation gradient represented by the patch size and the habitat amount in the landscape. We also analyzed the relationship between the diversity of generalists and specialists with the fragmentation using the effective number of species (exp (H')) from the Shannon diversity index (H'). Effective numbers derived from species diversity indices that share a common and intuitive set of mathematical properties that facilitate the interpretation of the diversity in an area, which is not possible through the direct employment of diversity indices, since different indices can lead the conflicting results when comparing diversity among areas (Jost 2006).

We used generalized linear models to test the association between patch size and habitat amount in the landscape (predictors) with species richness, total abundance and diversity (response variables) for each patch. In this case, the two transects of each path were considered as one sampling unit. For each response variable, we created nine regression models representing different combinations of the effect of patch size, habitat amount and their interaction. The models include: 1) null model (intercept only) where there is no effect of patch size, nor habitat amount; 2) only a patch size effect, despite of habitat amount in the surrounding landscape; 3) only habitat amount effect, with no effect of patch size; 4) effect of both, patch size and landscape; 4a) variation of model 4 with different slope in different landscapes; 5) patch size effect only in landscapes with 10 and 30% of habitat amount (corresponds to fragmentation threshold hypotheses proposed by Andrén 1994); 5a) variation of model 5, with different slopes between landscapes; 6) patch size effect only in landscapes with 30% of habitat amount (corresponds to the loss of ecological resilience model proposed by Pardini et al. 2010); and 7) patch size effect only in landscapes with 10% of habitat amount (this model encompasses our hypothesis for the Cerrado). The species richness and abundance cannot assume negative values and do not have a normal distribution when the values are close to zero. Therefore, we used a Poisson error to model the species richness and abundance. We use a Gaussian distribution for species diversity.

We compared the variance explained in species richness, abundance and diversity based on the Akaike information criterion with correction for small sample sizes (AICc). We consider as equally plausible models those ones with ΔAICc< 2 (Burnham & Anderson 1998).

We measured the turnover in species composition using the Bray-Curtis similarity index between all pairs of samples. To determine the association between the change in the species composition and the fragmentation gradient, we employed a redundancy analysis for distance measurements (db-RDA) using the Bray-Curtis index as the response variable.

We consider the patch average NDVI as a covariate in all analyzes. In this way, we were able to deal with differences in the vegetation density between patches and landscapes.

All analyzes were performed in the R software (R Development Core Team 2013). The Redundancy Analysis was performed using the capscale function in the Vegan package (Oksanen et al. 2012).

Results

Richness, abundance and diversity

We captured 921 individuals belonging to 20 small mammal species, eight marsupials and 12 rodent species. The total richness was 11 (eigh species each), 15 (10 and 12 species each) and 15 (12 species each; Appendix 4) in the landscapes with 10 %, 30 % and 50 % of habitat amount respectively.

In relation to the generalist richness, two models were selected, and both do not show patch size effect (Table 1). Although the model 3, that predicts a difference in species richness between landscapes, showed the lowest AICc, the null model (model 1) was also equally plausible. For specialist species richness, the model 3 also showed the smallest AICc value, but unlike the generalist species, the specialist had greater richness in landscapes with greater habitat amount (Figure 2). Further, the model 4 also explained the variation in the specialist species richness equally well (Table 1).

The model that best explained the variation in the abundance of generalist species was the model 4 that includes both the habitat amount effect and the patch size effect in all landscapes. The abundance was greater in landscapes with less habitat amount (Figure 2, Table 1). On the other hand, the specialist species abundance was higher in landscapes with higher habitat amount. Four models were equally plausible to explain the data variation (Table 1). Among them, the model 6 showed the lowest AICc value. It includes a patch size effect only in landscapes with 30% of habitat amount (Figure 2). However, different of what we expected, the relationship between abundance of generalist (in all landscapes) or specialist species (in landscapes with 30% of habitat amount) and patch size was negative, with larger patches showing lower abundance than smaller ones (Figure 2).

Table 1. Models tested to explain the richness, abundance and diversity of small mammals in six landscapes with different habitat amount in the Cerrado of Mato Grosso do Sul, Brazil. M1: null model (no patch size or landscape effect); M2: only patch size effect; M3: only landscape effect; M4: effect of both patch size and landscape, the patch size effect is present in all landscapes; M4a variation of M4 with different slope between landscapes; M5: patch size effect only in landscapes with 10 and 30% of habitat amount; M5a: variation of M5 with different slope; M6: patch size effect only in landscapes with 30% of habitat amount; and M7: patch size effect only in landscapes with 10% of habitat amount.

	Generalist species				Specialist species			
	Model	AICc	Δ AICc	*Wi*	Model	AICc	Δ AICc	*Wi*
Richness	**M3**	**172.49**	**0.00**	**0.27**	**M3**	**129.63**	**0.00**	**0.34**
	M1	**172.54**	**0.05**	**0.26**	**M4a**	**131.00**	**1.37**	**0.17**
	M7	174.68	2.19	0.09	M4	131.71	2.08	0.12
	M2	174.69	2.2	0.09	M6	131.82	2.19	0.12
	M5	174.76	2.27	0.09	M7	131.92	2.29	0.11
	M4	174.97	2.48	0.08	M5	132.08	2.45	0.10
	M6	174.97	2.48	0.08	M5a	134.19	4.56	0.04
	M4a	177.21	4.72	0.03	M2	141.46	11.83	0.00
	M5a	177.28	4.79	0.02	M1	143.92	14.29	0.00
Abundance	**M4**	**390.97**	**0.00**	**0.74**	**M6**	**218.06**	**0.00**	**0.30**
	M4a	393.08	2.11	0.26	**M3**	**218.71**	**0.65**	**0.22**
	M6	404.56	13.59	0.00	**M5a**	**219.29**	**1.23**	**0.16**
	M5	405.12	14.15	0.00	**M7**	**219.88**	**1.82**	**0.12**
	M5a	406.25	15.28	0.00	M4	220.82	2.76	0.08
	M3	423.54	32.57	0.00	M5	220.97	2.91	0.07
	M7	424.63	33.66	0.00	M4a	221.65	3.59	0.05
	M2	433.92	42.95	0.00	M1	289.68	71.62	0
	M1	473.52	82.55	0.00	M2	290.87	72.81	0
Diversity	**M3**	**134.06**	**0.00**	**0.26**	**M4**	**97.64**	**0.00**	**0.41**
	M7	**134.23**	**0.17**	**0.24**	**M4a**	**99.05**	**1.41**	**0.20**

M5	**135.97**	**1.91**	**0.10**	**M3**	**99.13**	**1.49**	**0.19**
M4	136.06	2.02	0.09	M7	101.55	3.91	0.06
M6	136.54	2.48	0.07	M5	101.59	3.95	0.06
M1	136.55	2.49	0.07	M6	101.62	3.98	0.06
M4a	136.8	2.74	0.07	M5a	104.15	6.51	0.02
M5a	136.83	2.77	0.06	M2	104.43	6.79	0.01
M2	137.93	3.87	0.04	M1	107.55	9.91	0.00

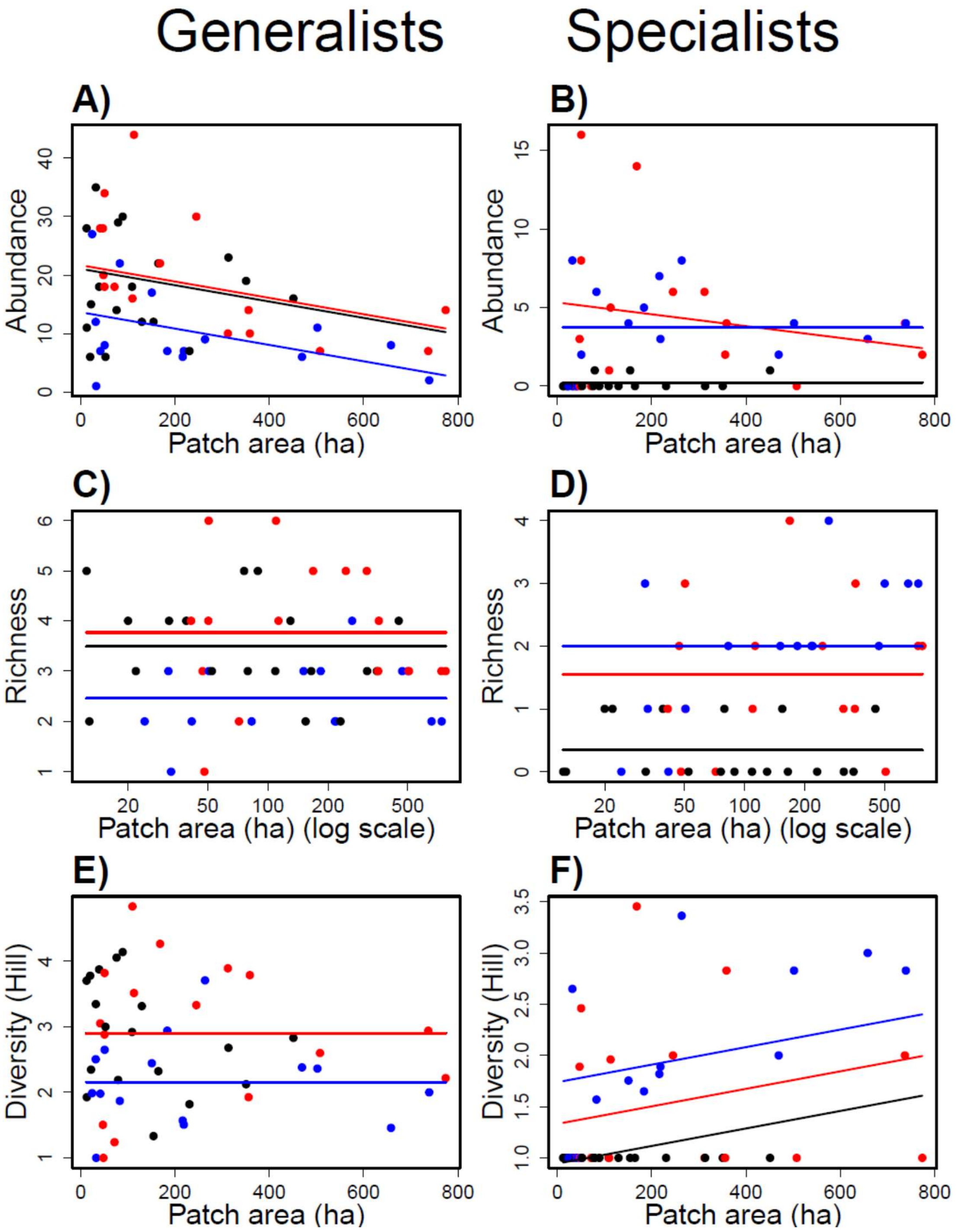


Figure 2. Effects of patch size and habitat amount in the landscape in richness, abundance and diversity of generalists and specialists small mammals present in woodland patches in a Cerrado region. The graphs correspond to the models with the smaller AICc for each response variable. Black: landscapes with 10% of habitat amount; Red: landscapes with 30% of habitat amount; and Blue: landscapes with 50% of habitat amount.

Three models were equally plausible to explain the generalist diversity (Table 1). Again, the model 3 showed the lowest AICc value, being the generalist diversity smaller in landscapes with high habitat amount (Figure 2). Regarding to specialist diversity, three models were selected (Table 1) and, between them, model 4 showed the lowest AICc value (Table 1). The diversity of specialist species is greater in landscapes with high habitat amount and there is a positive effect of patch size in all landscapes (Figure 2).

However it is noteworthy that, except for generalist abundance, the sum of the weights of models with AICc <2 was low for all response variables. Overall, we had little support to predict the richness and diversity of generalist species. However, for specialist species the sum of the models weights that consider the habitat amount in the landscape was high (see Table 1). In addition, considering the three response variables analyzed for the specialist group, the model 3, that considers only the habitat amount effect, had ΔAICc < 2 in all cases. On the other hand, the models that not considered an effect of habitat amount in the landscape (model 1 and model 2) have no weight or the lowest weight (Table 1). Therefore, for the specialist species the habitat amount is an important factor, while the effect of patch size was not consistently clear.

Species composition

The RDA axes, representing the relationship between the small mammals species composition and the environmental variables, explained 11% of the variation in the abundance of all species sampled ($P < 0.001$). The habitat amount in the landscape and the NDVI were more strongly associated with the turnover ($P = 0.005$) than patch size ($P = 0.04$).

Analyzing the triplot, it is possible to see the ordination of the patches in relation to the fragmentation effect in the first axis, with patch size and habitat amount in the landscape acting similarly on the species composition, although the effect of the last is greater than the first (Figure 3). In this case, lower scores represent smaller patches in landscapes with less habitat amount, while sampling units with higher scores represent larger patches in landscapes with highter vegetation cover. The generalist and specialist small-mammal compositions change in relation to this gradient with generalist species mostly related to smaller patches in landscapes with less habitat amount (left side of diagram) while specialist species are predominantly associated with larger patches in landscapes with greater vegetation cover (right side of the diagram). It is also possible to see that there is a relationship between the vegetation density and the species composition in the second axis with larger NDVI values in the upper. However, it is not possible to relate the NDVI with the species composition classified as generalists and specialists, but regardless of habit, most species are more closely related to patches with higher density of woody vegetation (higher NDVI).

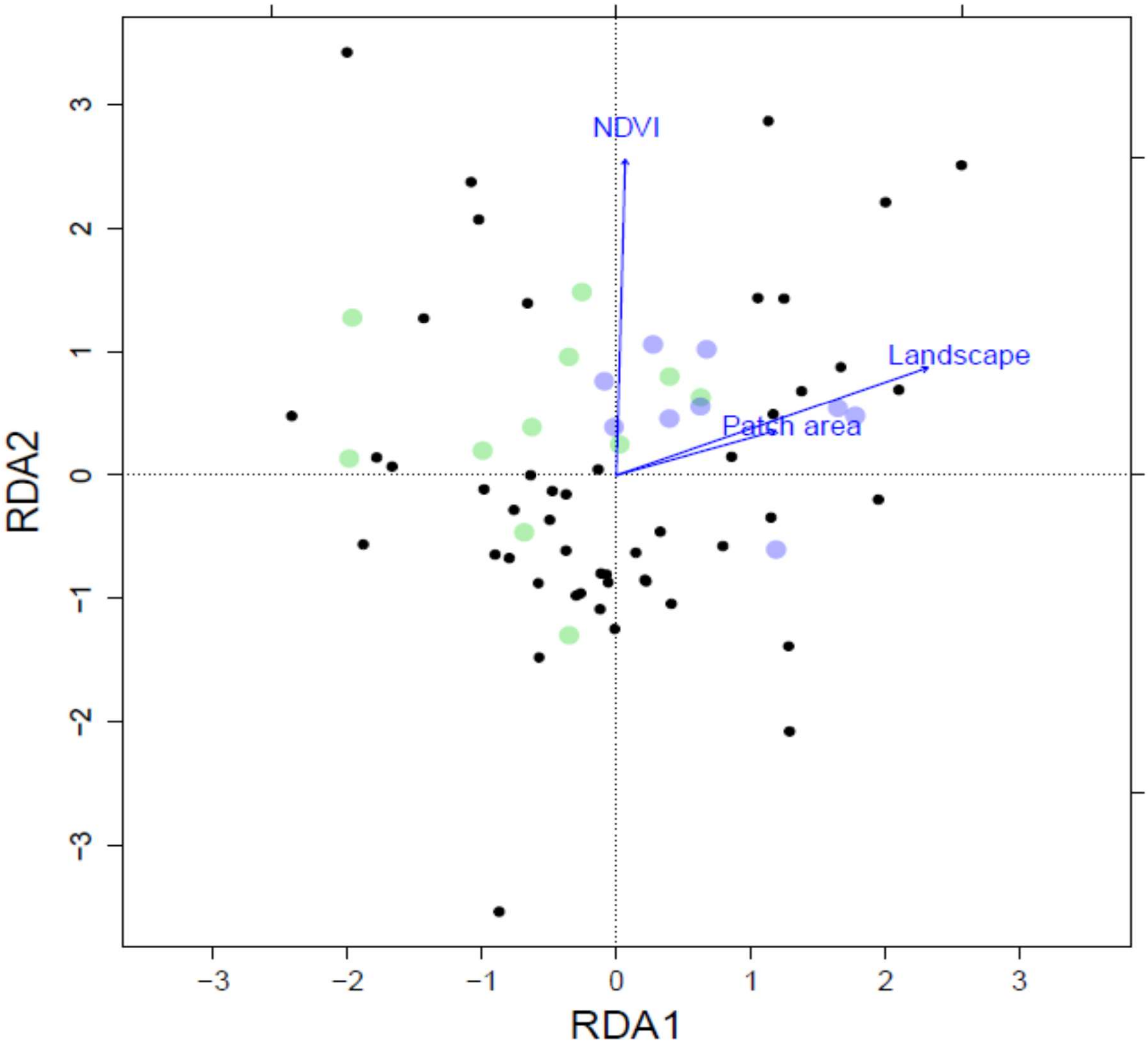


Figure 3. Triplot indicating the relationship between the small mammal species composition (calculated based on the dissimilarity of Bray-Curtis) with the effect of patch size, habitat amount in the landscape and vegetation density (NDVI). Green circles correspond to generalist species, blue circles correspond to specialist species, and black circles correspond to patches.

Discussion

Little attention has been given to the consequences of habitat loss and fragmentation in savannas or grasslands biomes, despite the rapid conversion of their natural areas into disturbed landscapes in recent decades (Bond & Parr 2010). This is the first study in the Cerrado with large sample (49 patches) that measured the effect of patch size in landscapes with different habitat amount. Overall, our results show that there is a substantial decreased in the richness of small-mammal specialist species as woodland areas are replaced by exotic pastures in landscapes of the Cerrado. On the other hand, generalist species become more abundant in smaller patches and landscapes with less habitat amount.

We do not corroborate our hypothesis that only in landscapes with less habitat amount (10% of remaining vegetation cover) the richness, abundance and species diversity would be related with patch size, but without decreasing the gamma diversity in the landscape. Nevertheless, our results were also distinct from those postulated by Andrén (1994) which predicts a patch size effect in species richness only below a certain threshold of habitat amount (around 20-30% of habitat cover in the landscape). We also did not find the same result of Pardini et al. (2010) for the Atlantic-Forest small mammals, where the authors found a patch size effect just in landscapes with intermediate level of vegetation cover. However, our results agree with the Pardini et al. (2010) in the sense that we lose specialist species richness in landscapes with severe habitat loss. The habitat amount in the landscape is the most important factor to determine the species richness, abundance and diversity for small mammals in the Cerrado. Except for generalist richness, all the selected models had the effect of the vegetation cover in the landscape. Thus, there is greater richness and abundance of specialist species in the most forested landscapes, while generalist species dominate the most deforested ones. On the other hand, the patch size effect varied considerably in relation to species group (generalist or specialist) and the response variable analyzed (richness, abundance or diversity). Overall, the richness is not related with patch size, but there was an increase in the generalist species abundance in smaller patches.

The decrease in species richness with a decrease in patch size is widely reported in fragmented landscapes for different groups of plants (e.g. Piessens et al. 2004, Galanes & Thomlinson 2009) and fauna (e.g. Parris 2006, Uezu & Metzger 2011). However, we did not find a clear relationship of richness and patch size in our samples. We believe that the lack of species-area relationship in our sample can be related with the regional characteristics of the sampled area or the sample area effect. Due to the regional characteristics where the Cerrado is inserted, with large ranches, the remnants of natural vegetation are also larger compared to other regions such as the Atlantic Forest (Galindo-Leal 2003, Ribeiro et al. 2009). In a comparison with Pardini et al. (2010) study, the average size of the patches in our study was 204.0 ha, while the patches sampled by Pardini et al. (2010) had an average size of 9.5 ha. Considering that the small mammals have small home ranges (e.g. Cáceres et al. 2012), the species richness cannot be directly related to the patch size in our study because even the small patches have enough size to maintain viable populations of several specialist species. Similarly, Fonseca & Robinson (1990) found no species-area relationship in the Atlantic Forest sampling larger patches (333 ha on average) than Pardini et al. (2010).

On the other hand, the lack of correlation between patch size and richness can be attributed to the sample area effect. A larger sampling area in a continuous habitat will contain more individuals than a smaller one and, for a given abundance distribution, it implies more species. Therefore, if large quantities of habitat were subsequently removed, leaving patches of different sizes, the species-area relationship in these patches would still be maintained due to the sample area effect (Fahrig 2013). Thus, our results are consistent with this statement because if the species richness is greater in larger patches just due to the sample area effect, we would expected that a standardized sampling effort of patches, regardless its size, result in a similar richness, as we found in this study. The habitat amount hypothesis (Fahrig 2013) postulates that species richness in patches with standardized sampling should increase with the total habitat amount in the "local landscape" of the sample. It also predicts that the number of species in a sample is independent of the particular patch area in which the sample is located, except in the proportion that this patch area contributes to the habitat amount in "local landscape" of the sample. Therefore, taking into account that the habitat amount in our landscapes (on a larger scale) reflect a greater habitat amount in the "local landscape" (around each sample unit), according to the habitat amount hypothesis, we would expected that patches inserted in landscapes with 50% of habitat amount would have more species than patches in landscapes with 30% of habitat amount and so on, regardless of patch size.

The generalist species were more abundant in smaller patches. The increase of some species abundance in small patches have already been documented for mammals (e.g. Malcolm 1988, Debinski & Holt 2000, Michalski & Perez 2007) and have different causes, such as predator release (Terborgh et al. 2001, Prugh et al. 2009), matrix tolerant species (Laurance 1995) and competitor release (Nupp & Swihart 2001). It is unlikely that a predator release effect is acting on small-mammal abundance, since it acts mainly on the mesopredator abundance through the extinction of top predators in communities, like cougars and jaguars (Prugh et al. 2009). Therefore, we would expect a decrease in the small-mammal abundance instead of an increase, since small mammals are common prey in the mesopredators diet in the region as small cats (*Leopardus* spp., Wang 2002), small canids (*Cerdocyon thous*, Pedó et al. 2006) and mustelids (*Eira barbara*, Presley 2000). In relation to the movement through the matrix, it is likely that at least some species, especially the generalist ones, can keep flow between patches (Gascon et al. 1999, Pires et al. 2002), but we would need to sample the matrix to confirm this hypothesis. Thus, we believe that the greater abundance of generalist species in smaller patches and landscapes with less habitat amount can be related to a competitor release effect on these sites, possibly linked to a greater mobility in the matrix by these generalist species. Considering that specialist species tend to be better competitors compared to generalist species (Manor & Saltz 2008), it would be expected that generalist species increase in abundance in smaller patches and landscapes with less habitat amount as a result of specialist extinction caused by habitat loss. Although we did not find a clear effect of specialist richness and abundance in smaller patches, possibly there is a deleterious effect on these populations on these sites. The fact that we found a positive relationship between patch size and specialist diversity reinforces this hypothesis.

The patch size and the habitat amount in the landscape have a similar effect on the Cerrado small mammal species composition, although the former is weaker than the latter. There is a change on the species composition, with generalist species being predominant, in terms of abundance, in smaller patches and in landscapes with less habitat amount, while specialists are rare or nonexistent in these areas, which confirms the previous results and are in agreement with other studies (see Harrinson & Bruna 1999 for review).

The vegetation density is also important in the small mammal species composition. Regardless of the species habit, generalist or specialist, the majority of species are associated with higher vegetation density patches, here represented by the NDVI. The more complex and dense the vegetation is, the greater the niches availability, which implies in a greater species richness and abundance in these areas when compared to more open habitats (August 1983).

Our results show that there is a habitat loss effect on small mammal communities, while specialist species decline in landscapes with less habitat amount, generalist species are more abundant. However, unlike the common pattern observed in most studies of fragmentation and habitat loss, the relationship with the patch size was unclear in the majority of cases. Therefore, our data showed that there is specialist species loss in landscapes with less vegetation cover in relation to landscapes with higher vegetation cover, but this species loss is independent of patch size. Thus, we conclude that for small mammals in the Cerrado, the habitat amount in the landscape is more important than the patch size. These results can be related with the Cerrado regional characteristics, with large ranches where the owners keep large patches and thus even our smaller patches have a reasonable size to maintain a high richness of small mammals. The lack of a patch-size effect is also in accordance with the habitat amount hypothesis (Fahrig 2013) which predicts that the habitat amount in the landscape is the main factor to predict species richness.

These results highlight the need to understand the long-term effect of fragmentation and habitat loss in the Cerrado species. The fragmentation process to which the region is being subjected is continuous and only a negligible portion of the biome is inserted in protected areas (8.43 %, MMA 2011). Against that background, we emphasize the need to carry out further studies about the effect of habitat loss and fragmentation on the biodiversity of this hotspot, considering not only the patch as sample unit, but also the surrounding landscape.

Chapter 2 - Testing the habitat amount hypothesis for small mammals in a Savanna region of South America

Abstract

According to the habitat amount hypothesis the species richness in a sample site would increase with the increase in the habitat amount in the local landscape of the sample site. On the other hand, changes in patch size and isolation would have no effect when the local habitat amount is constant. We tested the habitat amount hypothesis using a small mammal dataset recorded in 100 transects in a savanna region of Brazil. More specifically, we tested the strength of effect of habitat amount in the landscape, patch size and isolation to predict the specialist small mammal richness. We used generalized linear models considering the predictors together and singly using subsets of that data controlling for correlation between them. Our results showed that habitat amount is the major predictor of species richness in fragmented landscapes, as predicted by the hypothesis. The habitat amount effect was always positive and high, although patch size showed positive effect in species richness in landscapes with intermediate habitat amount. In turns, isolation has no effect on species richness. Considering the need to provide practical information for landscape managers, the habitat amount seems to be the most adequate predictor of species richness since it reflects the habitat loss effect summarizing the patch size and isolation effect in just one predictor.

Key-words: fragmentation threshold, isolation, patch size, scale of effect, species-area relationship.

Resumo

De acordo com a hipótese do “habitat amount”, a riqueza de espécies em uma unidade amostral aumenta com o aumento da disponibilidade de habitat na paisagem local desta unidade amostral. Por outro lado, o tamanho e o isolamento do fragmento no qual a unidade amostral encontra-se inserida não teria efeito sofre a riqueza de espécies. Nós testamos a hipótese do “habitat amount” utilizando um conjunto de dados de pequenos mamíferos capturados em 100 transecções no cerrado brasileiro. Mais especificamente, nós quantificamos o efeito da quantidade de habitat na paisagem e tamanho e isolamento do fragmento sobre a riqueza de pequenos mamíferos especialistas. Utilizamos modelos lineares generalizados considerando as preditoras em conjunto e isoladamente em subconjuntos dos dados controlando a correlação entre elas. Nossos resultados indicam que a quantidade de habitat é a principal preditora da riqueza de espécies nas paisagens fragmentadas. O efeito da quantidade de habitat foi sempre positivo e maior que as demais preditoras, embora o tamanho do fragmento tenha apresentado efeito positivo na riqueza de espécies nas paisagens com nível intermediário de perda de habitat. Por sua vez, o isolamento não teve efeito sobre a riqueza de espécies. Devido à necessidade de prover informações práticas as quais possam ser facilmente aplicadas em medidas de conservação, a quantidade de habitat parece ser a preditora mais adequada já que ela resume a mesma informação fornecida pelo tamanho do fragmento e seu isolamento em apenas uma única preditora.

Palavras-chave: limiar de fragmentação, isolamento, tamanho de fragmento, escala de efeito, relação espécie-área.

Introduction

The habitat loss and fragmentation are the major factors responsible for the current species extinction crisis (Barnosky et al. 2011). Its negative effects are a result of a combination between the decrease in total habitat available for the species and changes in the spatial configuration and quality of the remaining patches (Andrén 1994, Fahrig 2003). However, the fragmentation metrics and habitat loss area usually correlated because landscapes with less habitat amount are also normally more fragmented and vice versa. Therefore, it is difficult to conclude if either process have the same effect strength or if one process is more important than the other. Generally, studies that control this correlation have found a stronger effect of habitat loss than fragmentation (see Fahrig 2003 for a review). Therefore, the habitat loss in the landscape seems to be the major factor driven species responses to the conversion of pristine areas into anthropic ones.

The island biogeography theory (TBI) was proposed by MacArthur & Wilson (1967) to explain the species richness on islands. It predicts that smaller and more isolated islands have less species richness than larger or less isolated ones. However, the theory has been widely applied to predict the richness in forest patches of terrestrial systems (Haila 2002, Laurance 2008, Fahrig 2013). In this sense, the species-area relationship and extinction-colonization rates are considered as equivalent in terms of islands or habitat patches. However, different of islands, surrounded by an inhospitable matrix for terrestrial species, patches are separated by a matrix that can be used with different frequency depending on its composition and the species present in the patches (Umetsu & Pardini 2007, Umetsu et al. 2008). The species-area relationship in forest patches is probably more related to the sample area effect than to the extinction-colonization dynamics assigned to the island system (Fahrig 2013).

According to the sample area effect, any larger sampling area will contain more individuals in a region of continuous habitat and, for a given abundance distribution, it implies in more species. If large quantities of habitat were subsequently removed, leaving patches of different sizes, the species-area relationship in these patches would still be maintained due to the sample area effect (Fahrig 2013).

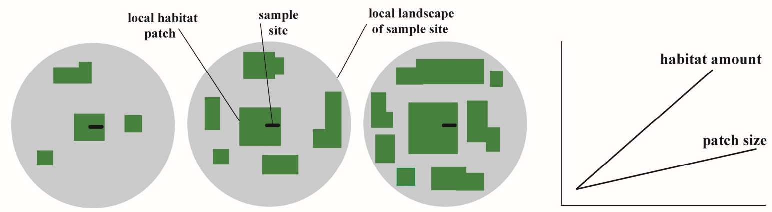
Due to the TIB patches were assumed to represent the natural units for studying richnes, abundance or presence of species. However, this view can be questioned on the base of numerous studies that actually species cross the border between patch and matrix frequently. Therefore, not the habitat patches, but the landscapeshould be used as units for the study of richness and abundance. In a hypothetical example, consider a linear species-area relationship (log of species richness per log of sample area). In a continuous region, a sample area of 50-unit size contains 10 species and a sampling area with 100-unit size contains 20 species (the double area, the double richness). If the region was fragmented leaving the same sampled areas (100 and 50-unit size patches), according to the sample area effect we would expected the same proportion of species richness in the larger and smaller patches found before the fragmentation, although some species would disappear in the region. Therefore, after fauna relaxation, the 50-unit patch would have fewer species (e.g 8 species, instead of the initial 10) and the 100-unit patch would still have the double species richness than the half size patch (e.g. 16 species, instead of 20). The point is that the proportion in species richness between these patches (in this example 2:1) would be kept constant. In a review Fahrig (2013) found six studies comparing the species-area slope in continuous and fragmented regions and they were similar in all the studies, although the richness were smaller in the entire fragmented regions. Therefore, she related this difference with the habitat amount surrounding the sample units. On the other hand, in island systems the species-area slope is steeper than the species-area slope in continuous habitat (Watling & Donnelly 2006). Thus, if we considered the same sample size, an island with 50-unit size would have less than the half species richness than a double-size island. It happens because besides the sample area effect, the island systems are subject to other processes (e.g. a higher extinction-colonization dynamics) that are not applied to terrestrial systems.

The habitat amount hypothesis (Fahrig 2013) postulates that species richness in patches with standardized sampling, despite of the patch size, should increase with the total habitat amount in the "local landscape" of the sample. Thereby, it predicts that the number of species in a sample is independent of the particular patch area in which the sample is located, except in the proportion that this patch area contributes to the habitat amount in the "local landscape" of the sample.

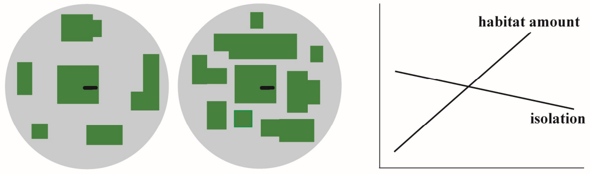
Fahrig (2013) proposes different ways to test the habitat amount hypothesis. One of these is to conduct an experiment (or select landscapes) in order to have landscapes with the same habitat amount but a wide range in size or isolation of the patches sampled. Therefore, it is possible to test the effect of the patch size or isolation controlling for the habitat amount effect. On the other hand, to test the strength of habitat amount effect, without a confounding effect of patch size or isolation, the research design should comprise landscapes with different habitat amount, holding the patch size or isolation constant. Important attention should also be given to: 1) the correct definition of the habitat for target species; 2) consider the correct scale of effect in which the habitat amount will be measured; and 3) control for other variables that can affect species richness like differences in the matrix composition between sites (Fahrig 2013).

Considering the importance of this issue to conservation actions since the patch size has been one of the most common predictors in the focus of conservation studies (e.g. Petit et al. 2004, Guldemond & van Aarde 2010, Munguía-Rosas & Montiel 2014, Magioli et al. 2015), we aim to test the habitat amount hypothesis using a small mammal dataset recorded in

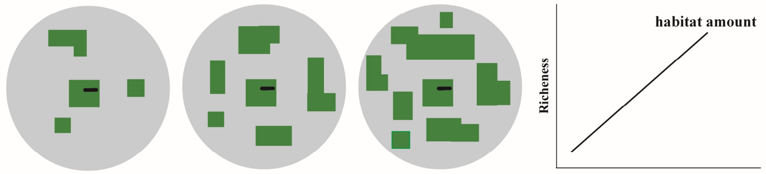
100 transects in a savanna region of Brazil. More specifically, we tested the following predictions. 1) Considered together, both habitat amount and patch size will show positive effects on species richness, but the former will have a stronger effect (Figure 1a). 2) On the other hand, isolation will show a negative effect on species richness but again a weaker effect than habitat amount (Figure 1b). When we consider subsets of the data set controlling for the correlation between patch size, isolation and habitat amount (see below), we expected that: 3) habitat amount will have a positive effect in species richness (Figure 1c e 1d); 4) patch size and 5) isolation will have no effect on species richness as long as the local habitat amount is kept constant (Figure 1e and 1f). Additionally, we compare through an information criteria approach a model considering habitat amount as predictor with a model considering patch size plus isolation together. According to the habitat amount hypothesis, we expected that habitat amount would have a better fit in predict species richness than patch size and isolation together.



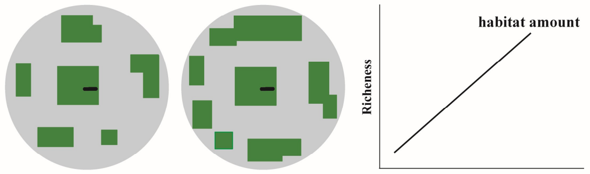
(a) increasing habitat amount and patch size



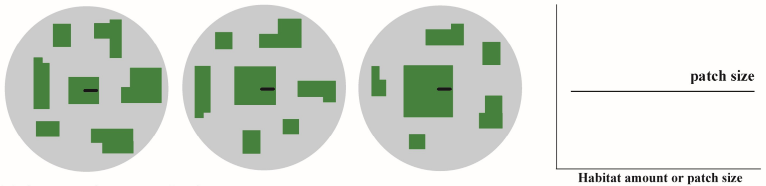
(b) increasing habitat amount and decreasing isolation



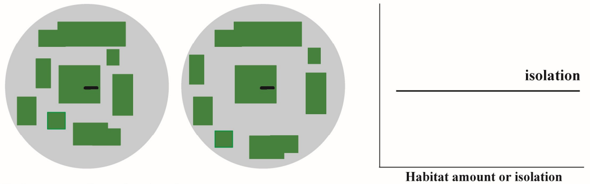
(c) increasing habitat amount



(d) increasing habitat amount



(e) increasing patch size



(f) increasing isolation

Figure 1. Predictions to test the habitat amount hypothesis (Fahrig 2013). In (a): the species richness will increase with the increase in habitat amount and patch size, but the first will have a higher effect than the last; (b) the species richness will increase with the increase in habitat amount and decrease in isolation, but the first will have a higher effect than the last; the richness will increase with an increase in habitat amount, even keeping the patch size (c) or isolation (d) constant; (e) patch size will not affect the species richness after controlling the habitat amount variation; and (f) isolation will not affect the species richness after controlling the habitat amount variation. Adapted from Fahrig (2013).

Material and methods

Study area

We sampled forest small mammals in a savanna region located in the central portion of South America. The Cerrado biome occupies 22 % of Brazilian territory, with smaller portions in Paraguay and Bolivia. The Cerrado contains different vegetation physiognomies, including grasslands, scrub-like savanna, woodland areas and gallery forests (Eiten 1982). This is one of the world's biodiversity hotpots considering its concentration of endemic plant species and exceptional loss of habitat (Myers et al. 2000). The Cerrado is under a rapid process of conversion of natural areas to anthropogenic land covers, especially croplands and grazed lands. It is estimated that 50% of the natural covers of the Cerrado have already been converted, and that about 80% is under some form of human use (Mittermeier et al. 1999, Machado et al. 2004, Klink & Machado 2005).

Sampling design

We used a mensurative experimental approach (McGarigal & Cushman 2002) to test the habitat amount hypothesis by examining the independent effect of habitat amount, patch size and isolation on small mammal richness.

We classified actual TM/Landsat-7 images of the southern Cerrado (between 20º17' and 21º15'S, and 54º53' and 56º31'W) using the GIS SPRING program (Camara et al. 1996). To reduce the variation in species composition between areas, the maximum distance bettwen landscapes was ≈ 160 km and all of them are inserted in the same river basin. Thus, differences in species composition between landscapes should be primarily related to differences in the habitat fragmentation and not to differences in species distribution range between areas.

Using a supervised classification, we classified the study region into a binary forest/nonforest map where forest included woodland areas. Woodland areas compose the main natural vegetation in the southern Cerrado (Silva et al. 2006); most of the open areas in this region are highly modified grazing lands.

Using the classified map we chose 50 patches in which we sampled small mammals in 100 transect lines looking for a broad variation in the predictors tested. In each transect we installed ten live-traps alternately on the ground (wire: 33 × 12 × 12 cm) and in the understory (Sherman: 30 × 9 × 7 cm) at 1.5 m height. The transect lines were 180 m long and distant in average 74 ± 48 km (minimum distance: 0.3 km; maximum distance: 160 km) from each other.

In total, we sampled each transect during five or six consecutive days on four different occasions, two in the rainy season (February / March 2012 and November / December 2012) and two in the dry season (July / August 2012 and June / July 2013). The sampling effort was 204 trap-nights in each transect line and 22,032 trap-nights in total.

Each transect was considered one sample unit where we measured the specialist species richness as response variable. We limited the set of study species to specialist species because habitat specialists are more susceptible to habitat loss than generalists are (Pardini et al. 2010, Matthews et al. 2014, see Chapter 1 and 3 in this thesis). The species classification was obtained from the literature based on the following criteria: 1) publications indicating the species as sensitive to habitat loss/fragmentation; 2) specificity regarding to habitat use (occurrence restricted to woodland areas); and 3) restricted distribution range (see references in Appendix 4). The small mammals captured were identified, marked with numbered ear-tags (Fish and small animal tag size 1, National Band and Tag Co., Newport, Kentucky) and released at the same point of capture. Techniques were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (protocol 30808-2) and are in compliance with guidelines published by the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2011).

We considered as predictors: the patch size in which the transect line was inserted, the isolation (mean distance of the transect to the nearest three patches) and habitat amount in the surrounding landscape (Figure 2; Appendix 5). As the scale of effect (Jackson & Fahrig 2012) for small mammals in the region were not available, we used a multi-scale approach. We measured the surrounding habitat amount (percentage of woodland areas) in 10 concentric circles ranging in radius from 250 m to 6000 m around the central point of each transect line. This range was selected based on the home ranges of the species used to calculate their dispersal distance (Bowman et al. 2002) and the corresponding scale of effect (Jackson & Fahrig 2012) (Appendix 6).

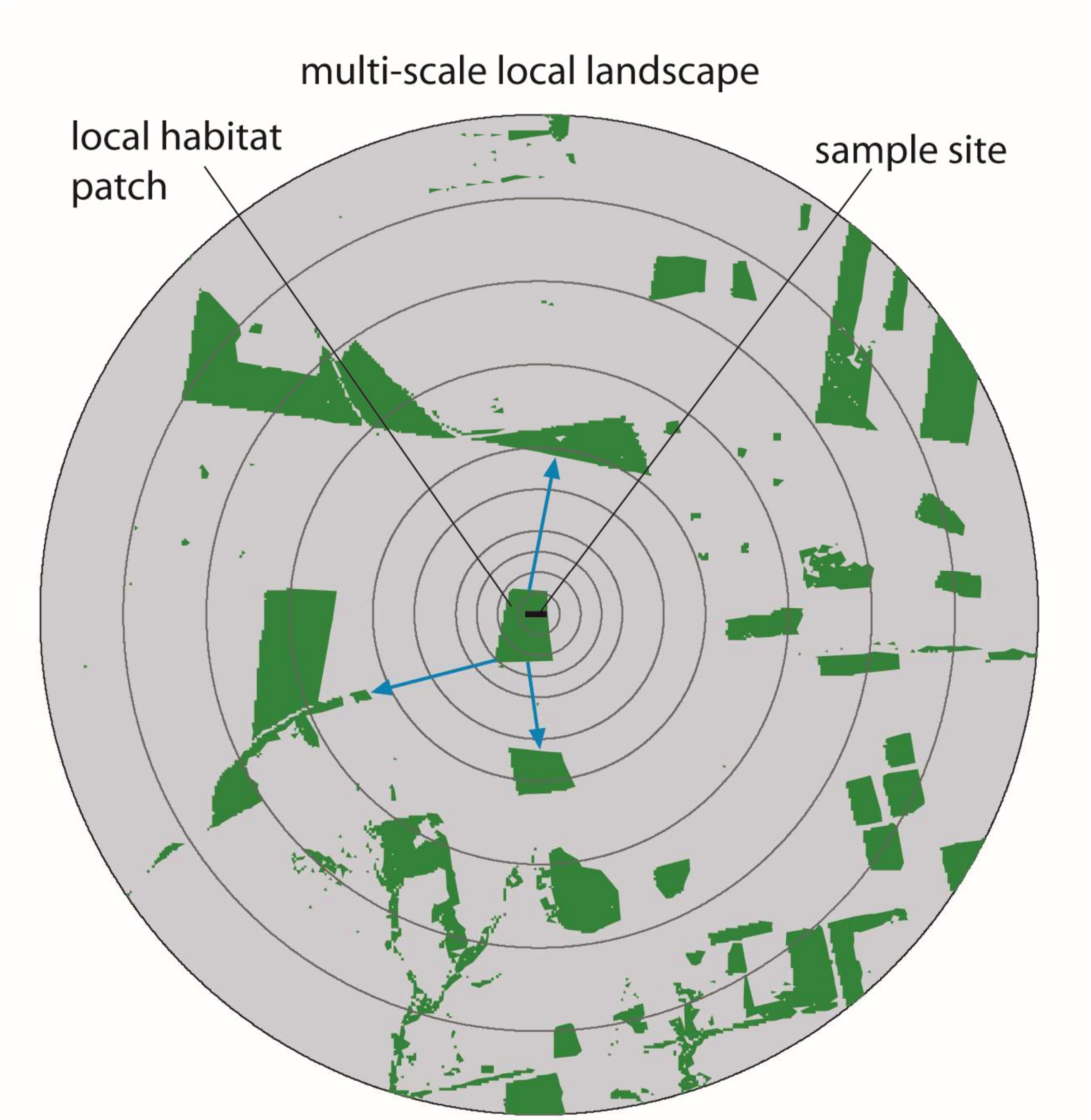


Figure 2. Example landscape centered on a 180 m transect to sample small mammals. The blue arrows correspond to the isolation mensured (mean distance to the three nearst patches). The landscape in witch the habitat amount was meansured is shown with radii 250 m, 500 m, 750 m, 1000 m, 1500 m, 2000 m, 3000 m, 4000 m, 5000 m and 6000 m around the center of the sampling transect.

Data analysis

At the largest landscape extents, many landscapes were overlapping. Therefore, we used a randomization approach to repeatedly select non-overlapping subsets of the sites. This avoids pseudoreplication, which would occur if it turned out that the scale of effect was one of the larger scales. It also avoided to use transects installed within the same patch in the same analysis, since they were usually closer to each other than transects installed in different patches. To obtain the randomly selected non-overlapping subsets, we used the software Focus (available at http://www.glel.carleton.ca) (Holland et al. 2004). Therefore, we were able to use all or most of the data points to find the correct scale of effect and test our predictions, even if only a small proportion were used in each individual regression because of spatial overlapping.

To find the scale of effect we conducted a linear regression on each of the 100 randomly selected non-overlapping subset generated by Focus. In this case, each non-overlapping subset had a sample size of 22 transects, as this was the largest number of possible spatially independent points at the largest spatial scale we considered (6000 m radius). We considered the scale of effect as the one at which the mean Pearson correlation coefficient (r) between habitat amount and species richness was largest. We opte to used Pearson coefficient instead of R^2 because R^2 does not differentiate between positive and negative relationships. Therefore, using R^2 is problematic as a measure of the strength of the regression because we are averaging over many regressions. Image that regressions at a given scale show both positive and negative relationships, as is likely in the case of a very weak relationship, the mean of measures of R^2 will be artificially high. This occurs because the values of this statistic from individual regressions are always positive, even if some of the regressions result in negative relationships (see Holland et al. 2004 for further explanation). We then used the best scale in subsequent analyses.

To test our predictions, we first standardized the habitat amount, the patch size and the isolation predictors to a mean of 0 and a standard deviation of 1 to allow comparison of regression coefficients. Considering that the correct scale of effect implied in landscapes overlap, we used again the Focus software to generate subsets of 100 randomly selected non-overlapping landscapes for each prediction we tested.

We then applied the lmList function of the lme4 package (Bates et al. 2014) in R program (R Development Core Team 2013) to conduct generalized linear models using a Poisson error distribution to test the following predictions:

1) When considered together, the habitat amount will show a stronger effect than patch size on species richness (Figure 1a).

2) Isolation will show a weaker (and negative) effect than habitat amount on species richness (Figure 1b).

3) The effect of habitat amount will remains high, after controlling the correlation with patch size or isolation (Figure 1c and d). To control for correlation between predictors we selected four subsets of the data with a wide range in habitat amount and a small range in patch size (subsets ha1 and ha2, Figure 3a) or isolation (subsets ha3 and ha4, Figure 3b).

4) To test if patch size has no effect on species richness, when controlling for the correlation with habitat amount (Figure 1e), we considered three subset in order to keep a small variation in the habitat amount, but a large variation in patch size (subsets ps1, ps2, ps3, Figure 3a).

5) Finally, to measure if isolation, when independent of habitat amount, has no effect on species richness (Figure 1f), we choose two subsets of the data in order to keep a small variation in the habitat amount, but a large variation in isolation (i1 and i2, Figure 3b).

Note that we used subset here to refer a subset of data points to test our prediction. After we choose the subsets considering all data set, we used again the focus to randomly selected non-overlapping subsets used to avoid landscape overlapping.

We applied a simple mean to summarize the beta coefficients of the randomly selected non-overlapping subsets for each prediction into one value. Therefore, we obtained a mean beta coefficient for each prediction arising from a set of regression analyses of randomly selected non-overlapping landscapes.

The number of sample units (transect lines) differed in each prediction tested because in some cases we were using just a subset of the data set, instead of all transect lines sampled (Figure 3). For example, when we tested the prediction 3, we had 28 sample units available in the subset ha1, instead of the total 100 transects sampled. Therefore, the randomly selected non-overlapping landscapes subsets ranged from nine to 13 sample units depending of the subset of the data considered (ha1 to ha4, ps1 to ps3, i1 and i2), instead of the 22 sample units used when we considered all data set in the randomization process to test the scale of effect or the predictions 1 and 2.

As the Focus randomly selected the non-overlapping subsets of landscapes, just taking into account the distance between sampling sites, some of them could show correlation between predictors by chance. Therefore, to make sure that we were really using independent subsets of non-overlapping landscapes, we also conducted a correlation test between predictors for each one. We excluded any randomly selected non-overlapping subset in which the correlation coefficient between predictors was > 0.10 before proceed with the GLM analysis.

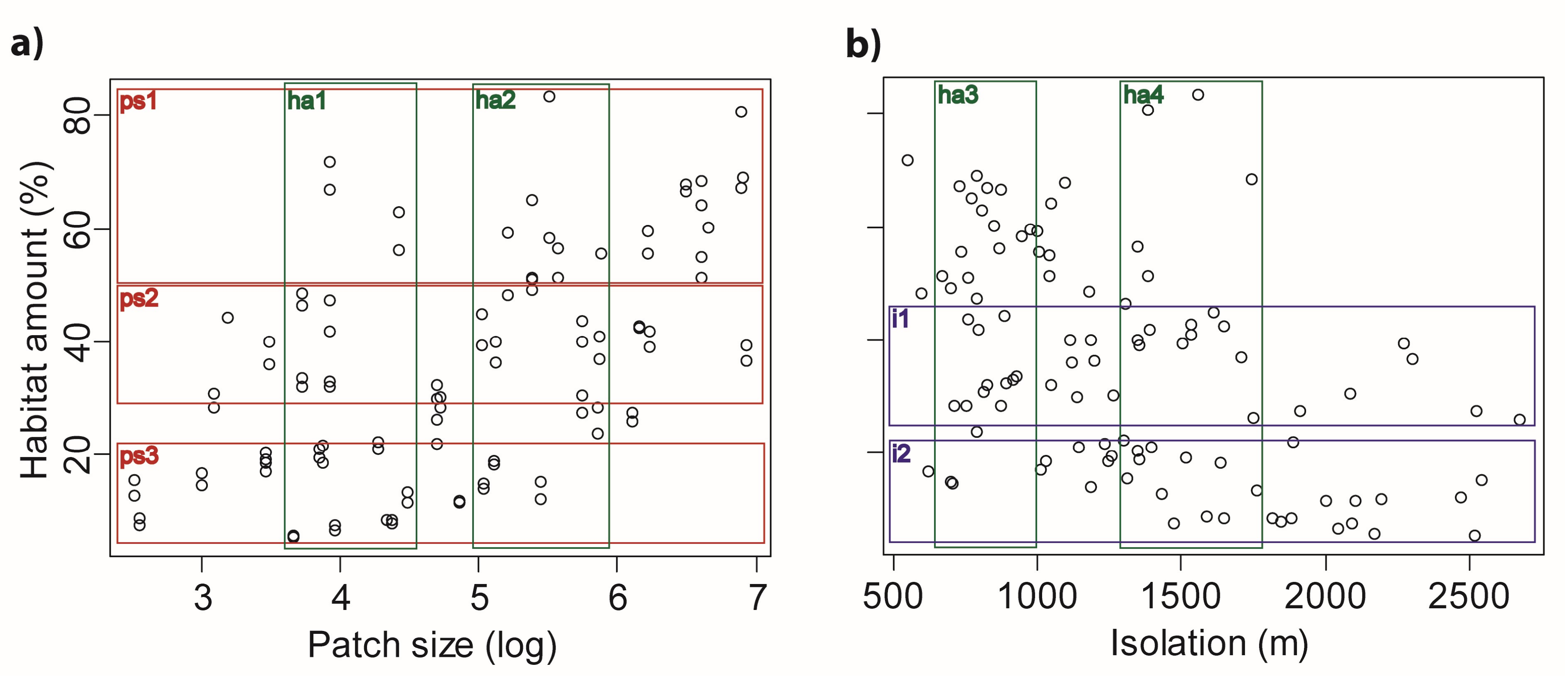


Figure 3. Subsets of the data used to test the isolated effect of habitat amount and patch size (a) and isolation (b). ha = habitat amount; ps = patch size; i = isolation. The habitat amount was measured considering the scale of effect for the species sampled. The isolation corresponds to the mean distance to the nearest three patches.

Finally, we tested if a model with just habitat amount as predictor would has a better fit than a model with patch size plus isolation together. We considered the AIC obtained for each randomly selected non-overlapping subset as indicator of the model fit. We considered the randomly selected non-overlapping subsets that included all data set (used to test the prediction 1 and 2) to conduct this analysis (totaling 200 randomly selected non-overlapping subsets). Then, we obtained a mean of the AIC values arising from the substration of the models with habitat amount ($M1_i$) from models with patch size plus isolation ($M2_i$) in a paired way using the following equation:

$$\mathrm{Mean\Delta AIC} = \sum_{\mathrm{i=0}}^{\mathrm{n}} (\mathrm{AIC\ M1}_i - \mathrm{AIC\ M2}_i)\ /\mathrm{n}$$

We expect that the MeanΔAIC will be < -2 according to the habitat amount hypothesis. However, is the MeanΔAIC > 2 the patch size plus isolation has a better fit than the habitat amount model; but if $-2 < \mathrm{Mean\Delta AIC} < 2$ both models are equally plausible.

Results

We captured 20 small mammal species in total, in which nine (four marsupials and five rodents) were classified as specialist species (Appendix 4). The scale of effect that best predicted the specialist species richness was the landscapes with 2000 m radius (Figure 4). Therefore, in the following analyses we considered just this scale.

We found a positive beta coefficient for both habitat amount (mean b = 0.58; st. error = 0.30) and patch size (mean b = 0.17; st. error = 0.30) in the multiple regression (Table 1; Figure 5). According to our first prediction, the effect of habitat amount was larger (by a factor of about 3.5) than the effect of patch size on species richness.

Similarly, when we considered the habitat amount and isolation effect together, we found positive beta coefficient for habitat amount (mean b = 0.68; st. error = 0.28). However, different of our second prediction, we found no effect of isolation on species richness (mean b = 0.06; st. error = 0.32) (Table 1; Figure 5).

On the assumption of independence of predictors, each one of the 100 randomly selected non-overlapping subsets obtained for each of the nine subsets to test the prediction 3, 4 and 5 (Figure 3) showed small correlations between predictors ($r < 0.10$). The exceptions were the subset h3 and ps1 in which we keep only 27 and 36 randomly selected non-overlapping subsets respectively for the subsequent analyses. We also excluded 11 and 28 randomly selected non-overlapping subsets for the subset ha2 and ha4 respectively, three and eight for the subsets ps2 and ps3 and 28 for the subset i2. None randomly selected non-overlapping subsets showed correlation ($r > 10$) between predictors in the subsets ha1 and i1, so we considered all 100 in the follow set of analyses.

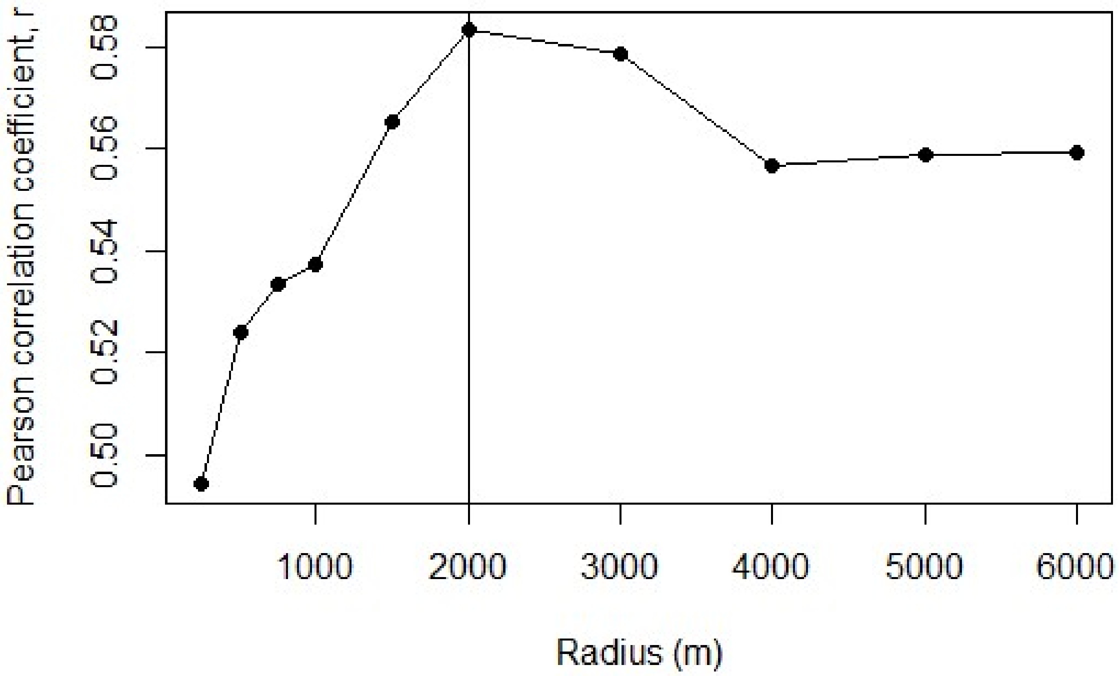


Figure 4. Scale of effect considering the habitat amount in landscapes with different buffer sizes for specialist small mammal species richness in a savanna region of Brazil.

Table 1. Mean coefficient values (b), mean standard error (st. error) and proportion (%) of p values <0.05 of the generalized linear model of the randomly selected non-overlapping subsets testing for: 1) habitat amount and patch size; 2) habitat amount and isolation; 3) effect of habitat amount in subsets of data controlling the patch size (ha1 and ha2) and isolation (ha3 and ha4) variation; 4) effect of patch size in subsets of data controlling the habitat amount variation (ps1, ps2 and ps3); 5) effect of isolation in subsets of data controlling the habitat amount variation (i1 and i2).

	Intercept			Patch Size			Habitat Amount			Isolation		
	B	st. error	p	b	st. error	p	b	st. error	P	b	st. error	p
Habitat amount + patch size	-0.39	0.30	3	0.17	0.30	3	0.58	0.30	44	-	-	-
Habitat amount + isolation	-0.45	0.29	22	-	-	-	0.68	0.28	83	0.06	0.32	0
Habitat amount (ha1)	-1.24	0.75	0	-	-	-	0.96	0.58	28	-	-	-
Habitat amount (ha2)	-0.01	0.29	0	-	-	-	0.48	0.28	22	-	-	-
Habitat amount (ha3)	-1.13	0.32	0	-	-	-	0.47	0.33	7	-	-	-
Habitat amount (ha4)	-0.15	0.37	0	-	-	-	0.48	0.34	23	-	-	-
Patch size (ps1)	0.48	0.39	14	-0.16	0.54	0	-	-	-	-	-	-
Patch size (ps2)	-0.10	0.30	0	0.46	0.34	5	-	-	-	-	-	-
Patch size (ps3)	-1.31	0.65	62	-0.30	0.82	0	-	-	-	-	-	-
Isolation (i1)	-0.34	0.33	1	-	-	-	-	-	-	0.14	0.33	0
Isolation (i2)	-0.09	0.35	1	-	-	-	-	-	-	-0.25	0.37	4

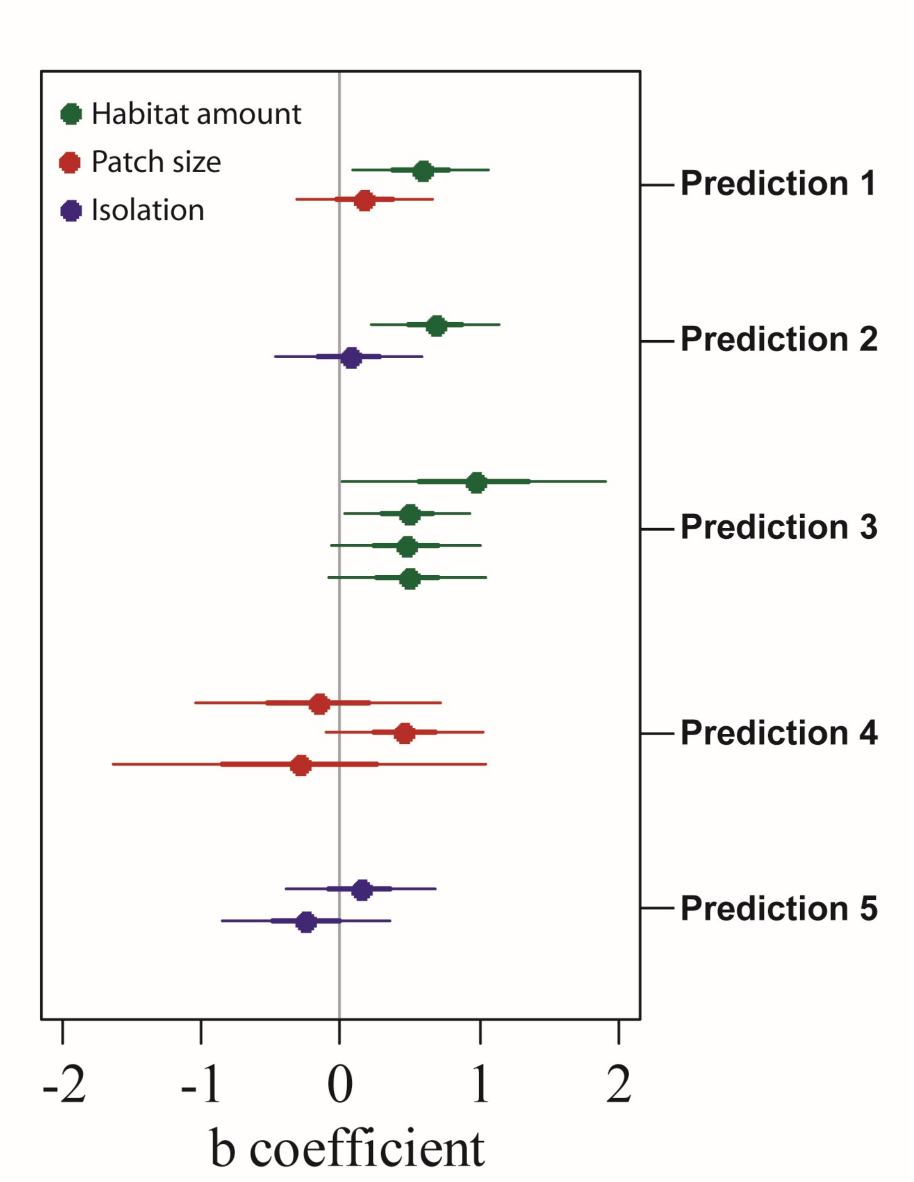


Figure 5. Mean beta coefficient (dot), mean standard error (thick line) and confidence interval (thin line) for habitat amount (green), patch size (red) and isolation (blue) to predict small mammals specialist species richness in fragmented landscapes in a Savanna region. The prediction numbers correspond to: 1) effect of habitat amount + patch size; 2) effect of habitat amount + isolation; 3) effect of habitat amount in four subsets controlling for patch size and isolation variation; 4) effect of patch size in three subsets controlling for habitat amount variation; 5) effect of isolation in two subsets controlling for habitat amount variation. See the subsets in Figure 3.

We corroborated our third prediction that habitat amount, even after controlling for the patch size and isolation variation, would show a positive effect on species richness. Both subsets that considered the effect of habitat amount by keeping a small variation in the patch size showed positive effect of habitat amount on species richness (b mean = 0.96; st. error = 0.58; b mean = 0.48; st. error = 0.28, respectively) (Table 1, Figure 5). In the same way, both subsets that considered the effect of habitat amount by keeping a small variation in the isolation showed positive effect of habitat amount on the species richness (b mean = 0.47; st. error = 0.33; b mean = 0.48; st. error = 0.34, respectively) (Table 1, Figure 5). Although the results were not significant in the majority of each randomly selected non-overlapping subsets (Table 1), all beta coefficients were consistently positive (Figure 6).

When we tested the patch size effect after controlling for habitat amount variation (prediction 4), the subsets ps1 and ps3 showed mean negative beta coefficients (b mean = -0.30; st. error = 0.82, and b mean= -0.16; st error = 0.54, respectively, Table 1). The variation in b coefficients between the randomly selected non-overlapping subsets was high with both positive and negative values (Figure 6). However, different of which we predicted, the subset ps2 showed a consistently positive effect on species richness (b mean = 0.46; st. error = 0.34) (Table 1, Figure 5 and 6).

Both subsets i1 and i2 used to test the isolation effect (prediction 5) showed no effect on species richness, with coefficients varying between positive and negative values (b mean = -0.25; st. error = 0.37, and b mean= 0.14; st error = 0.33, respectively) (Table 1; Figure 5 and 6).

The AIC of the models considering just the habitat amount as predictor were smaller than the models considering patch size plus isolation. The MeanΔAIC was - 5.44 (95 % CI = [-5.93; -4.96]), therefore, the habitat amount model is most plausible than the patch size plus isolation model.

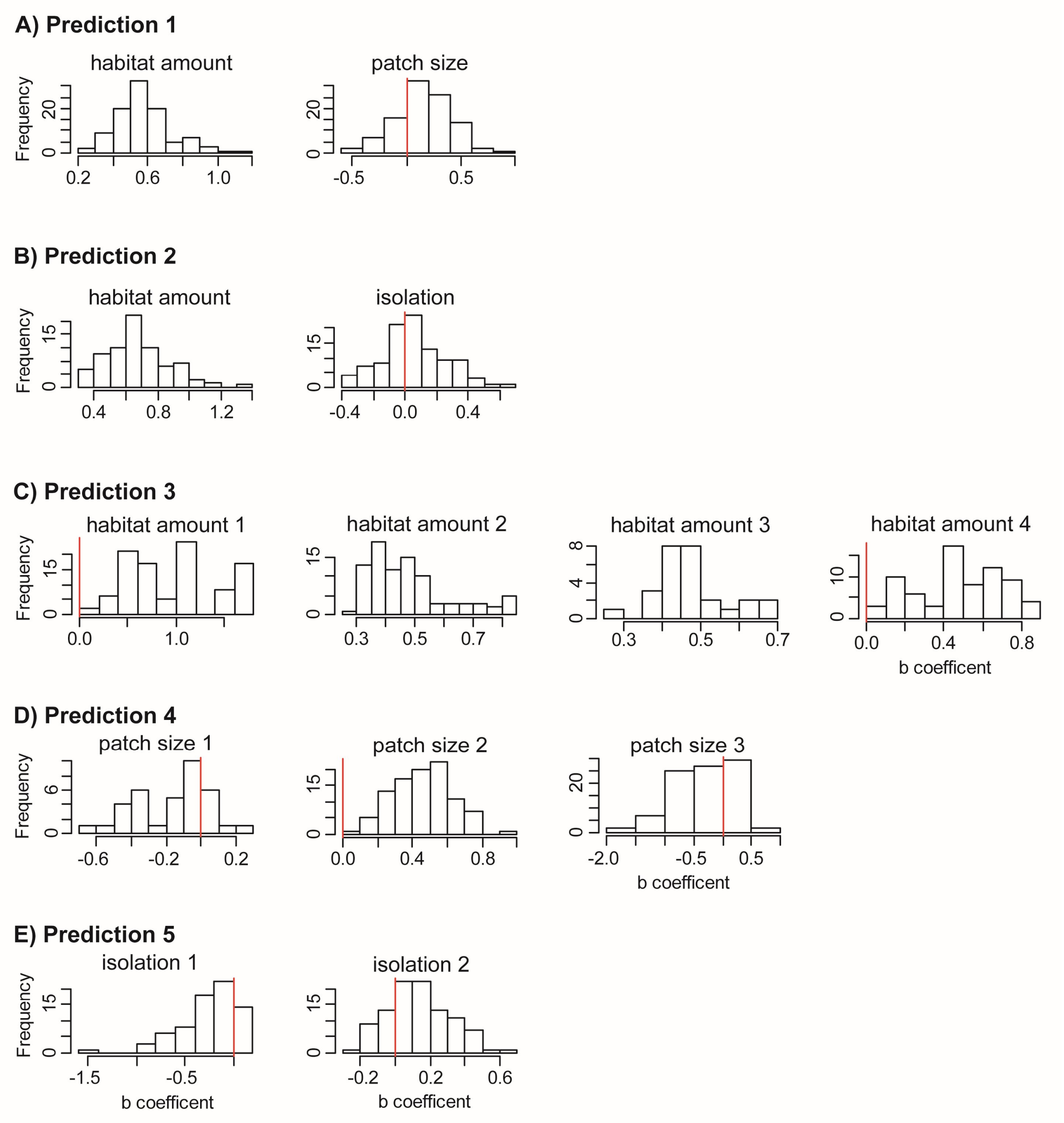


Figure 6. Frequency of beta coefficients for the randomly selected non-overlapping subsets of landscapes considered to test each prediction. The red line corresponds to zero values of b coefficient.

Discussion

The first step to quantify the habitat amount effect is to find the correct scale that delimits the landscape in which to measure the habitat amount. Different of patch size, whose scale is delimited by the patch boundaries, the landscape scale is not known a priori. Traits related to the species dispersal ability seem to be the best ones to predict the correct scale of effect (Jackson & Fahrig 2012). However, in the lack of this information, widely available traits, like body mass, can also be used as a proxy for dispersal capacity (Thornton & Fletcher 2014). Nevertheless, the majority of studies use arbitrary scales to measure the habitat amount or other landscapes-context predictors (Jackson & Fahrig 2015). If researches consider a suboptimal scale, they are probably underestimating the effects of landscape structure on species responses, which can lead to biased conclusions. Jackson & Fahrig (2015) showed that the majority of landscape studies do not include the correct scale range when they look for the scale of effect. In our study, the scale of effect that small mammal specialist species strongest responded to habitat amount in the landscape was a 2000 m radius around the sample site. We used the dispersal distance of all species captured to estimate the range of the multiscale in which we found the scale of effect. Therefore, we are confident about our estimate of habitat amount in these landscapes.

Although the majority of subsets of non-overlapping landscapes were not significant at $\alpha = 0.05$ (Table 1), we highlight that habitat amount coefficients were positive in all analyses carried out (Figure 6). On the other hand, the patch size and isolation coefficients, when controlled for habitat amount correlation, showed positive and negative values in similar proportions (Figure 6). Considering that habitat loss and fragmentation are highly correlated (Fahrig 2003), it is difficult to replicate landscapes in a broad scale keeping the predictors independent. Therefore, the lack of significance in the subsets of non-overlapping landscapes testing the habitat amount effect probably is a consequence of the reduced sample size. A small sample size increases the type II error through the increase in the standard error, which results in a low statistical power (Zuur et al. 2010). It is unlikely that we have found positive coefficients values for habitat amount in all subsets tested by chance. In turns, the variation between positive to negative values in the patch size and isolation coefficients indicated that its effect on species richness is much weaker than the habitat amount effect. Therefore, although showing some limitation, our results are in accordance with the habitat amount hypothesis (Fahrig 2013).

Our results showed that the habitat amount have a stronger effect than patch size or isolation for species richness in all predictions tested. However, in one subset (ps2, Figure 3 and 5) the patch size showed a consistent positive effect in species richness. The fragmentation threshold hypothesis (Andrén 1994) predicts that just below a certain threshold (around 30% of habitat cover in the landscape) the fragmentation effects would have an important effect in species richness. This would happen because, at this point, an increase in habitat loss results in an exponential increase in the distance between patches to such an extent that the landscape connectivity is eroded (Andrén 1994). Therefore, below this threshold patch size and isolation would act as good predictors to species richness. However, recently Pardini et al. (2010) showed that in an Atlantic Forest landscape below the fragmentation threshold (10% of habitat amount) the species-area relationship is not a good predictor anymore because regardless of patch size, just generalist species would remain in the landscape. The idea that the fragmentation effects are more important in intermediate values of habitat amount has been considered in other studies as well (Banks-Leite et al. 2014, Villard & Metzger 2014). In this sense, our results are in accordance with the regime-shift model proposed by Pardini et al. (2010) since we found positive effect of patch size just in landscapes with intermediate habitat amount (30-50% of habitat cover; subset ps2; Figure 3). Therefore, we did not disregard that patch size could have some importance in predicting species richness in specific situations (Fahrig 1998). In our case, this happened when the habitat amount assumed intermediate values in the landscape, as found in other studies (Pardini et al. 2010, Banks-Leite et al. 2014, Villard & Metzger 2014).

The species-area relationship is probably more detectable in landscapes with intermediate vegetation cover because in landscapes with high habitat amount, the species keep a constant flux in the entire landscape since the patches are usually close to each other. So even in the smaller patches viable populations persists though constant immigration. However, in landscapes below the fragmentation threshold the distance between patches increases in an exponential manner (Andrén 1994). Therefore, at this point the predictions of biogeographic island, in relation to patch size and isolation, could assume an important role because patches are more similar to true islands, at least for species with lower mobility. This threshold coincides with intermediate values of habitat amount in the landscapes. Nevertheless, an additional increase in habitat loss, summed with the population loss in smaller patches, let to a higher isolation that compromise the species persistence even in larger patches (Pardini et al. 2010). In this situation, even species with high mobility are also prone to extinction taking into account that the mortality in matrix is higher (Casagrandi & Gatto 1999, Fahrig 2001). In this case, successful immigration movements are less probably to occur for the majority of species leading to eminent extinction in the landscape level with minimal additional habitat loss (Pardini et al. 2010).

Recently, Hanksi (2015) argued that the habitat amount hypothesis may be valid just when the total habitat amount in the landscape is still high and for small spatial scales. As discussed above, our data showed positive effect of patch size just in landscapes with intermediate habitat amount, instead of landscapes with severe habitat loss as pointed by Hanksi (2015). In relation to the spatial scale, we analyzed the same data set used in the present study in another research considering a broad scale (see Chapter 1 in this thesis). The sample design was similar to that used by Pardini et al. (2010), and cited by Hanski (2015) as an example of the importance of spatial configuration across larger areas. I tested the fragmentation threshold hypothesis (Andrén 1994) and the regime-shift model (Pardini et al. 2010) considering six 150 km^2 landscapes with seven to nine patches of different sizes inserted in each landscape. Again, even analyzing this data set in a broad scale context, we found that habitat amount in the landscape was the major predictor of species response. In turn, patch size showed an inconsistent effect that varied a lot depending of the response variable and the species group analyzed. This result reinforces the habitat amount hypothesis as adequate even considering a local landscape, measured based on species scale effect, or a broad regional landscape. Interestingly, in that broad scale we do not detect an effect of patch size in specialist species richness in landscapes with intermediate habitat amount. This discrepancy let us to suggest two hypothesis: 1) the scale of effect is more appropriate, at least for the Cerrado species, to detect a threshold instead of a broad regional scale or, 2) as we found a patch size effect in the present study considering a range of 30 – 50% of habitat amount, the threshold in the Cerrado might be higher than 30% of habitat amount. However, with our data set these affirmations are just speculative and need further investigation.

To our knowledge, this is the first study to test the habitat amount hypothesis. As predicted by the hypothesis, our results showed that habitat amount is the major predictor to species richness in fragmented landscapes. Considering the need to provide practical information for landscapes managers, the habitat amount seems to be the most adequate predictors since it reflects the habitat loss process and summarize the patch size and isolation effect in just one variable (Fahrig 2013). However, in some specific situations, the species-area relationship can also exert an important role in predict species richness as well. In our case, in landscapes with intermediate habitat amount, which corroborates recently studies (Pardini et al. 2010, Banks-Leite et al. 2014, Villard & Metzger 2014). Therefore, further studies are need to test the habitat amount hypothesis in order to investigate if this pattern is widely applied; and more important, in which situations we can safely ignore the fragmentation patterns in the landscape (e.g. patch size, isolation). Considering that we based our conclusions in the species richness, maybe other descriptors of species response to habitat loss and fragmentation could show different responses to these predictors. We encourage future studies to focus on other descriptor of communities like composition, and functional and phylogenetic diversity to test not only this hypothesis, but also the role of patch size in predicting communities' response to deforestation. Additionally, species of different ecology and present in different biomes should also be considered to test the habitat amount hypothesis in order to investigate if this pattern can be widely applicable.

Chapter 3 - Patch size and habitat loss effect on the phylogenetic and functional structure of small mammal's metacommunities in the Brazilian Cerrado

Abstract

The habitat loss and fragmentation are the major current causes of biodiversity loss, however little is known about how metacommunities respond to the fragmentation process in a functional and phylogenetic perspective. We investigated if the small mammal phylogenetic community composition changes according to patch size and habitat amount in the landscape. We also investigated if the species traits express convergence and divergence assembly patterns along these gradients. We sampled small mammals in 54 woodland patches of different sizes and inserted in six landscapes with different habitat amount. We described the species based on traits that we believe are important for their adaptation to the environment. We applied an approach based on the scaling up of phylogeny and traits information of each species to the community level weighted by its abundance. After we described the community based into their phylogeny and traits composition, we correlated these matrices with the patch size and habitat amount predictors. Communities present in small patches are mainly associated with marsupials, while rodents are more common in the larger ones. In relation to traits convergence, communities present in smaller patches have species composition with longer muzzle and ear length, wider hind feet and generalist habit when compared with communities present in larger ones. Regarding to the habitat amount in the landscape, the average muzzle length and the relative abundance of generalist species are greater in landscapes with less habitat amount. On the other hand, the relative abundance of specialist species is lower in these landscapes. We also found that the functional diversity is positively correlated with the patch size and habitat amount in the landscape. Fragmentation and habitat loss affects the small mammal metacommunities in a directional and predictable way. Some traits show convergence along the gradient, in this sense, scansorial and arboreal species would be less affected by fragmentation, as well as the generalist species, relative to habitat and diet. This is the first study to relate phylogeny and species traits in a patch-landscape design.

Key-words: Didelphidae, species-area relationship, functional ecology, habitat amount, phylogenetic signal, Rodentia.

Resumo

A perda de habitat e a fragmentação são as principais causas atuais da perda da biodiversidade, entretanto pouco se sabe sobre como metacomunidades respondem ao processo de fragmentação em uma perspectiva funcional e filogenética. Nós investigamos se a composição filogenética de comunidades de pequenos mamíferos se altera de acordo com o tamanho do fragmento e a quantidade de vegetação remanescente na paisagem. Também analisamos se atributos funcionais das espécies expressam padrões de convergência e/ou divergência ao longo destes gradientes. Para tanto, descrevemos as espécies baseadas em atributos funcionais que são importantes a adaptação das espécies ao ambiente. Então, aplicamos uma abordagem de transferência da informação funcional e filogenética das espécies para o nível de comunidade, ponderada pela abundância das mesmas. Depois de descrever as comunidades baseados na sua filogenia e em seus atributos, correlacionamos estas matrizes com as preditoras, tamanho de fragmento e quantidade de habitat na paisagem. Encontramos que comunidades presentes em fragmentos menores são principalmente compostas por marsupiais, enquanto roedores são mais comuns nos fragmentos maiores. Em relação aos padrões de convergência, comunidades presentes em fragmentos pequenos possuem maior comprimento de focinho e orelha, patas mais largas e habito generalista quando comparadas a comunidades presentes em fragmentos maiores. A respeito da quantidade de vegetação na paisagem, em média o comprimento do focinho e a abundância de generalistas é maior em paisagens com menor quantidade de habitat. Por outro lado, a abundância de especialistas é menor nestas paisagens. Ainda, a diversidade funcional está positivamente relacionada tanto com o tamanho do fragmento quanto a quantidade de vegetação na paisagem. A fragmentação e perda de habitat afeta as comunidades de pequenos mamíferos de uma forma previsível e direcional. Alguns atributos apresentaram convergência ao longo do gradiente, neste sentido, espécies escansoriais e arborícolas seriam menos afetadas pela fragmentação, bem como espécies generalistas, tanto em relação ao habitat quanto a dieta. Este é o primeiro estudo a relacionar a filogenia e os atributos funcionais das espécies em um gradiente de fragmentação.

Palavras-chave: Didelphidae, relação espécie-área, ecologia funcional, quantidade de habitat remanescente, sinal filogenético; Rodentia.

Introduction

The species can be described by its taxonomic identity and also by morphological and physiological traits that reflect their responses to environmental factors (Lavorel & Garnier 2002). Therefore, we can characterize these traits as being functional and hence the patterns that model the communities described by these traits are also functional (Pillar & Orlóci 1993). The functional approach investigates how organisms are functionally structured in the communities, that is, what role they play in ecosystems and which functional traits are selected or filtered in the presence of an environmental disturbance (Podgaiski et al. 2013). Describing communities based on traits allows the identification of patterns of organization that can, to some extent, be extrapolated to communities with different species composition from those of the original research, which provides the generalization of knowledge required for conservation actions.

In general, the species community composition can be driven by neutral processes (e.g. dispersal limitation; Hubbell 2001) or by their niche based on habitat (e.g. environmental filters and biotic interactions; Cornwell & Ackerly 2009). From the niche perspective, the species communities' organization show two opposite trends. On the one hand, the action of environmental filters can generate an organization pattern with trait convergence, that limits the species present in the community to those more similar in certain traits (Keddy 1992). On the other hand, biotic interactions between species that compose a community can affect its structure, leading to species arrangements that can diverge more to each other, in terms of the functional traits than expected if they were randomly distributed. Biotic interactions generate similarity limitation between species (Diamond 1975), a pattern that results in trait divergence (Wilson 1999). A given set of traits can express convergence patterns for some traits and divergence for others or even the same traits can express both convergence and divergence at different points of the environmental gradient (Pillar et al. 2009).

The species can differ in their responses to the current environmental conditions. For this reason, phenotypic characteristics of the species that composes an assembly are simultaneously the result of their evolutionary history and their ecological response to the current environment. Thus, it is expected that closer phylogenetically species share more phenotypic characteristics than with the more distant ones. This tendency for phylogenetic conservation in phenotypic traits of phylogenetically related species, called phylogenetic signal (Blomberg & Garland 2002), can be measured for a given species pool as the covariance between the phylogeny and phenotypic traits values (Blomberg & Garland 2002, Blomberg et al. 2003). To measure the extent to which the phylogenetic signal in a set of phenotypic traits affects communities, Pillar & Duarte (2010) propose a process that expands the phylogenetic signal to a metacommunity level. Thus, it is possible to evaluate the interaction between phylogeny (P) and convergence of ecological traits (T) in a set of communities subjected to an environmental gradient (E) (Webb et al. 2002).

The habitat loss and fragmentation, which has occurred at an accelerated rate, is one of the major current causes of biodiversity loss worldwide (Barnosky et al. 2011). The theory of island biogeography (MacArthur & Wilson 1967) that predicts the species richness on islands has also been widely used to describe the effect of habitat fragmentation in continental areas (Andrén 1994, Haila 2002). In this context, larger or less isolated forest patches would have greater species richness than smaller and more isolated ones. Many fragmentation studies in the Neotropics have compared the richness and abundance of species in patches with different sizes and isolations (e.g. Malcolm 1997, Cáceres et al. 2010, Pardini et al. 2010), and the relationship with these predictors has already been well documented for small mammals (e.g. Malcolm 1997, Bentley et al. 2000, Pardini et al. 2005, Pardini et al. 2010). However, little is known about how the fragmentation process affects the functional and phylogenetic community structure.

The fragmentation can act as an environmental filter because it changes not only the size and isolation of a given patch, but also exposes the remaining species present in these patches to ecological changes, since the fragmentation modify the functional and structural traits of the patches. For example, the edge effect can cause disturbance in abiotic factors inside the patch (e.g. temperature, humidity, and light and wind incidence) (Laurance 1991, Davies-Colley et al. 2000, Dodonov et al. 2013). As a result of abiotic changes, the vegetation density and composition can also be altered (Benítez-Malvido & Martínez-Ramos 2003, Echeverría et al. 2007, Christianini & Oliveira 2013, Dodonov et al. 2013). Ultimately, these changes could change the community functional and phylogentical composition present in the patch. In turn, the intensity of this effect is directly related to patch size due to the relationship between area and perimeter, and thus this is more pronounced in smaller patches (Laurence et al. 2002).

Moreover, the habitat amount in a landscape can enhance the loss of species, since species that avoid moving in the matrix can have their population more isolated as the habitat amount decreases and the distances between neighboring patches increase (Andrén 1994, Pardini et al. 2010). Measures of patch isolation can be calculated in different ways: distance from the nearest patch, average distance between one patch to all others in the landscape, distance from the nearest patch weighted by its area, etc. However, between the several possible isolation measures, the amount of habitat at a suitable distance from the fragment (and measures of isolation that are highly correlated with it) is the variable that best predicts the rate of immigration between patches and ecological responses, including species richness (Fahrig 2013).

Therefore, in this study we used the patch size and the habitat amount in the landscape as environmental gradients. We expect that communities present in patches of different sizes and/or landscapes with different habitat amount will respond to local differences, which can entail a change in the species composition of these patches, through the generation of environmental filters and/or biotic interactions, such as an increase in interspecific competition because of the fragmentation process. To our knowledge, no study has compared communities present in forest fragmentation gradients, using their functional traits and its phylogenetic composition as communities' descriptors. Therefore, it is important to understand how biological communities are structured in terms of functional patterns and what are the relationships of such structures with habitat fragmentation, so present today.

In this context, we investigated how fragmentation affects the small mammals' communities in a phylogenetic and functional approach. By sampling small mammals in patches of different sizes and inserted in landscapes with different habitat amount, we aimed to answer the following questions: 1) is there a pattern in the phylogenetic community structure related to ecological fragmentation gradients (patch size and habitat amount in the landscape)?; 2) do the traits express convergence and divergence assembly patterns? and 3) witch traits have phylogenetic signal at the species pool level and between they, which ones express phylogenetic signal at the metacommunity level related to trait-convergence and trait-divergence assembly patterns? As small mammals are composed by two phylogenetically distant clades (rodents and marsupials), we expect that some traits show phylogenetic signal and, if they are involved in trait-convergence/trait-divergence assembly patterns, a phylogenetic community structure related with the environmental gradient is also expected. In general, as disturbance gradients can generate environmental filters (Podgaiski et al. 2013), we hypothesized that trait-convergence assembly patterns will be more important in structuring communities than divergence patterns. Therefore, in smaller patches and/or landscapes with less habitat amount, we expected a subset of traits composition that is present in the larger and/or more forested ones (Cáceres et al. 2010, Pardini et al. 2010); this species loss will be related with functional traits, which are favorable or deleterious along the fragmentation gradient. On the other hand, we expect that in larger and/or less fragmented landscapes, trait-divergence assembly patterns will be more prevalente, because communities facing a smaller effect of environmental filters would be mainly structured by biotic interactions such as competition, which would limit the similarity between species communities.

Material and methods

Study area

Using the GIS SPRING program, we classified actual TM/Landsat-7 images of south region of Cerrado (between the coordinates 20º17' to 21º15'S and 54º53' to 56º31'W) (Camara et al. 1996). We classified the study region into a binary habitat/nonhabitat map where habitat was defined as forest cover (woodland areas) using a supervised classification.

We sampled 54 savanna patches (mean size = 300.6 ± 381.1 ha) into six landscapes of 22,500 ha each (Appendix 7). The landscapes are similar in relation to topography and climate, but differ in the percentage of natural vegetation cover: two landscapes have 10, two 30 and two 50% of remaining habitat amount, which reflects in greater isolation between patches in landscapes with less habitat amount (Andrén 1994).

To reduce the variation in species composition between areas, the maximum distance bettwen landscapes was ≈ 160 km and all of them are inserted in the same river basin. Thus, differences in species composition between landscapes should be primarily related to differences in the habitat fragmentation and not to differences in species distribution range between areas. Woodland areas compose the main natural vegetation in the southern Cerrado (Silva et al. 2006); most of the open areas in this region are highly modified grazing lands composed by exotic species.We installed the transect lines just in woodland areas, since the gallery forest can have a particular fauna (Johnson et al. 1999) and were not present in all patches.

Data collection

Each patch was sampled with 20 live-traps distributed along two transect lines that were at least 300 meters distant from each other and at 50 m from the patch edge. In each transect we installed ten live-traps alternately on the ground (wire: 33 × 12 × 12 cm) and in the understory (Sherman: 30 × 9 × 7 cm) at 1.5 m height, baited with a mixture of bacon, pumpkin, cod liver oil and peanut butter. We conducted four field phases of five or six consecutive nights each, two in the rainy and two in the dry season along two years. The total sampling effort was 408 trap-nights in each patch and 22,032 trap-nights considering all patches.

The small mammals captured were identified, measured, sexed, marked with numbered ear-tags (Fish and small animal tag size 1, National Band and Tag Co., Newport, Kentucky) and released at the same point of capture. Techniques were approved by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (protocol 30808-2) and are in compliance with guidelines published by the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2011).

Functional traits

We considered two qualitative traits which have partitioned into four binary variables: vertical stratum use (0 for species predominantly trapped on the ground and 1 for understory); and habitat use (0 to generalist and 1 to specialist species, see below). We also considered five quantitative functional traits for each species: body mass (average mass of all adults trapped); tail length (average tail length divided by average body length); hind feet width (mean width divided by the average length of the hind feet); ear length (average ear length divided by the average body length) and muzzle length (average muzzle length divided by the average body length). We assume that these morphological traits are related to small mammal species adaptation to the environment. The body mass influences the prey size consumed and the dispersal distance capacity of the species (Dickman 1988, Cáceres et al. 2012). The tail and ear length and the width of the hind feet reflect the species capacity of use the vertical stratum. Therefore, longer tail and ear, and shorter wider feet tend to be related to more arboreal habit, while cursorial species have shorter tails and ears and longer narrow hind feet (Eisenberg & Wilson 1981, Camargo et al. 2012). As the diet of many small mammals species are unknown (e.g. almost all marsupial species are classified as insetivorous-omnivorous according to Paglia et al. 2012), we use the muzzle length as diet indicator. Shorter muzzle species tend to be more frugivorous while longer muzzle ones tend to be more insectivorous, with intermediate values presenting an omnivorous diet (Medellín 1991, Samuels 2009, Cáceres et al. 2014) (Appendix 8). All traits were measured in the field, except for the habit (generalist and specialist) that was obtained from the literature based on the following criteria: 1) publications indicating the species as sensitive or tolerant to fragmentation; 2) restricted distribution range or not, and 3) specificity regarding habitat use (restricted occurrence to woodland vegetation) (Appendix 8).

Data analysis

The analysis involving the species traits and the phylogeny is based on the scaling up of information regarding the data obtained for each species to the community level. We use the methodology described in Pillar et al. (2009) and Pillar & Duarte (2010) to analyze the functional patterns of organization in metacommunities, as well as its phylogenetic structure. We constructed matrices containing the traits measured by each species (matrix **B**), the abundances of species in communities (matrix **W**), the ecological gradient representing the habitat fragmentation measured by patch size (matrix $\mathbf{E_P}$) and remaining habitat amount in the landscape (matrix $\mathbf{E_L}$) and phylogenetic distance between species (matrix **SF**) based on Bininda-Emonds et al. (2007), with addition of Fabre et al. (2012) for rodents (Appendix 9). Therefore, we have a set of matrices: **B**, **W**, $\mathbf{E_P}$, $\mathbf{E_L}$ and **SF**.

The method used to determine the community phylogenetic structure (Pillar & Duarte 2010) is based on phylogenetic similarity matrix between species (matrix **SF**), which is used for defining a fuzzy matrix Q (in the range 0 to 1) (Pillar & Orlóci 1991). We define then **P** = Q'W by matrix multiplication, so the matrix **P** will contain the composition of communities after fuzzy weighting of species abundance by their phylogenetic similarity. We order the matrix **P** by principal coordinate analysis (PCoA) to detect possible phylogenetic patterns (Duarte 2011). The axes generated by PCoA that explained more than 10% in the variation of weighted phylogenetically species composition data were analyzed by analysis of variance, in order to verify if the phylogenetic community structure is associated with the environmental gradients. In this case, we considered the patch size (small, medium and large) and the habitat amount in the landscape (10, 30 and 50% of remaining vegetation) as factors.

We used the methodology described in Pillar et al. (2009) to identify the assembly functional patterns of metacommunities' organization, both related to convergence and divergence of traits. To calculate the convergence of traits (trait-convergence assembly pattern - TCAP), we defined by matrix correlation **T** = B'W. The elements in **T** are abundance weighted average values of the community traits (community weight mean - CWM) (Violle et al. 2007). To identify the divergence of traits (trait-divergence assembly pattern - TDAP) (Pillar et al. 2009), in a first step, we use the matrix of similarity between pairs of species in the range of 0 to 1 (matrix **SB**) based on the attributes **B** to define the fuzzy matrix **U** (Pillar & Orlóci 1991). By matrix multiplication, **X** = U'W will contain the species composition after fuzzy weighting by their traits similarities (each line in **X** refers to a species). The matrix **X** expressed both TCAP as TDAP (Pillar et al. 2009).

Through matrices correlation, we evaluate how the patterns in **T** (TCAP) and **X** (TCAP and TDAP) are related to the gradient **E**. We calculated the congruence level between TCAP and **E** using distance matrices correlation: ρ (D_T, D_E). A strong correlation indicates that factors directly or indirectly represented in **E** are involved in species ecological filters that, at least for the traits considered in the analysis, consistently produce TCAP along the gradient. In the same way, we also defined the correlation between ρ (D_X; D_E), then we removed the effect of component ρ (D_T; D_E) of ρ (D_X; D_E) by partial correlation matrix ρ (XE.T), which will result in the level of congruence between TDAP and **E**. A strong correlation in this case indicates that factors directly or indirectly represented in **E** causes limitation in the similarity of traits considered in the analysis (see Pillar et al. 2009 for further details).

We also evaluated the relationship between the environmental gradient and traits that showed TCAP using a regression analysis for the patch size gradient and an analysis of variance (ANOVA) for the habitat amount in the landscape. In this case, we use the CWM of each trait as response variable.

We ordered the matrix **X**, calculated based on the traits that showed TDAP, by principal coordinate analysis (PCoA). The PCoA was performed using Euclidean distance between sampling units and plotting the functional diversity (FD - calculated by Rao entropy; Botta-Dukát 2005) and the patch size gradient or habitat amount in the landscape (matrix **E**). We used the FD in order to represent the divergence pattern, since the higher is the functional diversity for a given set of traits the greater is its TDAP from these traits.

To measure the Phylogenetic Signal (PSM) related to TCAP, we first calculated the distance matrix D_P from the phylogenetic matrix **P**. Similarly, we also calculated the distance matrix D_T from the convergent trait structure described in **T**. A strong correlation in ρ (D_P; D_T) indicates that there is a strong phylogenetic signal, in other words, similar communities in terms of phylogenetic structure are also similar in relation to the average values of their traits.

In order to define the PMS related to the TDAP, we calculate the partial correlation between ρ (D_P; $D_X.D_T$) removing the effect of TCAP (D_T). A strong phylogenetic signal indicates that the communities' phylogenetic structure is an important role in the set of communities associated with biotic interactions (see Pillar & Duarte 2010 for more details).

We tested the statistical significance of all matrix correlation performed by permutation via null models as described in Pillar et al. (2009) and Pillar & Duarte (2010).

Before these procedures, we looked for a set of attributes that maximizes: 1) TCAP [ρ(TE)]; 2) TDAP [ρ(XE.T)]; 3) Phylogenetic Signal at the Metacommunity level (PSM) related to the TCAP; and 4) Phylogenetic Signal at the Metacommunity level (PSM) related to the TDAP, using the method developed by Pillar & Sosinski (2003). In this case, attribute sets maximizing the expression of each of the above patterns are obtained through an algorithm that considers all combinations of attributes. Then, for each gradient, we use in matrix **B** only those set of traits that maximized each of the four above-mentioned patterns.

We used the packages SYNCSA (Debastiani & Pillar 2012) and Vegan (Oksanen et al. 2012) in the R program (R Development Core Team 2013) to carrying out all the analysis.

Results

We captured 1023 individuals of 20 small mammals species, eight Didelphidae marsupials and 12 rodents, 11 of the Cricetidae family and one of Echymidae family. The Didelphidae were prevalent in communities, being present in 53 of the 54 sampled patches, while rodents were present in 46. In turn, the most prevalent species were the marsupials *Gracilinanus* *agilis*, *Didelphis albiventris* and *Thylamys macrurus*, present in 50, 38 and 35 patches, respectively.

The correlation between the phylogenetic structure and the patch size was significant (ro($\mathbf{PE}_{P}$) = 0.28; p = 0.04), but we have not found relationship between the phylogenetic structure and habitat amount in the landscape (ro($\mathbf{PE}_{L}$) = 0.09; p = 0.52). The first two PCoA axes explained 99% of the variation, the first being responsible for 96% and the second by 2% of the variation in the matrix **P**. The ordination plot shows that communities present in small patches are mainly associated with marsupials species (Didelphidae), while rodents (Sigmodontidae and Echimyidae) are more present or are more abundant in the larger ones (Figure 1). We analyzed only the first PCoA axis, which did not vary between landscapes (F = 1.77; p = 0.18), but varied significantly according to the patch size (F = 4.36; p = 0.02). The scores of small patches (<50 ha) differ from scores of the larger patches (> 500 ha) (Q = 4.41, p <0.01), but both did not differ from the medium ones (50-500 ha) (Q = 1.44; p = 0.10) (Appendix 10).

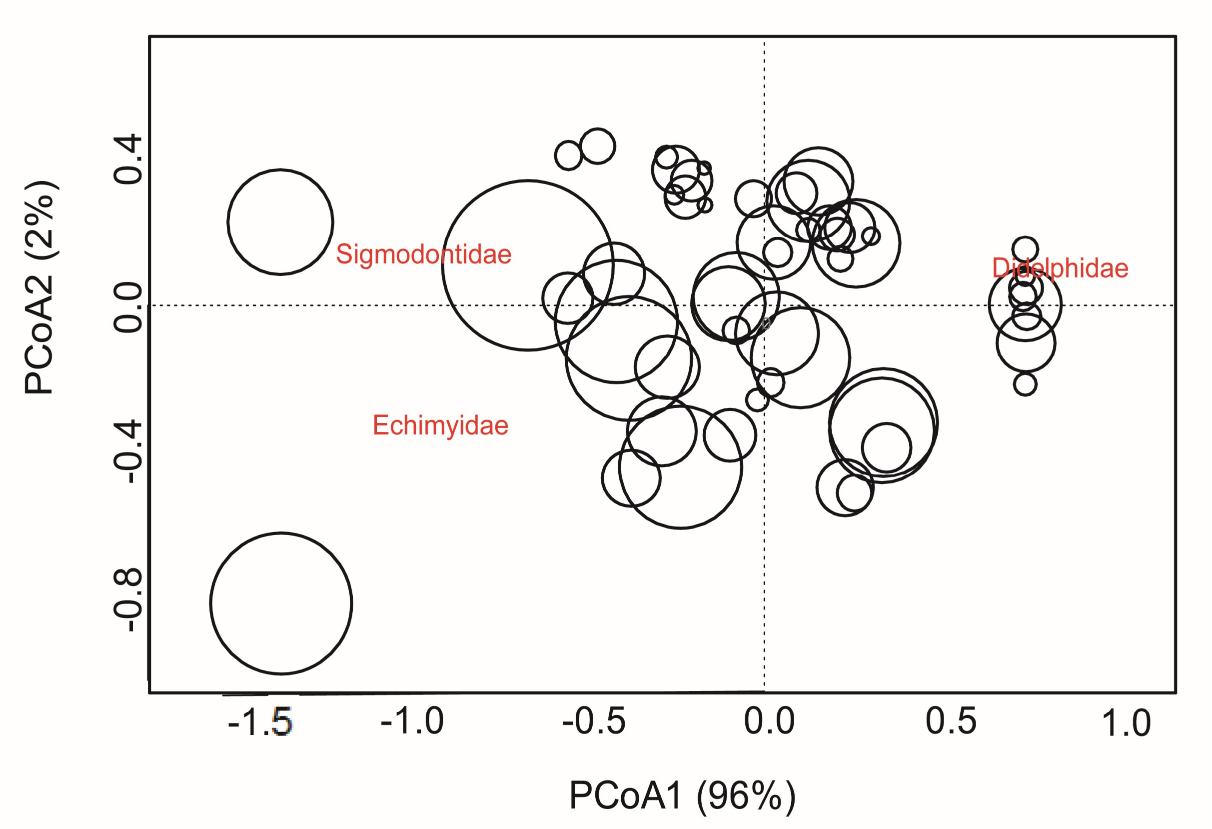


Figure 1. Principal coordinates analysis of phylogenetic structure (matrix P) of small mammal species occurring in a patch size gradient in the Cerrado, Mato Grosso do Sul, Brazil. Circle size represents patch size.

Four traits (muzzle and ear length, hind feet width and generalist habit) maximized the TCAP along the patch size gradient (ro(**TEP**) = 0.316; p = 0.01). In this sense, communities present in smaller patches tend to have species composition with longer muzzle and ear length, wider hind feet and generalist species when compared with communities present in larger patches (Figure 2). Regarding the gradient related to the habitat amount in the landscape, both the species habit (specialist and generalist species) and the muzzle length showed TCAP (ro(**TEL**) = 0.248; p <0.01) (Figure 3). In general, the average muzzle length and the relative abundance of generalist species are greater in landscapes with less habitat amount (Figure 3a and 3c). On the other hand, the relative abundance of specialist species is lower in these landscapes (Figure 3b).

The body mass and the ear and muzzle lengths together maximized the TDAP along the patch size gradient (ro(**XEP.T**) = 0.35, p <0.01). The ordination plot shows that the functional diversity is positively correlated with the patch size; it means that larger patches have greater functional diversity (divergence) in the three traits mentioned (Figure 4a). Regarding to the habitat amount gradient, again the body mass and the muzzle length, together with the generalist habit, maximized the TDAP along the gradient (ro(**XEL.T**) = 0.22; p <0.01). In general, the functional diversity is higher in landscapes with higher habitat amount (Figure 4b).

All morphological traits, except muzzle length, were more similar among close-relative species than among distant relatives at the species pool level (body mass (BF = 0.125; p = 0.01), tail (BF = 0.112; p = 0.05), ear (BF = 0.458; p <0.01) and hind feet (BF = 0.878; p <0.01)). However, the ecological traits we considered (vertical stratum and habitat use) are not conserved into clades because no one alone showed phylogenetic signal at the species pool level.

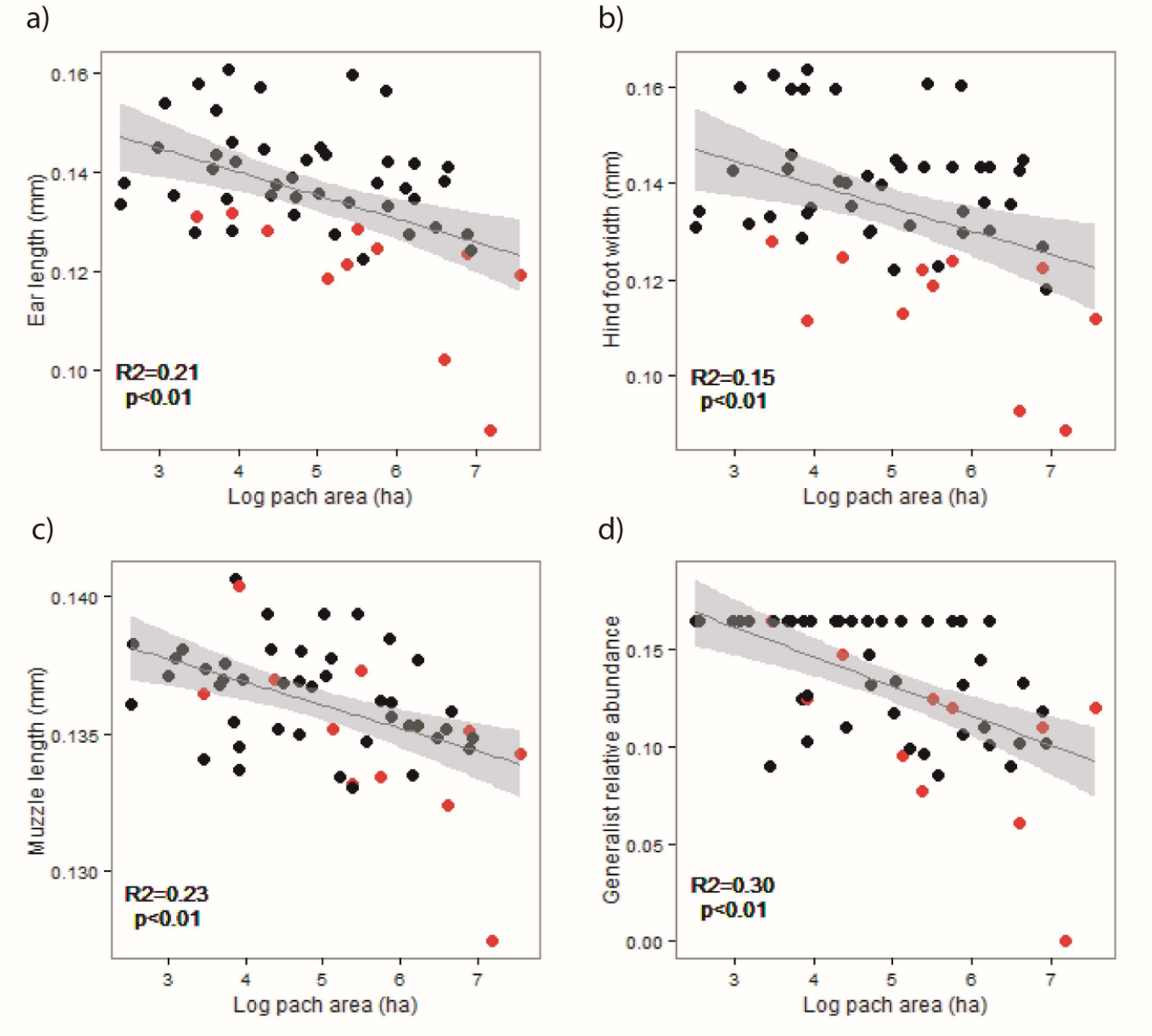


Figure 2. Trait-convergence assembly pattern found in small mammals metacommunities in a patch size gradient in the Cerrado of Mato Grosso do Sul. The diagrams show the relationship between the average trait values in the community (community weighted mean - CWM) with the patch size. We consider just the traits that maximize the expression of trait convergence in the gradient. Black dots are communities with greater marsupials' abundance and red dots are communities with greater rodents' abundance.

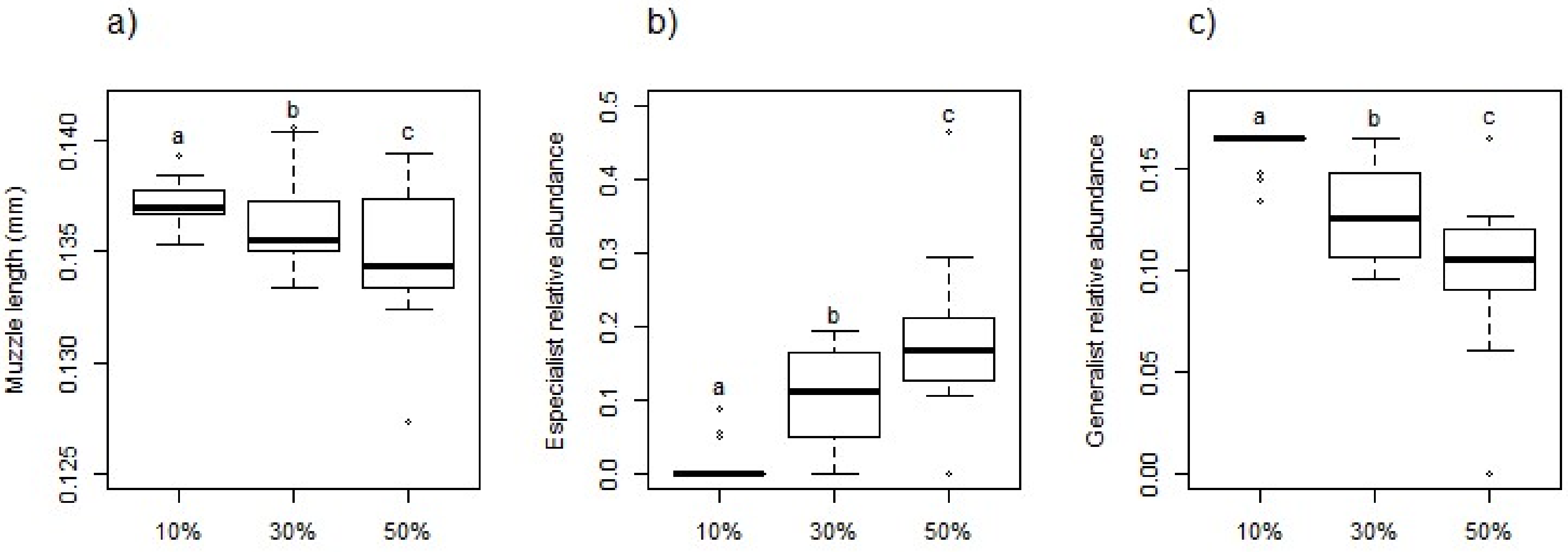


Figure 3. Trait-convergence assembly pattern found in small mammals metacommunities in a habitat amount gradient in the Cerrado of Mato Grosso do Sul. The diagrams show the relationship between the average trait values in the community (community weighted mean - CWM) with the habitat amount in the landscape; these are the traits that maximize the expression of trait convergence in the gradient. The box sets the 1st and 3rd quartile with the line in the median and the bars correspond to 1.5 times the value of the quartiles (about 2 standards deviations). The dots represent outliers. Different letters represent significant differences ($p < 0.05$) between landscapes with different habitat amount.

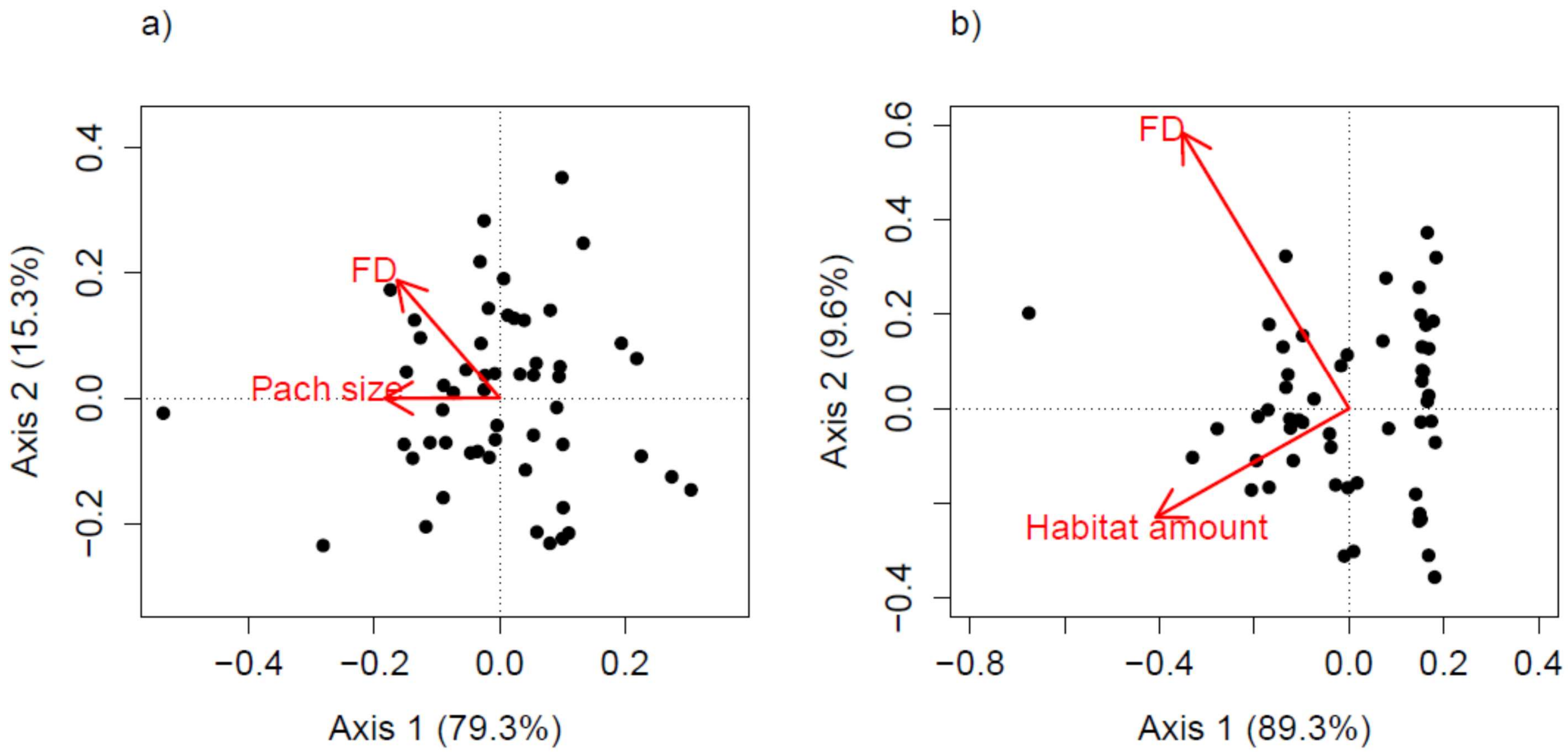


Figure 4. Trait-divergence assembly patterns (TDAP) found in small mammals metacommunities in a fragmentation gradient in the Cerrado of Mato Grosso do Sul. The biplots comprise an ordenation diagram (PCoA) of the small mammals metacommunities composition after weighting by traits that maximized the expression of TDAP related to patch size (a) and habitat amount in the landscape (b). FD: functional diversity.

In relation to the PSM, we found that the hind feet width and the muzzle and ear lengths together maximize the PSM related to TCAP. These attributes together have strong phylogenetic signal at the species pool level (ro (**BF**) = 0.73; p <0.01) but, despite the correlation between phylogenetic community structure and traits to be high, it was not significant (ro (**PT**) = 0.96; p = 0.08). Body mass, ear length and hind feet width maximize the PSM related to TDAP, but the correlation was not significant (ro (**PX.T**) = 0.93, p = 0.13), although this traits set also shows phylogenetic signal at the species pool level (ro (**BF**) = 0.74; p <0.01).

Discussion

To our knowledge, this is the first study to analyze the functional and phylogenetic patterns of small-mammal metacommunities along a fragmentation gradient. Although many studies in fragmented areas have reported that species richness is positively related to patch size (e.g. Pardini et al. 2005, Holland & Bennett 2009, Cáceres et al. 2010), our results show that the loss of species does not occur randomly, being rather related with both phylogeny and certain functional traits of the species.

The phylogenetic pattern along the communities subject to the patch size gradient shows that, in general, marsupials are more tolerant to fragmentation than rodents. This pattern has already been reported in studies conducted in the Atlantic Forest (Magnus & Cáceres 2012) and Cerrado (Cáceres et al. 2010), where positive relationships between species richness and patch size were observed only for rodents. The greater persistence of marsupials in small patches can be related to their greater dispersal ability through the matrix when compared to rodents (Pires et al. 2002, Passamani & Fernandez 2011). This trait allows the flow of individuals between isolated patches and consequently their persistence, whether in large or small ones. Moreover, we observed no relationship between phylogenetic structure and the habitat amount in the landscape, indicating that, in general, rodents can persist even in the comparably very fragmented landscapes, since these patches have a minimum size achievable to its persistence (this study represented by patches >100 ha). On the other hand, marsupial do not seen to be limited neither by habitat amount in the landscape nor by patch size. However, it is noteworthy that this is a general pattern of species prevalence between sites, and obviously there are rodent species tolerant to fragmentation, as well as marsupials that are sensitive to fragmentation in these areas.

We also observed a trait-convergence pattern along the gradient, which might indicates that patch size works as an environmental filter, selecting certain traits with respect to others. This is the case of the ear and muzzle length, width of the hind feet and generalist habit, which on average have higher values in small patches, decreasing as the patch size increases. To a certain extent, some of these traits also reflect a relationship between rodents and marsupials with patch size, since marsupials tend to have longer ears and wider feet than rodents on average (Figure 2a and 2b; Appendix 8). However, the muzzle length and generalist habit did not show phylogenetic signal, which means that they do not vary between clades of marsupials and rodents (Figure 2c and 2d; Appendix 8). Several studies suggest that cursorial small-mammal species are more affected by fragmentation than those species able to use the understory stratum (e.g. Pardini 2004, Viveiros de Castro & Fernandez 2004, Pardini et al. 2005, Püttker et al. 2012). Two of the above mentioned traits indirectly reflect the ability to use the vertical forest stratum, i.e., the longer the ear and wider the feet, more arboreal a given species is (Eisenberg & Wilson 1981, Camargo et al. 2012). In this sense, the small mammals of the Cerrado seem to respond to the fragmentation in a similar way as the species of forest biomes such as the Atlantic Forest, since our results shows that these traits are on average bigger in small patches than in larger ones. This indicates the predominance of scansorial and arboreal species in small-patch communities.

Fragmentation not only causes the reduction and isolation of a given patch, but also causes changes its functional and structural characteristics, including the change of plant species composition, the increase in edge effect, and changes in the forest density vegetation. These changes are stronger in small patches (Laurance et al. 2002). Pardini (2001) attributed the success of arboreal small mammal species into patches, compared to continuous areas, to the denser understory caused by the higher light input due to the more open canopy. Besides, Viveiros de Castro & Fernandez (2004) found that arboreal species have high ability to cross the open matrix composed by pasture. The abilities to use disturbed patches and to disperse through the matrix are important traits for tolerance to fragmentation (Laurance 1991, Pires et al. 2002, Lira et al. 2007, Passamani & Fernandez 2011). On the other hand, it is unclear which factors are affecting the persistence of cursorial species into small patches, but they probably should be associated with the physical changes previously mentioned. Small cursorial mammals depend directly on the environment structure at ground level; that is, it is the environment they use to forage, to shelter and to move. Thus, there are two distinct consequences in small patches: 1) the increase in the luminosity and the edge effect causes an increase in understory vegetation density, favoring the arboreal species (Pardini 2001), 2) the decrease in the vegetation and litter density on the ground level can contribute to the reduction of available resources to the cursorial species.

The muzzle length reflects an indirect relationship with the diet of a species. In general, specialist mammal's species in relation to diet have wider and shorter snout and jaw and/or shorter molar series than more generalist species (Medellín 1991, Samuels 2009, Cáceres et al. 2014). Strictly insectivorous species are exceptions, with longer and narrower snout and jaw than the others (Samuels 2009). In the present study there is no exclusively insectivorous species (specialist in relation to diet with long muzzle), but many of them are classified as insectivorous-omnivore, which are considered generalist in relation to diet and have intermediate muzzle size, being *Gracilinanus agilis* and *Thylamys macrurus* examples of such species (Paglia et al. 2012). In this sense, the patch size can be acting as an environmental filter, favoring species with longer than shorter muzzle, being the last ones mainly present in the larger patches. The availability of food resources is limited in smaller patches, particularly those of vegetable origin like fruits (Silva & Tabarelli 2000, Elias et al. 2012), thus favoring the predominance of omnivorous species, which in turn reflects in a higher average muzzle length in these sites. For these species, much of their diets are composed primarily by invertebrates, with the addition of other food items according to their availability in the environment. This behaviour indicates an environmental plasticity by these species, at least in relation to diet, possibly contributing to their persistence in smaller patches where this resource type is abundant (Didham 1997). Moreover, herbivorous or granivorous species (specialist in relation to diet with short muzzle) are rare or absent in smaller patches (Melo, G. unpublished data), being *Thrichomys pachyurus* and *Oecomys* spp. examples of such species (Paglia et al. 2012).

By analyzing the β diversity in a study with similar sample design to ours, Püttker et al. (2015) found homogenization of species composition in fragmented landscapes of Atlantic Forest, concluding that habitat loss works as an environmental filter for small-mammal communities. Our results also indicate that there is environmental filter acting in very fragmented landscapes, but in addition we show that some functional traits are directly subjected to this environmental filter. In this case, the habitat amount in the landscape functions as a filter for both, specialist species in relation to diet and habitat.

The fragmentation threshold hypothesis proposed by Andrén (1994) indicates that below a certain threshold (about 30% of the habitat amount in landscape) the species-area relationship is more evident than in less fragmented landscape (for example, our landscapes of 50% of habitat cover). Pardini et al. (2010) in a study conducted in the Atlantic Forest found that in severely fragmented landscapes (around 10% of the remaining vegetation) the loss of native vegetation leads to an extinction filter that results in the abrupt loss of specialist species in the landscape, regardless the remaining patches size. Püttker et al. (2012) related some ecological traits with a fragmentation vulnerability index for marsupials, and their results show that specialization in relation to habitat use was the most important variable to explain the species extinction in fragmented landscapes. Our results indicate that there are loss (or decrease in abundance) of habitat specialist species in landscapes with low habitat amount. Thus, both patch size and habitat amount in the surrounding landscape act as environmental filters for the small mammal species. In this case, cursorial and specialist species in relation to diet and habitat are the main ones affected by habitat loss and fragmentation process.

In addition to the convergence patterns along the fragmentation gradients, we also found divergence patterns considering both environmental gradients. In general, the less exposed to fragmentation the communities are, in relation to both patch size and habitat amount, the greater the species functional diversity present in these communities. With favorable environment for persistence of species susceptible to fragmentation, the generalist and dominant species in smaller patches and/or in the landscapes with less habitat amount become less abundant. In general, specialist species tend to be superior competitor than generalist ones (Dueser & Hallet 1980, Hallet et al. 1983, Marvier et al. 2004), and co-occurrence of these different functional types in larger patches and/or landscapes with high habitat amount increases the functional diversity at these sites.

We found phylogenetic signal at the species pool level for the majority of morphological traits. This means that phylogenetically related species tend to be more similar to each other based on their traits than would be randomly expected. As the small-mammal communities are composed of two distant clades, marsupials and rodents, it was expected a strong phylogenetic signal at the species pool level in relation to morphological traits. The marsupial morphology, with opposable thumb and long tail, is common throughout the group, which makes them relatively homogeneous morphologically (Medellín 1991, Rossi et al. 2012), but there are exceptions to these characteristics, such as the marsupial *Monodelphis domestica*. On the other hand, the rodents have a much larger morphological variation between species. However, unlike the morphological traits, the ecological traits showed no phylogenetic signal at the species pool level. In general, ecological traits tend to be more labile compared to morphological traits (Usseglio-Polatera et al. 2000, Poff et al. 2006). Although some morphological traits related to TCAP and TDAP have presented phylogenetic signal at the species pool level (e.g. feet width and ear length), we have not found phylogenetic signal at the metacommunity level.

In this research, we found evidence that Cerrado fragmentation affects the small mammals' metacommunities in a directional and predictable way, and we can conclude that, in general, rodents are the most affected group by the fragmentation process. Furthermore, some functional traits, such as feet width, ear and muzzle length and generalist/specialist habit show convergence along the gradient of fragmentation. In this sense, scansorial and arboreal species would be less affected by fragmentation, as well as the generalist species relative to habitat and diet. This is the first study to relate the functional traits and phylogeny of small mammals with the fragmentation process. Future studies can complement our results investigating these patterns in communities present in other regions, and considering other predictors that are also related to the fragmentation process, such as edge effect.

General conclusions

Our results showed that there is a strong habitat loss effect on small mammal communities in the Cerrado. Considering a wide scale (22,500 ha landscapes), specialist species decline in landscapes with less habitat amount, while generalist species are more abundant. However, we did not corroborate our prediction of a species-area relationship in landscapes with 10 % of habitat amount and high gamma diversity in all landscapes, despite the habitat loss. Actually, we found an unclear patch size effect in the majority of cases and a decrease in species richness (majorly for specialist species) in the landscape with less habitat amount. Thus, we conclude that for small mammals in the Cerrado, the habitat amount in the landscape is more important than the patch size. The lack of a patch-size effect could be related with the regional characteristic of the region (even the small patches are sufficiently large for the species considered) or in accordance with the habitat amount hypothesis, which predicts that the habitat amount in the landscape is the main factor to predict species richness.

Taking this in mind, we tested the habitat amount hypothesis considering a local landscape (2000 m radius buffer) and we found that our data are in accordance to it. The habitat amount had a positive effect in species richness, but the patch size and isolation had no effect, when controlling for habitat amount correlation. However, in some specific situations, the patch size can also exert an important role in predict species richness as well. In our case in landscapes with intermediate habitat amount. Therefore, further studies are need to test the habitat amount hypothesis in order to investigate if this pattern is widely applied; and more important, in which situations we can safely ignore the fragmentation patterns in the landscape (e.g. patch size, isolation).

We showed that Cerrado fragmentation affects the small mammals' metacommunities in a directional and predictable way, and we have showed that, in general, rodents are the most affected group by the fragmentation process.

Furthermore, the habitat loss and fragmentation act as an environmental filter to the species. Some functional traits, such as feet width, ear and muzzle length and generalist/specialist habit show convergence along the gradient of fragmentation. In this sense, scansorial and arboreal species would be less affected by fragmentation, as well as the generalist species relative to habitat and diet. On the other hand, the functional diversity is higher in larger patches and/or landscapes with higher habitat amount.

Interestingly, patch size showed an important effect when we analyzed the small mammal communities using a functional and phylogenetic approach. However, the same predictor has not showed and important effect when we considered more widely used species descriptors, like species richness and abundance. Therefore, our results indicated that some predictors cannot have a quantitative effect on species community descriptors, but show a qualitative effect, as found by us analyzing the functional and phylogenetic species alteration in a patch size gradient.

These results highlight the need to understand the long-term effect of fragmentation and habitat loss in the Cerrado species. The fragmentation process to which the region is being subjected is continuous and only a negligible portion of the biome is protected as conservation units. Against that background, we emphasize the need to carry out further studies about the effect of habitat loss and fragmentation on the biodiversity of this hotspot. Our results showed the need to consider the surrounding landscape as sample unit, not only the patch size and isolation, since the former has more effect in species response to the fragmentation process. We also highlight the need to use qualitative descriptors of species response to fragmentation, since quantitative ones cannot show more specific patterns.

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APPENDICES

Appendix 1. Tukey's pairwise comparisons (Q below diagonal, p above diagonal), mean and standard deviation (sd) of patches size (ha) sampled in the six fragmented Savanna landscapes with different proportions of forest cover in Mato Grosso do Sul state, Brazil (ANOVA F = 1.329; p = 0.27).

	Landscape						Patch size	
	1-10%	2-10%	1-30%	2-30%	1-50%	2-50%	Mean	Sd
1-10%		1	0.317	0.999	0.824	0.872	124.95	108.18
2-10%	0.136		0.369	0.999	0.869	0.909	134.84	152.55
1-30%	2.941	2.805		0.520	0.954	0.927	338.13	290.46
2-30%	0.494	0.358	2.447		0.951	0.972	160.75	156.29
1-50%	1.727	1.590	1.214	1.233		1	250.12	264.24
2-50%	1.579	1.442	1.362	1.085	0.148		239.38	230.27

Appendix 2. Tukey's pairwise comparisons (Q below diagonal, p above diagonal), mean and standard deviation (sd) of distance (meters) of the sampled patch to nearest patch in the six fragmented Savanna landscapes with different proportions of forest cover in Mato Grosso do Sul state, Brazil (ANOVA F = 1.136; p = 0.35).

	Landscape						Distance of near patch	
	1-10%	2-10%	1-30%	2-30%	1-50%	2-50%	Mean	Sd
1-10%		0.996	0.646	0.575	0.414	0.974	485.11	540.24
2-10%	0.705		0.904	0.860	0.724	0.999	370.67	811.58
1-30%	2.167	1.462		1	0.999	0.969	133.50	144.42
2-30%	2.324	1.618	0.156		0.999	0.947	108.13	146.01
1-50%	2.691	1.985	0.523	0.367		0.857	48.57	26.73
2-50%	1.064	0.358	1.103	1.260	1.627		312.50	426.13

Appendix 3. Tukey's pairwise comparisons (Q below diagonal, p above diagonal), mean and standard deviation (sd) of mean distance (meters) of each patch sampled to all other patches in the same landscape in the six fragmented Savanna landscapes with different proportions of forest cover in Mato Grosso do Sul state, Brazil (ANOVA F = 5.995; p < 0.01).

	Landscape						Mean distance of the sampled patch	
	1-10%	2-10%	1-30%	2-30%	1-50%	2-50%	Mean	Sd
1-10%		0.990	0.423	0.007	0.038	0.091	1729.13	975.35
2-10%	0.548		0.226	0.002	0.014	0.036	1857.04	742.24
1-30%	2.671	3.219		0.447	0.832	0.959	1105.72	633.09
2-30%	5.285	5.833	2.614		0.987	0.912	495.50	224.89
1-50%	4.375	4.923	1.704	0.910		0.999	707.97	402.77
2-50%	3.857	4.405	1.186	1.428	0.518		828.92	637.20

Appendix 4. Number of individuals generalist and specialist non-volant small mammals sampled in fragmented Savanna landscapes with different proportions of forest cover in Mato Grosso do Sul state. Brazil. G = generalist; S = specialist.

Family / Species	Landscape			Classification*
	10 %	30 %	50%	
Didelphidae				
Cryptonanus sp.	0	0	1	G
Didelphis albiventris	73	27	17	G
Gracilinanus agilis	133	155	82	G
Marmosa constantiae	0	0	3	S
Marmosa murina	0	3	0	S
Monodelphis domestica	0	6	5	S
Philander opossum	0	0	1	S
Thylamys macrurus	24	61	30	G
Echymidae				
Thrichomys pachyurus	1	27	28	S
Cricetidae				
Calomys callosus	6	10	3	G
Calomys tener	1	0	0	G
Cerradomys maracajuensis	0	4	1	G
Cerradomys scotti	6	6	0	G
Hylaeamys megacephalus	0	23	5	S
Nectomys rattus	1	0	1	G
Oecomys bicolor	1	2	2	S
Oecomys mamorae	1	7	12	S
Oecomys roberti	0	3	0	S
Oligoryzomys nigripes	0	2	0	G
Rhipidomys macrurus	77	55	15	G

*Alho CJR. 2005. Intergradation of habitats of non-volant small mammals in the patchy Cerrado landscape. Arquivos do Museu Nacional 63: 41-48.

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Appendix 5. Predictors values for each transect line sampled. The habitat amount refers to the scale of effect for the species considered (2000 m radius).

Sample unit	Habitat amount (%)	Patch size (ha)	Isolation (m)
1	39.42	1023.07	2273.50
2	36.58	1023.07	2299.75
3	43.58	312.12	760.75
4	39.99	312.12	1116.25
5	55.42	358.77	1006.25
6	60.04	774.10	850.00
7	54.95	737.17	1044.50
8	64.17	737.17	1048.50
9	36.96	356.00	1705.25
10	40.69	356.00	1535.50
11	20.76	47.08	1394.00
12	19.43	47.08	1255.50
13	22.13	71.66	1297.25
14	20.82	71.66	1146.25
15	18.36	48.10	1244.50
16	21.42	48.10	1232.50
17	23.60	350.74	787.25
18	28.26	350.74	755.00
19	28.36	21.85	709.00
20	30.58	21.85	810.75
21	14.90	154.36	700.25
22	13.91	154.36	1183.25
23	11.94	230.61	2470.00
24	15.00	230.61	2545.00
25	8.40	76.03	1815.50
26	8.20	76.03	1884.00
27	7.37	52.42	2093.75
28	6.52	52.42	2042.50
29	11.52	129.59	2102.25
30	11.72	129.59	2196.00
31	16.61	19.97	619.75

32	14.38	19.97	703.00
33	13.12	89.01	1762.00
34	11.41	89.01	2003.50
35	68.99	992.04	788.50
36	63.06	82.90	807.75
37	56.24	82.90	870.50
38	49.05	218.67	696.75
39	64.99	218.67	774.50
40	59.29	183.66	1002.25
41	48.28	183.66	596.25
42	68.49	739.21	1744.75
43	51.38	739.21	1044.00
44	44.34	24.19	885.50
45	42.66	469.39	1535.00
46	42.37	469.39	1649.50
47	39.77	32.79	1345.00
48	35.88	32.79	1122.00
49	30.54	313.35	2085.50
50	27.38	313.35	1911.75
51	21.91	108.90	1887.50
52	26.03	108.90	1750.00
53	18.51	32.03	1028.25
54	16.80	32.03	1011.50
55	12.57	12.39	1430.75
56	15.36	12.39	1313.75
57	18.05	164.63	1634.25
58	18.87	164.63	1354.25
59	5.14	39.05	2520.00
60	5.48	39.05	2169.25
61	8.37	79.27	1650.25
62	7.74	79.27	1848.75
63	7.42	12.79	1474.75
64	8.69	12.79	1585.25
65	25.82	451.11	2674.50
66	27.48	451.11	2521.50

67	51.04	216.30	759.00
68	51.23	216.30	670.00
69	55.49	502.01	735.00
70	59.40	502.01	978.00
71	31.88	41.60	822.75
72	33.37	41.60	929.25
73	51.31	263.65	1385.25
74	56.53	263.65	1350.25
75	39.45	150.79	1503.25
76	44.79	150.79	1613.25
77	66.65	658.20	871.00
78	67.90	658.20	1098.50
79	20.28	31.79	1347.00
80	18.98	31.79	1514.50
81	41.69	50.71	797.50
82	47.39	50.71	792.25
83	36.38	168.28	1200.75
84	39.85	168.28	1185.75
85	29.75	109.73	1137.25
86	32.27	109.73	890.50
87	30.10	112.93	1266.25
88	28.36	112.93	872.25
89	38.88	507.60	1354.25
90	41.65	507.60	1389.50
91	83.35	245.22	1555.00
92	58.45	245.22	942.75
93	80.57	984.22	1381.50
94	67.34	984.22	727.00
95	66.85	50.36	825.25
96	71.88	50.36	551.75
97	48.63	41.30	1179.25
98	46.29	41.30	1303.75
99	32.94	50.55	914.50
100	32.02	50.55	1046.25

Appendix 6 – Definition of the range of our multi-scales in witch to look for the correct scale of effect for specialist small mammals captured in woodland patches in a savanna region. In bold the minimum and maximum value found.

Genus	Home range (m^2)#	√ Home range (m)	Max. dispersal distance (MDD)	0.3* MDD	0.5*MDD
Oecomys	1750	41.83	1673.2	502.0	836.6
Hylaemys	1350	36.74	1469.6	**440.9**	734.8
Thrichomys	6710	81.90	3276.0	982.8	1638.0
Marmosa	13500	116.19	4647.6	1394.3	2323.8
Monodelphis	1500	38.73	1549.2	464.7	774.6
Philander	28000	167.33	6693.2	2008.0	**3346.6**

The home range for all specialist species captured are not available, so we used the home range for the closed species (same genus) available. Our estimate probably covers the home range for those species (or genus) witch home range values were not known because they have intermediate body mass (see Appendix 8).

We used the home ranges of the species to calculate their maximum dispersal distance (MDD = 40*linear dimension of home range; Bowman et al. 2002). We then used the MDD to calculate the scale of effect that corresponds to 30 - 50 % of the maximum dispersal distance (Jackson & Fahrig 2012). So, we used the minimum (440.9 m) and maximum (3346.6 m) values found as the range of our multi-scales. To make sure we were really considering the correct range to look for the scale of effect, we extrapolated these values to 250 m and 6000 m.

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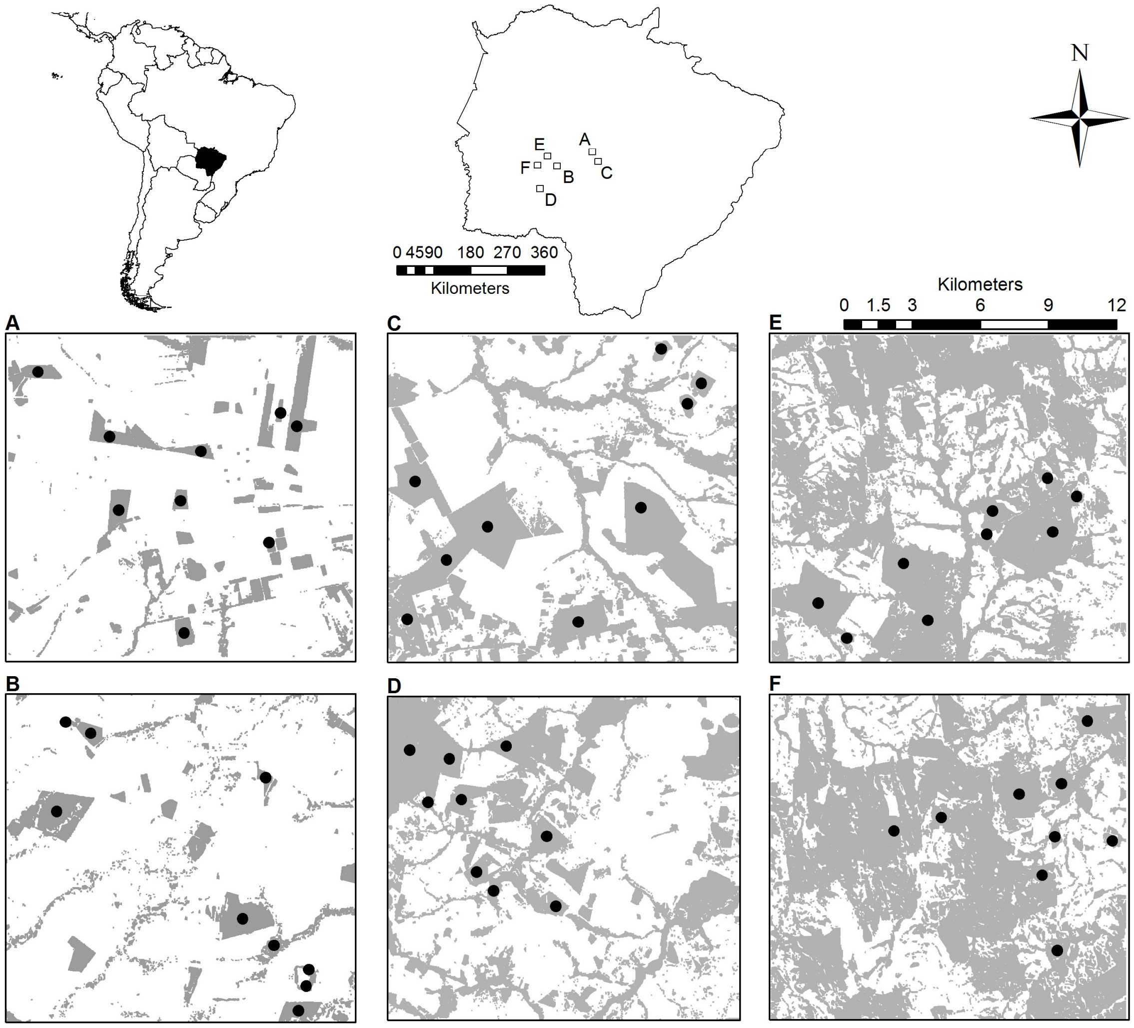

Appendix 7. Landscapes with 10% (A and B), 30% (C and D) and 50% (E and F) of habitat amount indicating the distribution of the 54 sampled patches (dots). In gray areas of natural remaining vegetation (woodland).

Appendix 8. Functional traits of small mammals species sampled in Cerrado woodland patches in Mato Grosso do Sul. Mass = body mass (average mass of all adults); Tail = average tail length divided by average body length; Foot = mean hind feet width divided by the average length of the hind feet; Ear = average ear length divided by the average body length; Muzzle = average muzzle length divided by the average body length; Habit = generalist or specialist in relation to habitat use (see references below); Vertical Use = ground (Gr) predominanted capture on the ground and (Un) predominanted capture in the understory.

Family/Species	**Mass (mm)**	**Tail (mm)**	**Foot (mm)**	**Ear (mm)**	**Muzzle (mm)**	**Habit***	**Vertical Use**
Didelphidae							
Cryptonanus sp.	14	1.358	0.589	0.204	0.126	Ge	Gr
Didelphis albiventris	453	0.988	0.672	0.190	0.122	Ge	Gr
Gracilinanus agilis	22	1.353	0.671	0.214	0.128	Ge	Un
Marmosa constantiae	79	1.348	0.737	0.161	0.110	Sp	Un
Marmosa murina	45	1.419	0.624	0.194	0.125	Sp	Un
Monodelphis domestica	62	0.517	0.577	0.144	0.122	Sp	Gr
Philander opossum	300	1.156	0.705	0.149	0.120	Sp	Gr
Thylamys macrurus	37	1.204	0.683	0.210	0.125	Ge	Un
Echymidae							
Thrichomys pachyurus	299	0.859	0.332	0.106	0.114	Sp	Gr
Cricetidae							
Calomys callosus	34	0.743	0.314	0.151	0.124	Ge	Gr
Calomys tener	15	0.592	0.338	0.163	0.132	Ge	Gr
Cerradomys maracajuensis	99	1.190	0.355	0.144	0.120	Ge	Gr
Cerradomys scotti	85	1.165	0.347	0.144	0.121	Ge	Gr
Hylaeamys megacephalus	53	0.944	0.301	0.164	0.137	Sp	Gr
Nectomys rattus	222	1.106	0.381	0.145	0.117	Ge	Gr
Oecomys bicolor	27	1.131	0.381	0.154	0.127	Sp	Un
Oecomys mamorae	68	1.195	0.433	0.134	0.119	Sp	Un
Oecomys roberti	64	1.135	0.369	0.138	0.113	Sp	Un

Oligoryzomys nigripes	20	1.291	0.278	0.156	0.123	Ge	Un
Rhipidomys macrurus	69	1.189	0.422	0.143	0.123	Ge	Un

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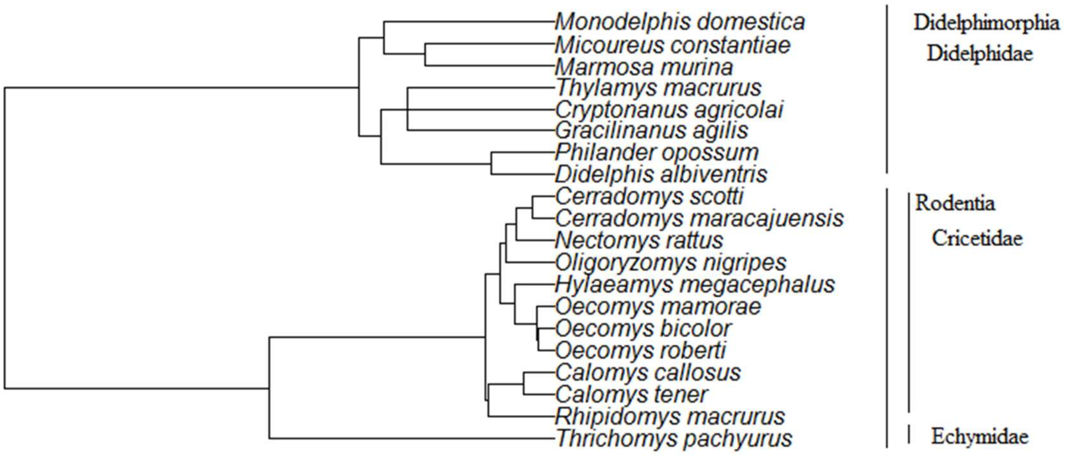
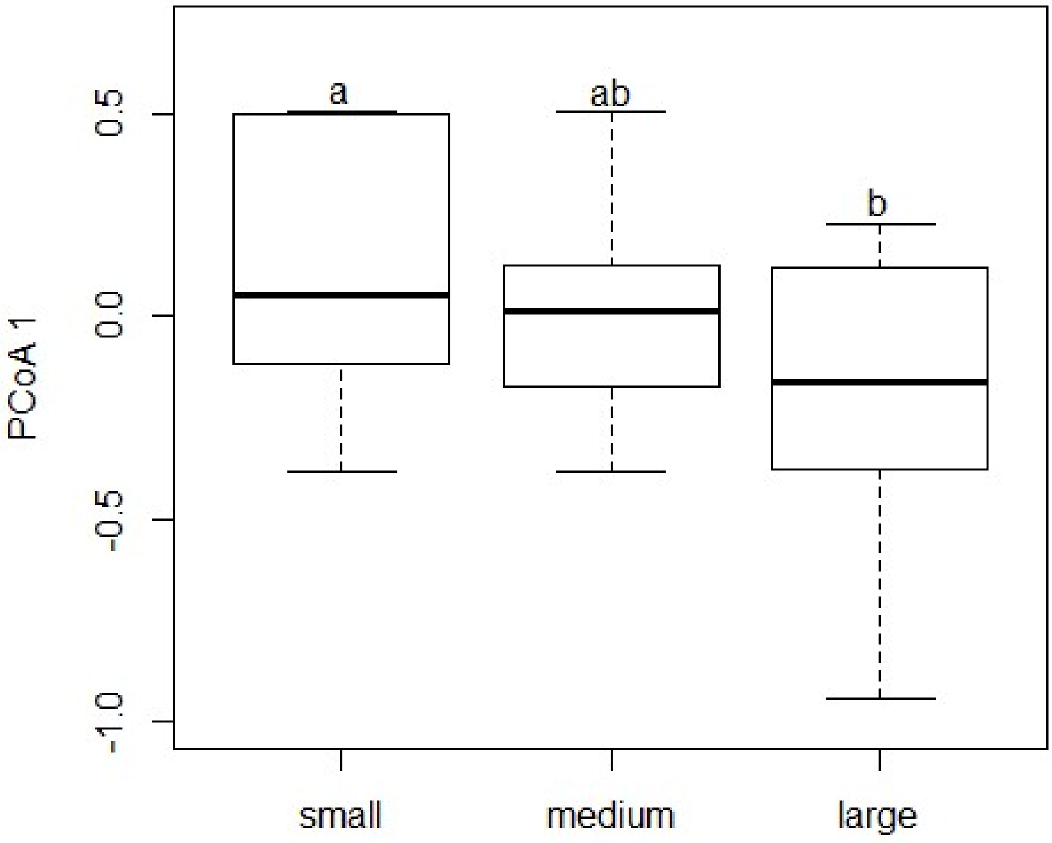
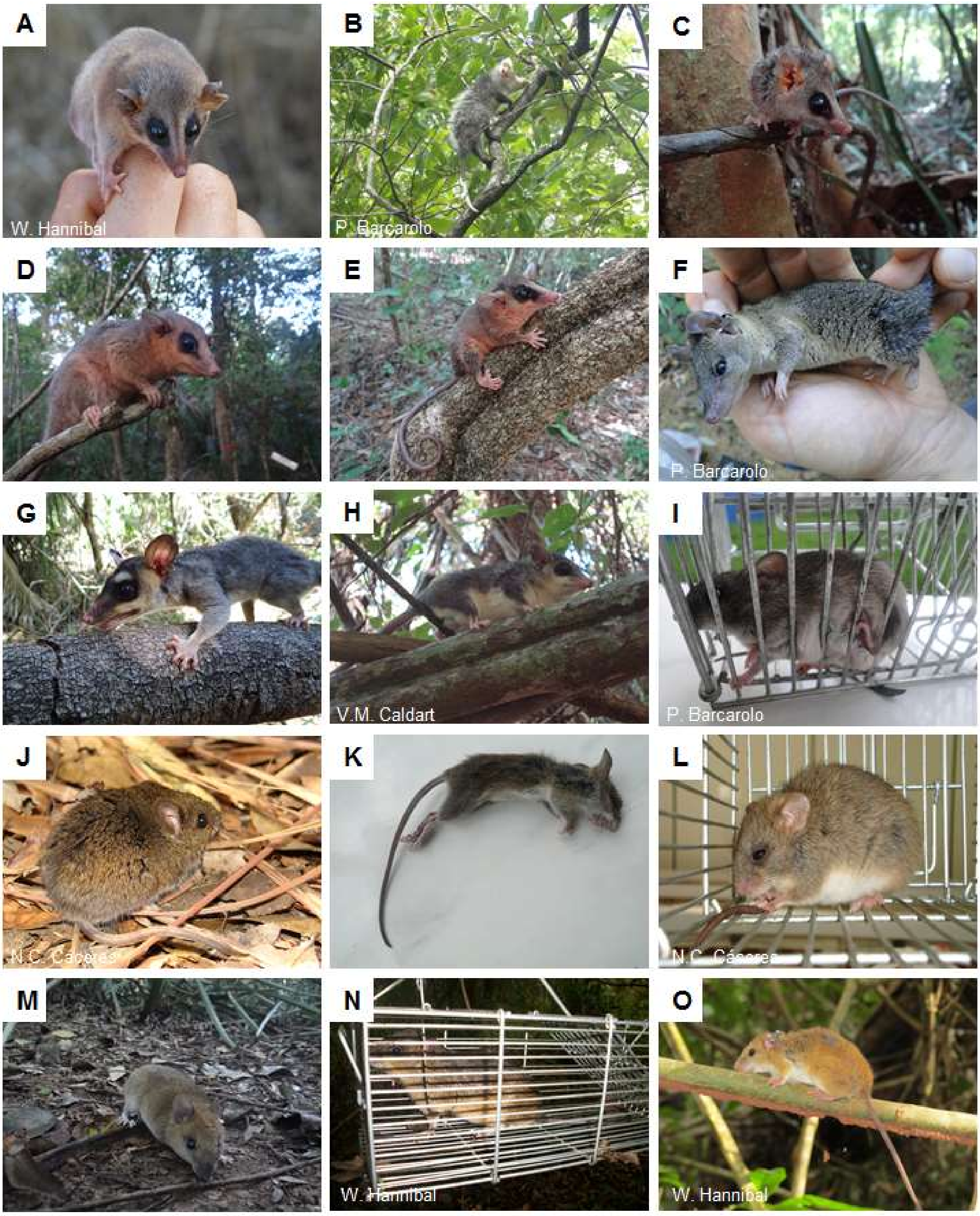


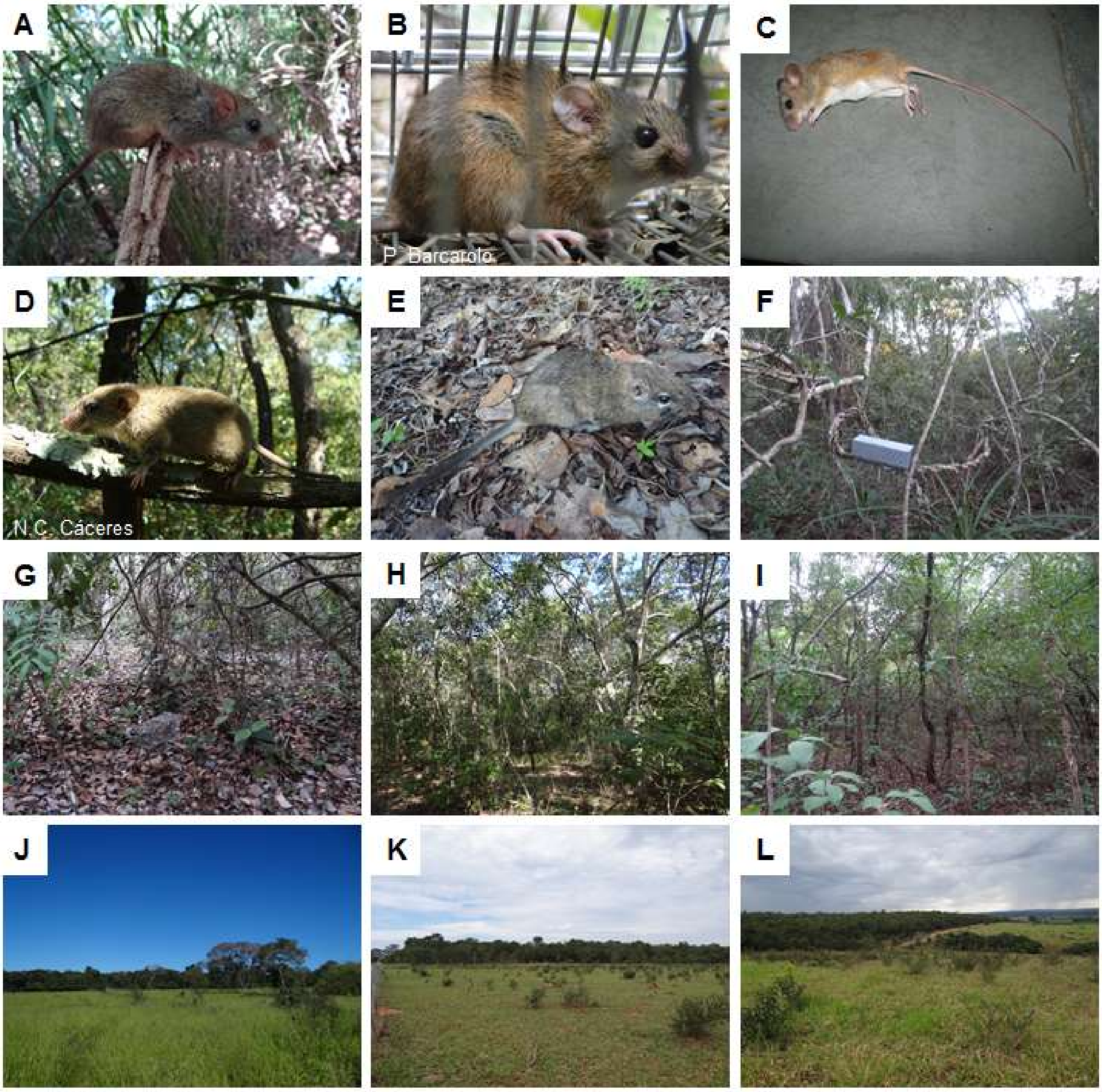
Appendix 9. Small mammals phylogeny of the species pool captured in fragmented landscapes of savanna in Mato Grosso do Sul.



Appendix 10. Analysis of variance of the first PCoA axis of the phylogenetic structure matrix of metacommunities present in a patch size gradient in the Cerrado, Mato Grosso do Sul, Brazil. Different letters represent significant differences ($p < 0.05$) between patch size.



Appendix 11. Small mammal species recorded in woodland patches of Cerrado, Mato Grosso do Sul, Brazil. A: *Cryptonanus sp.*; B: *Didelphis albiventris*; C: *Gracilinanus agilis*; D: *Marmosa constantiae*; E: *M. murina*; F: *Monodelphis domestica*; G: *Philander frenatus*; H: *Thylamys macrurus*; I: *Calomys callosus*; J: *C. tener*; K: *Cerradomys maracajuensis*; L: *C. scotti*; M: *Hylaeamys megacephalus*; N: *Nectomys rattus* and O: *Oecomys bicolor*.



Appendix 12. Small mammal species recorded in woodland patches of Cerrado, Mato Grosso do Sul, Brazil. A: *Oecomys mamorae*; B: *O. roberti*; C: *Oligorizomys nigripes*; D: *Rhipidomys macrurus*; E: *Thrichomys pachyurus*. In F a Sherman trap installed in the understory and in G a wire trap on the ground. In H and I the interior view of woodland two patches sampled. In J, K and L three woodland patches sampled and the grassland exotic pasture as matrix.