

UNIVERSIDADE ESTADUAL PAULISTA **"JÚLIO DE MESQUITA FILHO" UNESP** "JULIO DE MESQUITA FILHO" INSTITUTO DE BIOCIÊNCIAS – RIO CLARO



PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

MAMMAL ECOLOGY IN FRAGMENTED LANDSCAPES: BEYOND THE EFFECTS OF HABITAT AMOUNT

ANDRÉ LUIS REGOLIN

Rio Claro - SP Setembro - 2020



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Orientador: Milton Cezar Ribeiro

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor

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TÍTULO DA TESE: MAMMAL ECOLOGY IN FRAGMENTED LANDSCAPES: BEYOND THE EFFECTS OF HABITAT AMOUNT

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As Indagações

"A resposta certa, não importa nada: o essencial é que as perguntas estejam certas." Mario Quintana, Caderno H.

"Pense fora da caixa, pisoteie a caixa, enfie a porra de uma faca afiada nela." Bansky, Guerra e Spray.

Resumo

A conversão de áreas naturais para uso antropogênico da terra causa perda, fragmentação e degradação de habitat, as quais são as principais ameaças para a conservação de mamíferos terrestres em todo o mundo. Nesta tese buscamos compreender aspectos sobre a ecologia de mamíferos terrestres em paisagens fragmentadas através de um estudo teórico (capitulo 1) e dois estudos empíricos, sendo um sobre estrutura de comunidades (capítulo 2) e outro sobre modelagem de uso de habitat (capítulo 3). No capítulo 1, elaborado no formato de um ensaio, apresentamos e discutimos potenciais influências da fragmentação de habitat sobre o processo de dispersão de sementes sobre morcegos neotropicais. Identificamos lacunas no conhecimento, sugerimos maneiras de preenchê-las e apresentamos potenciais aplicações relacionadas à conservação. No capítulo 2, avaliamos como assembleias de mamíferos são estruturadas em paisagens fragmentadas heterogêneas, combinando análises da estrutura da paisagem com medidas de heterogeneidade espacial. Especificamente, quantificamos a importância de métricas da paisagem, calculadas a partir de mapas temáticos, e de descritores de heterogeneidade espacial intraclasse, estimados utilizando imagens satélites não classificadas, para explicar a riqueza de espécies e a dissimilaridade da composição de espécies entre paisagens. Descobrimos que, contrário às nossas expectativas, a configuração da paisagem foi o principal fator que afetou a riqueza de espécies, seguido pela heterogeneidade espacial e, por último, pela composição da paisagem. O aninhamento das espécies foi explicado, em ordem de importância, pela heterogeneidade espacial, configuração da paisagem e composição da paisagem. Embora as políticas de conservação tendem a se concentrar principalmente na quantidade de habitat, defendemos que o manejo da paisagem deve incluir estratégias para preservar e melhorar a qualidade do habitat em manchas naturais e a incrementar a complexidade da vegetação na matriz circundante, permitindo que as paisagens abriguem maior diversidade de espécies. Investigamos, no capítulo 3, como o uso de habitat por mamíferos herbívoros e frugívoros é moldado pela interação entre a quantidade e qualidade do habitat no Pantanal. Ainda, avaliamos se a contribuição da qualidade do habitat varia conforme a sensibilidade das espécies à perda de habitat. A qualidade do habitat foi mais importante do que a quantidade de habitat na determinação do uso do habitat pelas espécies. A qualidade do habitat foi a melhor preditora de uso de habitat para quatro das seis espécies, mas o uso de habitat não foi explicado apenas pela quantidade de habitat. A quantidade de habitat influenciou apenas quando considerada em conjunto com covariáveis de qualidade do habitat e apenas para espécies mais sensíveis à modificações do habitat. As

espécies menos sensíveis foram melhor modeladas apenas pelas covariáveis de qualidade do habitat. Os programas de conservação devem incorporar tanto a qualidade quanto a quantidade do habitat ao lidar com espécies sensíveis e priorizar o gerenciamento da qualidade do habitat ao focalizar espécies menos sensíveis.

Palavras-chave: Dispersão de sementes, heterogeneidade espacial, fragmentação de habitat, qualidade de habitat, morcegos.

Abstract

The conversion of natural areas to anthropogenic land use causes habitat loss, fragmentation and degradation, which are the main threats to the conservation of terrestrial mammals worldwide. In this dissertation we aim to understand some aspects of terrestrial mammals ecology in fragmented landscapes through a theoretical study (chapter 1) and two empirical studies, one about community structure (chapter 2) and other regarding habitat use modeling (chapter 3). In chapter 1, a theoretical essay, we present and discuss potential influences of habitat fragmentation on the process of seed dispersal by Neotropical bats. We identify knowledge gaps, suggest ways to advance in this topic and present potential applications related to conservation. In chapter 2, we evaluate how mammal assemblies are structured in fragmented heterogeneous landscapes, combining analyzes of the landscape structure with measures of spatial heterogeneity. Specifically, we quantify the importance of landscape metrics, calculated from thematic maps, and of infraclass spatial heterogeneity descriptors, estimated using unclassified satellite images, to explain species richness and the dissimilarity of species composition between landscapes. We found that, contrary to our expectations, landscape configuration was the main factor affecting species richness, followed by spatial heterogeneity and, finally, landscape composition. Species' nesting was explained, in order of importance, by the spatial heterogeneity, landscape configuration and landscape composition. Although conservation policies tend to focus mainly on the amount of habitat, we argue that landscape management should include strategies to preserve and improve the quality of habitat in natural patches and to increase the complexity of vegetation in the surrounding matrix, allowing landscapes harbor higher diversity of species. In chapter 3, we investigate how the use of habitat by herbivorous and frugivorous mammals is shaped by the interaction between the amount and quality of the habitat in the Pantanal. Furthermore, we evaluate whether the contribution of habitat quality varies according to the sensitivity of species to habitat loss. The quality of the habitat was more important than the amount of habitat in determining habitat use (occupancy) by species. Habitat quality was the best predictor of habitat use for four of the six species, but habitat use was not explained only by the amount of habitat. The amount of habitat influenced habitat use only when considered in conjunction with habitat quality covariates and only for species more sensitive to habitat changes. The least sensitive species were best modeled solely by habitat quality covariates. Conservation programs must incorporate both quality and quantity of habitat when dealing with sensitive species and prioritize habitat quality management when focusing on less sensitive species.

Keywords: bats, habitat fragmentation, habitat quality, seed dispersal, spatial heterogeneity.

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Introdução

Perda, fragmentação e degradação de áreas naturais são inevitáveis a nível global devido ao contínuo crescimento da população humana (Haddad et al. 2015). O processo de fragmentação do habitat, gerado pela expansão do uso antrópico sobre áreas naturais, altera a estrutura da paisagem pela perda de habitat, aumento do isolamento, intensificação do efeito de borda (Fahrig 2003), modificação da heterogeneidade do mosaico de manchas (Brady et al. 2011, Driscoll et al. 2013) e redução da qualidade do habitat (Mortelitti et a. 2010). As modificações na estrutura paisagem reduzem a oferta de alimentos e abrigos (Arroyo-Rodríguez & Mandujano 2006), reduzem a mobilidade das espécies (Driscoll et al. 2013) e aumentam o risco de predação na matriz (Brady et al. 2011), afetando desde os padrões de uso do habitat pelos animais (Lyra-Jorge et al. 2010) até o funcionamento do ecossistema (Jorge et al. 2013). A capacidade de habitats naturais remanescentes de sustentar a biodiversidade e os serviços ecossistêmicos depende da quantidade e qualidade do habitat, e do seu grau de conectividade (Haddad et al. 2015).

O estudo dos padrões espaciais das modificações antrópicas sobre processos ecológicos está no escopo da disciplina 'Ecologia de Paisagens', que visa à aplicação para a conservação da diversidade biológica e do manejo de recursos naturais (Risser et al. 1984). Os primeiros estudos dessa disciplina foram marcados por uma baixa resolução temática das análises de paisagens, i.e. a dicotomia entre habitat e não habitat (Boscolo et al. 2016). Esta simplificação analítica se justificava pelas limitações tecnológicas de sensoriamento remoto da época e pelo referencial teórico em vigor, o modelo de matriz-corredor-mancha que foi desenvolvido com base na teoria de biogeografia de ilhas (Boscolo et al. 2016). Neste paradigma, a maioria dos estudos de ecologia de paisagens buscou avaliar os processos relacionados aos padrões de área coberta por habitat na paisagem (i.e., composição) e ao seu arranjo espacial (i.e., configuração) (Chiarello 1999).

Posteriormente, a classificação mais detalhada de paisagens foi incorporada pelo modelo do mosaico heterogêneo, objetivando avaliar a importância da variedade de tipos de uso e cobertura do solo (Boscolo et al. 2016, Metzger 2001). Neste modelo, paisagem é definida como "um mosaico heterogêneo formado por unidades interativas, sendo esta heterogeneidade existente para pelo menos um fator, segundo um observador e numa determinada escala de observação" (Metzger 2001). Embora seja um aspecto central no conceito de paisagem, a variedade de fatores que geram heterogeneidade espacial tem sido relativamente pouco investigada em estudos ecológicos (Boscolo et al. 2016). Esforços têm focado na análise da permeabilidade da matriz e como isso afeta, por exemplo, a conectividade da paisagem (Ferreira et al. 2018) e os efeitos de borda (Martello et al. 2016). Tais avaliações qualitativas da matriz contribuem significativamente para a compreensão de diversos processos ecológicos em paisagens fragmentadas com uso humano mais intenso, mas ainda fornecem pouca atenção a variação da qualidade do habitat (St-Louis et al. 2014).

Qualidade do habitat é capacidade do ambiente de prover recursos e condições adequadas para a sobrevivência de indivíduos e persistência de populações (Hall et al. 1997). A importância da qualidade do habitat na manutenção de processos ecológicos em paisagens fragmentadas tem sido insuficientemente explorada (Mortelliti et al. 2010). A carência de estudos sobre o tema se justifica, em partes, pelo fato de alguns autores considerarem indistinguíveis a qualidade e a quantidade de habitat (Theobald et al. 2011). A escassez de estudos é intensificada pela inconsistência nos conceitos e a ausência de protocolos padronizados para mensurar qualidade de habitat (Mortelliti et al. 2010), tornando ainda mais difícil a tarefa de compreender a sua importância.

É necessário aumentar o nível de complexidade dos modelos teóricos e das análises de paisagem para avaliar o papel qualidade de habitat conjuntamente a variedade de fatores de heterogeneidade da paisagem (Boscolo et al. 2016). Contraditoriamente, há atualmente uma tendência de retomada de uma simplificação de análise ecológica das paisagens, a qual tem sido impulsionada por uma hipótese que propõe que a riqueza de espécies é definida principalmente pela quantidade de habitat na paisagem (Fahrig 2013). Alguns estudos têm corroborado a hipótese da quantidade de habitat para diferentes grupos taxonômicos em diversos sistemas (Melo et al 2017, Regolin et al 2017). No entanto, é preciso repensar sobre os paradigmas que sustentam tal proposição para que ecologia de paisagens vá além dos efeitos da quantidade de habitat.

Objetivos e estrutura da tese

Nesta tese buscamos compreender como aspectos sobre a ecologia de mamíferos terrestres em paisagens fragmentadas através de um estudo teórico (capitulo 1) e de dois estudos empíricos, sendo um sobre estrutura de comunidades (capítulo 2) e outro sobre

modelagem de uso de habitat (capítulo 3). No capítulo 1, elaborado no formado de um ensaio, apresentamos e discutimos potenciais influências da fragmentação de habitat sobre o processo de dispersão de sementes sobre morcegos neotropicais. Identificamos lacunas no conhecimento, sugerimos maneiras de preenchê-las e apresentamos potenciais aplicações relacionadas à conservação. No capítulo 2, avaliamos como assembleias de mamíferos são estruturadas em paisagens fragmentadas heterogêneas, combinando análises da estrutura da paisagem com medidas de heterogeneidade espacial. Especificamente, quantificamos a importância de métricas da paisagem, calculadas a partir de mapas temáticos, e de descritores de heterogeneidade espacial infraclasse, estimados utilizando imagens satélites não classificados, para explicar a riqueza de espécies e a dissimilaridade da composição de espécies entre paisagens. Investigamos, no capítulo 3, como o uso de habitat por mamíferos herbívoros e frugívoros é moldado pela interação entre a quantidade e qualidade do habitat no Pantanal. Ainda, avaliamos se a contribuição da qualidade do habitat varia conforme a sensibilidade das espécies a perda de habitat.

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Capítulo 1

Seed dispersal by Neotropical bats in human-disturbed landscapes^{\dagger}

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Short summary

Bats are crucial for the maintenance of ecosystem functions and services within human-modified landscapes. They are important seed dispersers, especially where large birds and large mammals are functionally or locally extinct. However, the roles of bats in fragmented landscapes are misunderstood, particularly in Neotropics. In the present study, we discuss the potential influences of the habitat-fragmentation process on seed dispersal by Neotropical bats. With the development of these studies, we will better understand the bat-modulated seed dispersal process, supporting regeneration and restoration programs that benefit from bat-based functions.

Abstract

In human-modified landscapes, where large bird and mammal species are often functionally extinct, bats are the main seed dispersers. However, the role of seed dispersal by bats for the maintenance of habitat dynamics in fragmented landscapes is still not understood, with information lacking on landscape-level effects of plant–bat interactions. We present some key topics related to spatial ecology of bats and discuss the potential influence of habitat fragmentation on several aspects of seed dispersal by Neotropical bats. We suggest that future studies need to evaluate bat–plant networks along habitat-loss and fragmentation gradients at the landscape level, including changes in land-cover types and habitat structural complexity, going beyond patch-based analysis. By advancing on the comprehension of ecosystem functioning in fragmented landscapes, we will better understand the bat-modulated seed-dispersal process, supporting regeneration and restoration programs that benefit from bat-based functions.

Keywords: Chiroptera, ecological networks, ecosystem services, gradients, habitat loss, restoration, tropical ecology.

Introduction

Modification of landscape structure as a result of habitat loss and fragmentation affects several ecological processes, such as, for example, the seed dispersal by animals (McConkey and O'Farrill 2012). Some landscape conditions, mostly, the loss of habitat and the increased isolation of habitat patches, inhibit seed-disperser movement (Driscoll et al. 2013). They may also affect the survival of animals, because animals can be exposed to new threats from the surrounding anthropogenic matrix (Niebuhr et al. 2015).

Birds, followed by large-sized mammals and bats, are among the most important seed dispersers in Neotropics, regarding plant species richness and dispersal efficacy (Bueno et al. 2013; Galetti et al. 2013; Bello et al. 2017; Barros et al. 2019). Many species of bird and large mammal are affected by habitat-fragmentation process and hunting (i.e. defaunation; Dirzo et al. 2014). However, several fruit-eating bats persist in fragmented landscapes because of their high abundance, great mobility, and plasticity of habitat use (García-García et al. 2014; Muylaert et al. 2016; Voigt et al. 2017). Even so, the role of bats in seed dispersal in fragmented landscapes is still not understood, because the effects of habitat fragmentation on bat-fruit interactions have not been sufficiently explored, what difficult the accurate measurement of seed-dispersal services they provide. Here, we, first, present an overview of seed dispersal by Neotropical bats. Then, we discuss some key topics and potential patterns related to the influence of habitat fragmentation on seed dispersal by Neotropical bats. Finally, the importance of further studies on bats within fragmented and heterogeneous landscapes is highlighted, with suggestions on how to assess the contribution of bats to landscape-level maintenance of ecological processes, with a focus being on seed dispersal.

Seed dispersal by Neotropical bats

Bats belong to the second largest order of mammals, after rodents (>1400 bat species have been described; Fenton and Simmons 2014; Simmons and Cirranello 2019), and have diverse ecosystem functions, providing pollination, arthropod pestsuppression (biological control) and seed-dispersal services (Kunz et al. 2011). Half of the 204 species of the Phyllostomidae family, the leaf-nosed bats, is seed dispersers or primarily frugivores, with different levels of dietary specialisation for fruits (Fenton and Simmons 2014). The main frugivorous species belong to subfamilies Stenodermatinae and Carollinae, whereas other fruit-eating species vary in the quantities of fruit ingested, such as nectarivores in the *Glossophaga* genus and omnivores, such as, for example, *Phyllostomus*, Phyllostominae (Muscarella and Fleming 2007; Silva et al. 2008). Thus, seed dispersal is not restricted to the fruit-eating specialist species within Phyllostomidae, and also species from predominantly nectarivorous and animalivorous subfamilies may occasionally feed on fruits and, therefore, contribute to seed dispersal. The main seed-dispersal agents are from genus *Artibeus*, *Sturnira* and *Carollia*, owing to their abundance and wide distribution, a high diversity of bat species in these genera, high richness of dispersed plant species, and the amount of dispersed seeds (Galindo-González et al. 2000; Silva et al. 2008; Farneda et al. 2015).

Neotropical bats disperse mostly seeds of small-sized (e.g. genera *Piper*) and greenish fruits (e.g. genera *Ficus*) containing high levels of protein and lipids, following the typical chiropterocoric patterns (Cazetta et al. 2012; Sarmento et al. 2014). The top five plant families dispersed by bats in the Neotropics are Solanaceae, Moraceae, Urticaceae, Piperaceae and Clusiaceae (=Hypericaceae; Muscarella and Fleming 2007). The bat-dispersed plant seeds can be from early to late successional stages, although pioneer species are more frequently found on bat faecal samples (Medellín and Gaona 1999; Galindo-González et al. 2000). However, because the evaluation of the bat–seeds relationship is predominantly based on faecal-sample analyses, the contribution of bats to the dispersal of large seeds, which are transported in the mouth without being ingested, is underestimated (Mello et al. 2005; Melo et al. 2009).

Bats are important agents of seed dispersal and forest regeneration because they usually defecate during flight (Medellín and Gaona 1999; Galindo-González et al. 2000; Muscarella and Fleming 2007; Peña-Domene et al. 2014), spreading seeds over long distances. For instance, a 21-g Sturnira lilium fruit-bat can fly over 4 km in fragmented areas within the Neotropical savanna over a single night (maximum Euclidean distance, P. K. Rogeri, unpubl. data). Beyond the high abundance and diversity of species of dispersed plants, bats may deposit the seeds in favourable places for germination (Medellín and Gaona 1999; Arteaga et al. 2006), and, therefore, are efficient seed dispersers.

Several common specific plant-bat interactions, such as those between *Artibeus* and *Ficus* and *Cecropia*, *Carollia* and *Piper*, and *Sturnira* and *Solanum* (Andrade et al. 2013), are frequently recorded in different habitat types (Oliveira et al. 2019), including,

for example, forest edges, riparian forests, pastures, forest and coffee plantations and sugarcane. However, these interactions rely on preference and opportunistic behaviour of bats (Andrade et al. 2013; Muylaert et al. 2014), because fruit availability varies over time and space (Silva et al. 2008). Despite the high diet diversity of fruit-eating bats, these specialised interactions may be very strong, mainly regarding the plant genera cited above (Lobova et al. 2009), and contribute to the nestedness of bat–fruit interaction networks.

Bat-fruit interaction networks in human-disturbed landscapes

Across spatial-temporal scales, bats interact with many plant species, while maintaining frugivory-based ecological processes (Bascompte 2010; Dáttilo and Rico-Gray 2018). These multiple interactions can be quantified and visualised as interaction networks. Network theory has its own emergent properties, as the nested and modular patterns of species interactions (Bascompte 2010; Mello et al. 2015, 2019). Bat-fruit interaction networks are typically nested, that is, specialist bat species interact mostly with specific subsets of those plant species with which the generalist bat species interact (Bascompte 2010; Dáttilo and Rico-Gray 2018). In addition, these networks show a modular structure where groups of bat species are strongly associated with a particular set of plant species, conferring them high levels of robustness in response to cumulative extinctions (Mello et al. 2011). Species of the subfamilies Stenodermatinae and Carollinae have the most important functional roles in these networks because they interact strongly and with more plant species than do other bat species (Mello et al. 2019) and connect network modules acting as hubs. Therefore, the loss of primarily frugivorous bats can cause great changes to the bat-plant network structure, affecting seed dispersal (Mello et al. 2011).

One of the main reasons driving the loss of frugivores in a certain habitat is the fragmentation of the tropical forests (Farneda et al. 2015; Muylaert et al. 2016), and, here, we describe how this could affect seed-dispersal interactions. The vulnerability of bats to fragmentation of tropical forests may vary according to species and traits, where small-sized frugivores seem to be less vulnerable to habitat loss and fragmentation when they have friendly matrices, such as the regenerating areas dominated by Cecropia and Vismia, surrounding old-forest patches in Amazon Farneda et al. (2015). In the cerrado (Brazilian savanna) fragmented landscapes, the reduction of woody vegetation cover

negatively affects the abundance of animalivorous bats, as well as the abundance of nectarivores, whereas frugivorous bats peak in abundance at intermediate woody vegetation-cover levels (Muylaert et al. 2016). Studies conducted in the Atlantic Forest and cerrado biodiversity hotspots in Brazil and Paraguay found high abundances of frugivorous bats in landscapes with intermediate levels (~50%) of forest fragmentation (Gorresen and Willig 2004; Muylaert et al. 2016). This probably occurs because of the positive effects of the amount of forest edge on bat abundance; forest edges are rich in the top five bat plants that compose their diets (Muylaert 2014).

Bat-fruit networks may be highly connected in landscapes with an intermediate habitat cover (~50%) because of the highest amount of edge area (Fahrig 2003), the highest landscape composition heterogeneity (Corro et al. 2019) and the highest diversity of bat species (Muylaert et al. 2016; Fig. 1). Edge areas have a higher availability of pioneer fruit species than do core areas (Oliveira et al. 2004) and more heterogeneous landscapes host high levels of plant diversity because they harbour plants from different land-use classes (Corro et al. 2019). However, it is important to highlight that this value (i.e. 50% of habitat cover) is close to the habitat-amount threshold found for bats within fragmented landscapes of south-eastern Brazil (47%, Muylaert et al. 2016). Thus, network structure can change abruptly by either a loss or replacement of species, leading to changes in seed-dispersal processes. Therefore, the structure of a plant-bat network has clear implications for how it may respond to an anthropogenic landscape change (Bascompte 2010), because it can be shaped by fragmentation, but may also resist this process to some unknown extent.

A recent study compared bat–fruit network data from the Atlantic Forest (Laurindo et al. 2019) between fragmented and continuous forests, where nestedness and modularity did not differ, despite the fact that modularity has had greater variation in fragmented sites. By extrapolating this relationship for a gradient analysis of habitat-cover effects on network structure, we hypothesise that there would be a gradual increase in modularity in response to forest cover because of the increase in bat–fruit specialised interactions (Fig. 1). Bat–fruit interactions are highly specialised, and these relationships should increase with the amount of habitat because of higher plant-genera richness, with a consequent higher network modularity (Mello et al. 2011; Andrade et al. 2013). However, nestedness should increase in disturbed areas, because the reduced availability of fruit diversity implies resource sharing of mainly pioneer species that do

not impose morphological or chemical restrictions to bats (Muscarella and Fleming 2007). Once nestedness represents a niche-breadth regime of a biological community, nested networks tend to have the highest niche overlap (Dáttilo and Rico-Gray 2018).



Figure 1. Hypothetical mutualistic networks of frugivorous bats and plants across a gradient of forest cover. Nodes represent different bat and plant species. Gray nodes are locally extinct species. Higher levels of chiropterocoric plant species and frugivorous bat species richness probably confer higher diversity of interactions to landscapes with intermediate forest cover.

Efforts to evaluate the effects of habitat fragmentation on chiropterochory and plant–bat networks are scarce worldwide. Melo et al. (2009) compared two sites with contrasting anthropogenic disturbance levels and found that the seed rain was less abundant at the more disturbed landscape; yet, there were no differences in the diversity of plant species within the seed rain when comparing the two disturbance levels. Taking into account the efforts to evaluate the effects of land cover on seed dispersal by bats, studies that evaluate bat–plant networks along fragmentation gradients (e.g. landscapes varying from 10% to 90% habitat cover, considering the 'scale of effect', i.e. the spatial extent at which species respond best to the landscape structure; Jackson and Fahrig 2015) are needed. This seems to be the main knowledge gap related to fragmentation effects on seed dispersal, given that the amount of habitat is probably the main factor determining species richness in the landscape (Fahrig 2013).

Other landscape attributes, such as the quality and permeability of anthropogenic matrix, may also be important for shaping bat–plant interaction networks (Driscoll et al. 2013). Changes in the land-cover type beyond the 'focal' native-vegetation patches must be further investigated. For example, the complexity of landscape and vegetation structure in the matrix is the main factor influencing both fauna and flora in landscapes with low forest-cover levels (Brady et al. 2011; Medeiros et al. 2016; Boscolo et al. 2017). However, it is unknown whether matrix-quality effects extend to bats as well. So far, little is known about the influence of the mosaic composition of landscapes on bat–plant networks. However, in structurally simplified environments such as agroforests, bat–plant networks are more vulnerable because of a reduced abundance of fruits (Hernández-Montero et al. 2015). Nonetheless, it is important to note that these authors evaluated only two sites, limiting our capacity of extrapolation for broader contexts.

Assessing the effects of habitat fragmentation on bat-fruit interactions networks

The influence of the amount of habitat, anthropogenic matrix type, and the complexity of vegetation structure on bat-plant mutualistic networks is poorly understood. Future studies could evaluate bat-plant networks by using literature georeferenced data (e.g. the Atlantic-Frugivory dataset (Bello et al. 2017), seeddispersal interactions within Brazilian Atlantic Forest (Emer et al. 2018), bat-interaction databases (Geiselman et al. 2015; Mello et al. 2019), and the review by Castaño et al. (2018)). To investigate the response of the bat-plant network structure to habitat fragmentation, it is necessary to select a set of landscapes that cover a meaningful fragmentation gradient. This set must ideally include changes in land-cover types and habitat structural complexity, going beyond patch-based analysis. In patch-scale studies, the biological response variable is related to attributes of the individual habitat patch in which the species are sampled (e.g. patch area, patch shape and patch quality). In contrast, at the landscape level, the influence on response variables is explained by the composition (i.e. the amount of different land-cover types present in the study landscapes) and configuration (i.e. the spatial arrangement of the landscape units) of the landscape, which is an area delimited by distances that are biologically relevant to the sampling point (the 'scale of effect'), and encompasses patches of different types and proportions of different habitats (Arroyo-Rodríguez and Fahrig 2014; Jackson and Fahrig 2015). To minimise potential sampling bias resulting from differences in the

methods among studies, it is recommended to control analytically the vegetation types and the vertical stratum in which the samples are recorded or collected (Medellín and Gaona 1999; Gregorin et al. 2017).

Applications

Understanding the effects of habitat fragmentation on bat-fruit interaction networks can be applied to (1) estimate the potential for natural regeneration and (2) accelerate assisted succession (restoration) in human-disturbed landscapes (Chazdon and Guariguata 2016; Howe 2016). Recognising and integrating of the role of bats in maintaining or (re)establishing plant diversity can lower the program costs and improve its effectiveness; currently, the program proceeds with uncertainty regarding plantanimal interactions (Howe 2016). By assessing the response of mutualist networks to modifications on landscape structure, changes in communities by a loss or turnover of species of bats and plants will be predictable (Dáttilo and Rico-Gray 2018). Thus, it will be useful to identify areas with the highest natural regeneration potential, by predicting which plant-species seeds will be dispersed and where they will be deposited on the basis of models that simulate the movement of bat individuals in accordance with landscapes structure (e.g. Ribeiro 2010). However, the interpretation of these models must be cautious, because the use of fruit resources by fruit-eating animals does not imply effective seed dispersal; to estimate seed-dispersal effectivity, fieldwork experiments and observations are required (Medellín and Gaona 1999; Howe 2016). Regarding restoration programs, the studies we propose will support the selection of plant species with characteristics that facilitate bat dispersal into, or their migrating through, the landscapes that are likely to be the most useful in conserving or restoring biodiversity (Chazdon and Guariguata 2016; Howe 2016).

Conclusions

On the basis of the discussions presented, we encourage future studies to assess bat-plant networks in landscapes with a varying level of landscape heterogeneity, consisting of units with different structural complexity levels, and those across habitatamount gradients and other disturbance levels. A comprehensive understanding of these networks could bring insight into the dynamics of bat-fruit networks. With the development of these studies, we will better understand the bat-modulated seeddispersal process, supporting regeneration and restoration programs that benefit from bat-based functions.

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Conflicts of Interest

The authors declare no conflicts of interest.

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Capítulo 2

Spatial heterogeneity and habitat configuration overcome habitat composition influences on alpha and beta mammal diversity^{\dagger}

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Abstract

The effects of habitat fragmentation on different taxa and ecosystems are subject to intense debate, and disentangling them is of utmost importance to support conservation and management strategies. We evaluated the importance of landscape composition and configuration, and spatial heterogeneity to explain α - and β -diversity of mammals across a gradient of percent woody cover and land use diversity. We expected species richness to be positively related to all predictive variables, with the strongest relationship with landscape composition and configuration, and spatial heterogeneity, respectively. We also expected landscape to influence β -diversity in the same order of importance expected for species richness, with a stronger influence on nestedness due to deterministic loss of species more sensitive to habitat disturbance. We analyzed landscape structure using: i) landscape metrics based on thematic maps and ii) image texture of a vegetation index. We compared a set of univariate explanatory models of species richness using AIC, and evaluated how dissimilarities in landscape composition and configuration and spatial heterogeneity affect β -diversity components using a Multiple Regression on distance Matrix. Contrary to our expectations, landscape configuration was the main driver of species richness, followed by spatial heterogeneity and last by landscape composition. Nestedness was explained, in order of importance, by spatial heterogeneity, landscape configuration, and landscape composition. Although conservation policies tend to focus mainly on habitat amount, we advocate that landscape management must include strategies to preserve and improve habitat quality and complexity in natural patches and the surrounding matrix, enabling landscapes to harbor high species diversity.
Resumo

Os efeitos da fragmentação de habitats em diferentes taxa e ecossistemas estão sujeitos a intenso debate, e esclarecê-los é de extrema importância para subsidiar estratégias de conservação e manejo. Avaliamos a importância da composição e configuração da paisagem em escala grossa e da heterogeneidade espacial dentro do habitat para explicar a diversidade $\alpha \in \beta$ de mamíferos em um gradiente de porcentagem de cobertura de vegetação lenhosa e de diversidade de uso da terra. Esperamos que a riqueza de espécies seja positivamente relacionada a todas as variáveis explanatórias, sendo a relação mais forte com medidas de composição, com medidas de configuração da paisagem em escala grossa e com a heterogeneidade espacial dentro do habitat, respectivamente. Também esperamos que a paisagem influencie ambos os componentes da diversidade β (substituição e aninhamento), na mesma ordem de importância esperada para a riqueza de espécies, e com uma maior influência no componente de aninhamento devido à perda determinística de espécies mais sensíveis ao distúrbio no habitat. Registramos ocorrências de mamíferos de pequeno, médio e grande porte em 20 paisagens no Brasil e analisamos a estrutura da paisagem usando: i) métricas da paisagem baseadas em mapas temáticos de cobertura da terra e ii) medidas de textura de imagem de um índice de vegetação calculadas a partir de imagens não classificadas. Comparamos um conjunto de modelos explicativos univariados de riqueza de espécies usando o Critério de Informação de Akaike e avaliamos como as diferenças entre pares de paisagens em medidas de composição e configuração da paisagem e medidas dentro de habitat de heterogeneidade espacial afetam os componentes da diversidade β usando uma regressão múltipla em uma matriz de distância. Descobrimos que, contrário às nossas expectativas, a configuração da paisagem foi o principal fator que afeta a riqueza de espécies, seguido pela heterogeneidade espacial e, por último, pela composição da paisagem. O aninhamento das espécies foi explicado, em ordem de importância, pela heterogeneidade espacial, configuração da paisagem e composição da paisagem. Embora as políticas de conservação tendem a se concentrar principalmente na quantidade de habitat, defendemos que o manejo da paisagem deve incluir estratégias para preservar e melhorar a qualidade do habitat em manchas naturais e a incrementar a complexidade da vegetação na matriz circundante, permitindo que as paisagens abriguem maior diversidade de espécies.

Keywords: biodiversity conservation, image texture, fragmentation, habitat modeling,

habitat quality, landscape, Mato Grosso do Sul, species losses

Introduction

The modern biodiversity crisis has been mainly attributed to the process of habitat fragmentation (Haddad et al., 2015), which changes landscape composition, configuration, and habitat quality, by affecting both natural vegetation patches and the anthropogenic matrix (Fahrig, 2003; Fischer & Lindenmayer, 2007; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013). The harmful effects of habitat loss on biodiversity are widely recognized among the scientific community, but the importance of habitat fragmentation per se and habitat degradation is subject to debate due to differences in conceptual foundations, statistical models, study systems, and resulting interpretations (Villard & Metzger, 2014; Fahrig, 2017; Fletcher-Jr et al., 2018). Habitat fragmentation *per se* is the sub-division of habitat patch (Fischer & Lindenmayer, 2007) and habitat degradation is the deterioration of habitat quality (Mortelliti, Amori, & Boitani, 2010). Some researchers have proposed that the effects of fragmentation per se are notable under certain levels of habitat cover, which is called fragmentation threshold (Andrén, 1994; Swift & Hannon, 2010). Others have hypothesized that the effects of the process of habitat fragmentation depend exclusively of the amount of habitat within the landscape (Fahrig, 2013; Melo, Sponchiado, Cáceres, & Fahrig, 2017). However, studies assessing the role of habitat quality are still largely unexplored (Mortelliti, Amori, & Boitani, 2010), so the importance of the variability of vegetation heterogeneity within-habitat is possibly underestimated (Kupfer, Malanson, & Franklin, 2006; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013). Consequently, conservation recommendations beyond reducing habitat loss have not reached a consensus, posing significant challenges for landscape management and biodiversity conservation (Fletcher-Jr et al., 2018). In Neotropical regions, nature management is particularly more challenging due to i) high ecosystem complexity associated to a mega biodiversity (Lewinsohn & Prado, 2005), ii) the highest global rates of forest loss (Hansen et al., 2013), and iii) lack of consistency in environmental policies, especially in Brazil (Brancalion et al., 2016). Thus, it is critical that we understand how structural modifications in fragmented landscapes drive the organization of assemblages in tropical ecosystems.

Historically, landscape ecology theories and models were strongly influenced by Island Biogeography and Metapopulation theories, wherein patches of native vegetation are considered as islands of habitat immersed in an inhospitable matrix, and, consequently, patch area and isolation drive metapopulation dynamics (MacArthur & Wilson, 1967; Hanski, 1998; Kupfer, Malanson, & Franklin, 2006; Fahrig, 2013). Based on this approach, conservation strategies have been focused on the preservation of large remnants of natural vegetation, and, eventually, on enhancing the matrix to connect these areas through ecological corridors (Fischer & Lindenmayer, 2006). This paradigm, however, has been challenged by recent studies, emphasizing the importance of explicitly considering differences between land cover types, contrary to the simplistic classification of habitat and non-habitat (Boscolo, Ferreira, & Lopes, 2016). Classifying different land use types is important because species occurrence may be driven by ecological requirements of non-substitutable resources from different habitat types (landscape complementation) and by substitutable resources from more than two habitat types (landscape supplementation; Dunning, Danielson, & Pulliam, 1992). The degree of matrix permeability also differs among land cover types because of variation in provision of food resources, water, shelters, and the presence of stepping stones (Russel, Swihar, & Craig, 2007; Brady, Mcalpine, Possingham, Miller, & Baxter, 2011; Ferreira, Peres, Bogoni, & Cassano, 2018). Thus, the anthropogenic matrix is not uniformly inhospitable for survival and reproduction of many species, nor an impenetrable barrier to its movement and dispersal (Kupfer, Malanson, & Franklin, 2006; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013). Nevertheless, the matrix permeability varies from species to species, once landscape perception itself is species-traits dependent (Gehring & Swihart, 2003; Goheen, Swihart, Gehring, & Miller, 2003; Hansbauer, Storch, Knauer, Pimentel, & Metzger, 2010; Kellner, Swihart, Duchamp, & Swihart, 2019). In this regard, even patches of natural vegetation can differ in habitat quality due to natural variation or anthropogenic degradation, producing spatial heterogeneity within habitat patches (Mortelliti, Amori, & Boitani, 2010). Therefore, explicitly incorporating spatial heterogeneity gradients in landscape analysis approaches can improve our understanding of the relationship between species diversity and landscape/environmental conditions, leading to management and conservation strategies that combine natural environments and human land use in an integrated and functional

way (Fischer & Lindenmayer, 2006; Fahrig et al., 2011; Boscolo, Ferreira, & Lopes, 2016).

The intensity of anthropogenic land use is a primary concern for the conservation of terrestrial mammal worldwide (Pekin & Pijanowski, 2012). Mammalian species are highly diverse in terms of diet, trophic levels, body mass, and habitat use patterns, and are key components of tropical ecosystem (Paglia et al., 2012; Dirzo et al., 2014). Mammalian species richness has been shown to be sensitive to changes in landscape structure (Goheen, Swihart, Gehring, & Miller, 2003; Russel, Swihar, & Craig, 2007; Brady, Mcalpine, Possingham, Miller, & Baxter, 2011; Haddad et al. 2015; Melo, Sponchiado, Cáceres, & Fahrig, 2017; Regolin et al., 2017; Berl, Jacob, Kenneth, Elizabeth, & Robert, 2018), allowing the modeling of this diversity component using distinct scenarios of land use. Other components of species diversity, however, have different responses to environmental variation and change (e.g. Dornelas et al. 2014), but are understudied in comparison with alpha diversity (Mori, Isbell, & Seidl, 2018). Although measures of alpha diversity (such as richness, abundance, and occurrence probability) are the main response variables in most studies, recent research has shown that beta diversity (dissimilarity between communities) is an essential variable to understand the processes that shape assemblage differences (Baselga, 2010). The beta diversity reflects two different phenomena: turnover and nestedness. The turnover component measures species replacement between communities, whereas nestedness refers to a non-random process of species loss between communities (Baselga, 2010). Therefore, understanding how beta diversity varies within a spatially heterogeneous system can contribute to our understanding of landscape functioning (Mori, Isbell, & Seidl, 2018).

In this study, we assessed how mammalian communities are structured over heterogeneous fragmented landscapes, by combining analyses of landscape structure with measures of fine spatial heterogeneity. Specifically, we quantified the importance of coarse-scale measures of landscape structure with measures of within-habitat spatial heterogeneity in explaining mammal species richness, and the role of landscape variables in species compositional dissimilarity. We defined landscape composition as the amount of different land cover types present in the study landscapes, and landscape configuration as the spatial arrangement of landscape units (Villard & Metzger, 2014), while spatial heterogeneity was quantified using proxies of vegetation structural complexity (Wood, Pidgeon, Radeloff, & Keuler, 2012). We expected a positive relationship between species richness and landscape composition, configuration and spatial heterogeneity, with decreasing contributions from the former to the last respectively (Figure 1A). We also expected that β -diversity components (nestedness and turnover) would increase linearly with the differences among predictive variables between pairs of landscapes, with the same order of importance expected for species richness. Nestedness should be more strongly influenced by landscape differences than turnover due to deterministic losses of species more sensitive to environmental modifications (Figure 1B). Our expectations were based on the following assumptions: i) natural vegetation cover captures resource availability and environmental conditions that produce species occupancy (Fischer & Lindenmayer, 2007); ii) higher composition heterogeneity (diversity of land use types) increases the occurrence probability for species that use two or more vegetation types (landscape supplementation and complementation; Dunning, Danielson, Pulliam, 1992); iii) Landscape & supplementation and complementation also depend on landscape configuration, and are favored in patchy landscapes due to higher incidence of abrupt transitions between different land use types (edge areas; Fahrig, 2017); iv) edge areas have biotic and abiotic conditions that are different from both the matrix and the patch core region, with either positive or negative effects on species (Murcia, 1995; Berl, Jacob, Kenneth, Elizabeth, & Robert, 2018); and v) structural complexity is positively related to resource and shelter availability for both habitat patches and the matrix, and ultimately affect species movement capacity (Russel, Swihar, & Craig, 2007; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013).



Figure 1. Expected patterns between α (A) and β -diversity (B) of mammalian species and predictive variables of landscape composition, configuration and spatial heterogeneity in 20 heterogeneous fragmented landscapes in western Brazil.

Methods

Study areas

Our study was conducted on 20 landscapes located in Mato Grosso do Sul State, western Brazil, covering an area of 534,598 hectares. We distributed the landscapes across a gradient of seasonal Atlantic Forest, *Cerradão* and Cerrado *stricto sensu* cover (hereafter 'woody cover'), while also considering land use composition heterogeneity (Figure 2). The sampled landscapes are within an ecotonal region, with biogeographic influences from the Atlantic Forest, Cerrado and a small portion of the dry Chaco in the southwest. Both Atlantic Forest and Cerrado are biodiversity hotspots for conservation priorities (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Some landscapes are also biogeographically influenced by Amazon forest (Chiquitana forest). The study region is under constant anthropogenic pressure and has been undergoing intensive conversion of natural areas to anthropogenic land uses, especially croplands and pastures (Klink & Machado 2005; Roque et al., 2016). The deforestation ranges from 22,000 to 30,000 km²/year, which is higher than rates in Amazon (Klink & Machado, 2005).



Figure 2. Land use maps of 20 study landscapes in south-western Brazil where terrestrial mammals were studied to understand the effects of landscape composition (woody cover, landscape heterogeneity), configuration (edge density, patch density), and spatial heterogeneity (satellite image texture) on α - and β -diversity.

Mammal diversity data

We performed four field expeditions in April 2009, August 2009, May and June 2010, and July and August 2010. This effort was carried over 20 landscapes, distant from each other between 20 km to 634 km, yielding 20 independent samples of terrestrial mammal occurrence with body sizes varying from small (<1 kg) to large (Figure 2). On each expedition, we sampled mammals in five landscapes during five consecutive days and four nights using the following complementary methods: i) identification of vestiges, such as tracks (identified according to Angelo, Paviolo, Blanco, & Bitetti, 2008), feces, teeth, and others bones (bones were collected and compared to collection material for identification); ii) direct observation; iii) camera trapping; and iv) capture of small mammals with live traps. The sampling goal was not to estimate abundances, but to get a tally of species in each landscape for calculating species richness and composition.

For the first two methods, we performed walks on foot or by car at different periods of day and night, covering the different environments within each landscape. For the third method, we installed between 11 and 16 camera traps (Tigrinus®, Timbó, Santa Catarina State, Brazil) at 30-40 cm above the ground, in tree trunks of forest or Cerrado patches in each landscape. Cameras were placed on transect lines of 110 m in length containing two cameras in each extremity (in the border and in the interior of each forest fragment), operating 24 hours a day, during four consecutive days and nights. Transect lines were distant at least 150 m from each other (in small areas), but usually a minimum distance of 300 m was set. The total sampling effort was of 1,128 traps-night, with the mean effort per landscape being 56 ± 7 traps-night. We captured rodents and marsupials (<1 kg, Cricetidae, Echimyidae and Didelphidae families) using 65 wire (33x12x12 cm) and Sherman live-traps (30x9x7 cm). Traps were installed in forest ground (wire) and understory (Sherman), between 1.5 and 2 meters above the ground, during four consecutive nights, totaling 6,800 trap-night overall and 340 trapsnight per landscape. We baited the traps with a mixture of pumpkin, bacon, peanut butter and cod liver oil. In each landscape, we installed the traps along transects between the camera trap sampling points, 10 m apart from each other in the same transect, separated at least 150 m from each other transect line and at least 20 m from the nearest patch edge. Captured animals were identified and subsequently released. When necessary, we collected voucher specimens for identification, which were deposited in the mammalian collection of the Universidade Federal de Santa Maria (UFSM).

Land use and land cover maps

We generated an 8-km buffer around the camera trap sampling points within each landscape to delimit landscape extent. We chose this extent based on previous studies reporting landscape structure effects on small-, medium- and large-sized mammal assemblage composition within the Atlantic Forest (e.g., Lyra-Jorge, Ribeiro, Ciocheti, Tambosi, Pivello, 2010; Beca et al. 2017; Melo, Sponchiado, Cáceres, & Fahrig, 2017; Regolin et al. 2017), as well as to avoid spatial overlap (Jackson & Fahrig, 2015). We mapped land cover for each landscape using orthorectified images from the RapidEye satellite constellation, with 5m spatial resolution. Images were selected preferably from the dry season, due to lesser cloud cover and greater contrast between land use classes (47 images acquired between January 2011 and August 2013). Image processing was performed over all five spectral bands (blue, green, red, red edge and near infrared) and included: i) atmospheric correction using the 'Quick Atmospheric Correction – QUAC' algorithm implemented in the ENVI 5.0 software and ii) unsupervised classification using the 'Auto Class' software (github.com/JohnWRRC). Auto Class uses the GRASS function 'i.segment' to generate image segments and the K-means Clustering function of the 'foreign' R package (R Core Team, 2017) to group the segments into classes according to the mean and standard deviation of pixel values. We then converted this unsupervised map into a thematic classification by supervised visual interpretation and manual editing, based on image visualization at 1:2,500 cartographic scale, generating a final map with 11 classes (Figure 2).

Landscape structure metrics

The produced land cover maps in raster format were used as inputs for landscape structure metric calculations. We used the 'raster' R package (Hijmans, 2017) to load the raster data and define custom functions to calculate the following landscape structure metrics: (i) woody cover — percent woody (forest plus cerrado) cover in the landscape, (ii) patch density — ratio between the number of woody patches and total landscape area, (iii) edge density — ratio between area of woody patch edges and landscape area, and (iv) landscape diversity — Shannon index for mosaic of patches including all cover types. Woody cover and landscape diversity are used as measures of woody habitat composition, whereas edge density and patch density are measures of woody habitat configuration (Villard & Metzger, 2014).

Within-habitat spatial heterogeneity

We estimated within-habitat spatial heterogeneity by calculating image texture measures from the normalized difference vegetation index (NDVI). NDVI is a spectral index sensitive to photosynthetically active vegetation, which is related to plant biomass productivity (Justice et al., 1998). We calculated NDVI using the red and near-infrared spectral bands of RapidEye images (5-m spatial resolution) using the 'spatial.tools' R package (Greenberg, 2018). Image textures are statistical descriptors of the spatial relationship among pixel values within an image region, thus capturing spatial heterogeneity (St-Louis et al. 2009; 2014). When calculated using NDVI, texture therefore represents spatial variability in photosynthetically active vegetation within a given area (Wood, Pidgeon, Radeloff, & Keuler, 2012). Texture measures calculated from high resolution images have been related with descriptors of vegetation heterogeneity such as leaf-area index and foliage height diversity (Colombo, Colombo, Bellingeri, Fasolini, & Marino, 2003; Wood, Pidgeon, Radeloff, & Keuler, 2012). Particularly, textures can yield larger explanatory power for species richness than classified images because it captures fine-scale variability within coarse habitat classes in areas of gradual transition between vegetation types (St-Louis et al. 2009; Wood, Pidgeon, Radeloff, & Keuler, 2013).

We calculated 12 texture measurements from NDVI, using the 'r.texture' GRASS GIS function, being seven first order metrics: (i) sum average, (ii) entropy, (iii) difference entropy, (iv) sum entropy, (v) variance, (vi) difference variance, (vii) sum variance; and five second-order metrics based on a pairwise matrix of spatial relationships among pixels (grey-level co-occurrence matrix; Haralick, 1979), (viii) angular second moment, (ix) inverse difference moment, (x) contrast, (xi) correlation, and (xii) information measures of correlation. Each texture was calculated in four directions (0, 45, 90 and 135 degrees) considering a central pixel and its neighbors within the specified window, and then average of texture metrics were calculated to summarize all directions. We derived textures using four different moving window sizes on each pixel (3x3, 5x5, 7x7 and 9x9 pixels of 5m).

Data analysis

We first evaluated potential spatial autocorrelation and multicollinearity among explanatory variables (Supplementary material Appendix 1, Figs. A1, A2 and A3), and then selected seven uncorrelated predictive variables ($|\mathbf{r}| < 7$, as suggested by Dormann et al., 2013); two representing woody habitat composition: wood cover and landscape diversity; two representing woody habitat configuration: edge density and patch density; and three representing within-habitat spatial heterogeneity (texture measurements): correlation, sum entropy and difference entropy of the 3x3 moving window size that represents more local environmental information (Table 1).

Table 1.	Descr	ription of	the	seven r	non-correlated	predicti	ve variab	les of	f landscaj	pe s	structure
measure	nents	assessed	to	explain	mammalian	species	richness	and	changes	in	species
composit	ion in	20 fragm	ente	d landsca	apes in wester	n Brazil.					

Metric type	Landscape	Landscape metric description			
	metric name				
Landscape	Woody cover	Percentage of Atlantic Forest, Cerradão and Cerrado			
composition		stricto sensu in the landscape area.			
	Landscape	Shannon index for mosaic of patches including all cover			
	diversity	types.			
Landscape	Edge density	Ratio between area of woody edges and landscape area.			
configuration					
	Patch density	Ratio between the number of patches of woody and total			
		landscape area.			
Within-habitat	Correlation	Linear dependency of pixel values on those of			
spatial		neighboring pixels (Haralick 1973, Wood, Pidgeon,			
heterogeneity		Radeloff, & Keuler, 2012).			
	Sum entropy	Entropy is the system level disorder. The greater the			
		entropy, the greater the heterogeneity. Measures the			
		disorder related to the gray level-sum distribution of the			
		image (Haralick 1973, Wood, Pidgeon, Radeloff, &			
		Keuler, 2012).			
	Difference	Measures the disorder related to the gray level			
	entropy	difference distribution of the image (Haralick 1973,			
		Wood, Pidgeon, Radeloff, & Keuler, 2012).			

Mammal species richness– We fitted generalized additive models (GAMs) to quantify how mammalian species richness relate to heterogeneous fragmented landscapes, using the 'gam' function of the 'mgcv' R package (Wood, 2011) and assuming a Poisson distribution for count data (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We choose GAMs as they are able to capture non-linear and linear effects (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We computed seven univariate models, each including one of the four landscape structure metrics or the three spatial heterogeneity variables as predictors. We also included a null model representing a neutral response of richness to landscape structure (intercept only), totalizing eight competing models. We then compared the set of models using Akaike's Information Criterion corrected for small samples (AICc), to select the best explanatory model using the 'Ictab' function of the 'bbmle' R package (Bolker & R Development Core Team, 2017). All models with Δ AICc <2 were considered equally plausible to explain the patterns, i.e., a given landscape predictor influences species richness as much as the other included on best model list (Burnham & Anderson, 2002). We evaluated model weight (*w_i*) of plausible models as a proxy of predictor importance, since model weight can be interpreted as the probability of a model to be the best among competing models (Wagenmakers & Farrell, 2004). We also reported deviance explained to access model fit.

 β -diversity–We estimated total β -diversity and partitioned it in two components - turnover and nestedness - using a presence-absence assemblage matrix as input to the 'beta.pair' function of the 'betapart' R package (Baselga, 2010; Baselga & Orme, 2012). Total β -diversity was calculated as Sorensen's dissimilarity index (β_{sor}), turnover as Simpson dissimilarity index (β_{sim}), and nestedness (β_{nes}) as the difference between total β -diversity (β_{sor}) and turnover (β_{sim}). We used a multivariate linear regression (' –MRM) (Linchstein, 2007) using the dissimilarities matrices (beta diversity components), using the 'adonis' function of the 'vegan' R package (Oksanen et al., 2017) with 9,999 permutations to test the effect of predictive variables (landscape structural metrics and spatial heterogeneity) on β -diversity measures (turnover and nestedness). We considered that predictors affected beta diversity components where the significance levels of the coefficients were equal or lower than 0.05. We calculated the adjusted coefficient of multiple determination (\mathbb{R}^2), which is the ratio of the sum of squares of distances of the estimated values to the mean, to the sum of squares of distances of the original response variable values to the mean — adjusted by the numbers of degrees of freedom of the numerator and denominator of the coefficient of multiple determination (Legendre & Legendre, 2012). We opted to analyze the effect of the landscape on beta diversity through a frequentist approach - evaluating the p-value and the R² - as recent research has criticized the use of model selection for multivariate data on genetics and beta diversity (Franckowiak et al., 2017; Rocha et al., 2019)

Results

Overview

We recorded a total of 48 species of terrestrial mammals from 20 families and nine orders (Supplementary material Appendix 1, Table A1). Species richness per landscape ranged from eight to 25 (16 ± 4 ; mean \pm sd). The richest groups registered were rodents and carnivores, both with 12 species, followed by marsupials, with eight species. We recorded six ungulates, of which the most frequently were brocket deers (*Mazama gouazoubira* and *M. americana*) and the lowland tapir (*Tapirus terrestris*). The yellow bearded capuchin (*Sapajus cay*) was frequently detected, while three other primate species were rarely recorded. Regarding Xenarthra, we recorded three species of armadillos and two of anteaters. Finally, we verified the occurrence of the tapeti rabbit (*Sylvilagus brasiliensis*) in most studied landscapes.

Landscape structure influence on mammal richness

Among the set of eight competing models, three were equally plausible to explain species richness (Table 2): landscape configuration – edge density ($\Delta AICc = 0.0$; $w_i = 0.374$), spatial heterogeneity – sum entropy ($\Delta AICc = 0.3$; $w_i = 0.316$), and landscape composition – woody cover ($\Delta AICc = 1.1$; $w_i = 0.211$). We found a positive linear relationship between species richness and landscape configuration – edge density (Figure 3A) and also for spatial heterogeneity – sum entropy (Figure 3B). In addition, we also observed a positive relationship of woody cover on species richness below 30% of woody cover, with no effect above this threshold (Figure 3C).

Table 2. Set of eight competing univariate models to explain mammalian species richness in 20 fragmented landscapes in western Brazil. Two models refer to landscape composition (woody cover, landscape heterogeneity), two to habitat configuration (edge density, patch density), three to spatial heterogeneity (correlation, sum entropy, and difference entropy), and a null model with intercept-only that represents absence of effect. Model selection statistics include: Δ AIC is the relative difference in AIC values compared with top-ranked model; K is the number of parameters; w_i is the AIC model weight; and Deviance explained is proportion of null deviance explained by the model.

Model	ΔAICc	K	Wi	Deviance explained
Landscape configuration (edge density)	0.0	2	0.374	38.7%
Spatial heterogeneity (sum entropy)	0.3	2	0.316	37.1%
Landscape composition (woody cover)	1.1	4.04	0.211	61.9%
Landscape composition (landscape heterogenity)	4.4	2	0.041	17.7%
Spatial heterogeneity (correlation)	5.4	2.73	0.025	22.5%
Null	5.7	1	0.021	<< 0.0001%
Landscape configuration (patch density)	7.6	2	0.008	2.84%
Spatial heterogeneity (difference entropy)	8.8	2.78	0.004	7.26%



Figure 3. Best-supported models for explaining mammalian species richness in heterogeneous fragmented landscapes of western Brazil: (A) landscape configuration (edge density), (B) spatial heterogeneity (sum entropy), and (C) landscape composition (woody cover). Green shading is the confidence interval.

Patterns of β -diversity

Total β -diversity was composed mainly by turnover (0.78±0.13 sd) with a small proportion of nestedness (0.22±0.10 sd). Nestedness (β_{nes}) was driven by spatial heterogeneity (sum entropy), landscape configuration (edge density), and landscape composition (landscape heterogeneity and woody cover) – see Table 3 and Figure 4. Turnover (β_{sim}) was not explained by any predictive variable.

Table 3. Coefficients of determination (\mathbb{R}^2) using Multiple Regression on distance Matrix for each predictive variable to explain β diversity components (turnover and nestedness) of mammalian communities within twenty fragmented landscapes of western Brazil. Significant pvalues (<0.05) are in bold.

Prodictivo variables	β diversity	
redetive variables	Nestedness (β_{nes})	Turnover (β_{sim})
Landscape composition		
Woody cover	0.278 (p=0.025)	0.052 (p=0.475)
Landscape heterogeneity	0.314 (p=0.028)	0.075 (p=0.233)
Landscape configuration		
Patch density	0.023 (p=0.438)	0.069 (p=0.286)
Edge density	0.412 (p=0.008)	0.023 (p=0.821)
Spatial heterogeneity		
Correlation	0.176 (p=0.10)	0.040 (p=0.574)
Sum Entropy	0.565 (p<0.001)	-0.037 (p=0.998)
Difference Entropy	0.097 (p=0.243)	0.032 (p=0.709)

Discussion

Species assemblage in heterogeneous fragmented landscapes of tropical ecosystems are shaped by many ecological processes acting simultaneously. Consequently, identifying the main drivers of changes in mammalian species richness (α -diversity) and variation in communities' composition (β -diversity) is challenging (Mori, Isbell, & Seidl, 2018). Our results contradicted our expectations; landscape configuration (edge density) was the main driver of species richness, followed by spatial heterogeneity (sum of entropy) and landscape composition (woody cover). The order of importance of predictive variables explaining β -diversity was also different from our expectations; loss of species between communities (β_{nes}) was driven mainly by spatial

heterogeneity (sum of entropy), followed by landscape configuration (edge density) and landscape composition (woody cover and landscape heterogeneity). In accordance to our third prediction, β_{nes} responded more strongly than β_{sim} to differences in predictive variables.

Although several studies have reported that landscape composition – especially the amount of natural vegetation – as the main drivers of biodiversity patterns (Fahrig, 2013), the role of landscape configuration [such as fragmentation *per se* (Fahrig, 2003)] beyond the effect of landscape composition has been recently debated. While some studies highlight the predominant effect of habitat amount (Fahrig, 2003; 2013), others advocate that habitat configuration has an important additional effect on biodiversity (Villard & Metzger, 2014; Hanski, 2015; Fletcher-Jr et al., 2018). Furthermore, some authors also advocate that the effects of habitat fragmentation and loss on biodiversity are mediated by habitat quality (Kupfer, Malanson, & Franklin, 2006; Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013). We corroborate here the importance of habitat quality by showing how spatial heterogeneity in fragmented landscapes strongly contributes to explain mammalian species richness and changes in species composition.



Figure 4. Relationship between mammalian species nestedness and (a) spatial heterogeneity (sum entropy), (b) landscape configuration (edge density), (c) landscape composition (landscape heterogeneity), and (d) landscape composition (woody cover) in heterogeneous fragmented landscapes of western Brazil. Blue shading is the confidence interval. The x-axes represent absolute differences in explanatory variables.

Reliability of field data

Although a higher sampling effort on each landscape would decrease our variability resulting in a smaller error in species detection, a larger sample size (more landscapes) would result in a higher statistical power by increasing our degrees of freedom. We choose to increase sample units in detriment of a larger sampling effort in each landscape considering that the predictors (landscape metrics and measurements of spatial heterogeneity) were logistical easier and financial cheaper to measure than the response variable (Fahrig, 2005). In this way, we were able to sample 20 independent landscapes, which is a high number of independent sample units in comparison to other studies sampling mammals at landscapes scale (see examples in the review of Presley, Cisneros, Klingbeil, & Willig, 2019). Although our sampling effort in each landscape could limit the detection of rare or cryptic species, we used an equal sampling effort along the landscapes, so we consider our results are not bias and represent the relationship of the most representative local mammal species and landscape patterns.

Habitat composition influence

Species richness was positively associated with landscape configuration and spatial heterogeneity, but the relationship with percent woody cover was nonlinear. Richness was positively influenced by woody cover up to approximately 30% of total cover, followed by a slow decline of species above this threshold. This pattern is consistent with empirical studies showing similar thresholds of species diversity, where decreases of habitat amount result in abrupt decreases of species richness (e.g., Radford, Benett, Cheers, 2005; Banks-Leite et al., 2014; Ochoa-Quintero, Gardner, Rosa, Ferraz, & Sutherland, 2015). Our results indicate that, for landscapes below this 30% threshold, increasing native vegetation cover must be the main strategy to improve mammal diversity.

Woody cover, which we expected to be the strongest predictor of β -diversity, had the weakest effect on species richness and β_{nes} . The contribution of landscape composition to explain species richness and loss of species between communities seems to be larger in other landscapes with ample differences in habitat amount (e.g., 5-95%) and low landscape use diversity. An example is the study by Beca et al. (2017), who related mammals occurrence and richness to measures of landscape structure of forest patches immersed in a homogeneous matrix of biofuel plantation within the Brazilian Atlantic Forest. However, our study had a limited range of variation in habitat amount (5-55%) and higher heterogeneity of both native vegetation and matrix components than Beca et al. (2017), who classified land use types in two classes, forest and matrix. Therefore, the simpler view that habitat amount can alone support landscape management is unlikely to be applicable to heterogeneous landscapes under intense anthropic use in tropical ecosystems.

The positive relationship between landscape heterogeneity (Shannon index) and β_{nes} , which reflects natural and human land use diversity, refers to the processes of landscape complementation and landscape supplementation (*sensu* Dunning, Danielson, & Pulliam, 1992). The former occurs when species persistence depends on nonsubstitutable resources that are available in two or more different habitat types. For example, the crab-eating raccoon (Procyon cancrivorus) feeds in water bodies and shelters in the forest interior. On the other hand, landscape supplementation exists when species occurrence is favored by the provision of substitutable resources in different habitat types. It occurs, for example, when jaguars (Panthera onca) and pumas (Puma concolor) prey on cattle and sheep livestock in addition to wild mammals. Therefore, mammalian species loss can be related to a lack of structurally complex matrices where species can find complementary or supplementary resources. However, species-specific responses to landscape structure must be noted (Goheen, Swihart, Gehring, & Miller, 2003; Hansbauer, Storch, Knauer, Pimentel, & Metzger, 2010) and, consequently, effects of landscape composition may vary according to species traits (e.g., niche breadth and mobility; Kellner, Swihart, Duchamp, & Swihart, 2019) and temporal variation in matrix structure (e.g., crop cycles within agriculture matrix; Berl, Jacob, Kenneth, Elizabeth, & Robert, 2018).

Habitat configuration effects

Our results go beyond the paradigms of habitat composition, and evidence the role of the configuration of natural vegetation patches for the maintenance of species richness. We found a positive relationship between edge density and the number of mammalian species, which suggests a positive effect of habitat fragmentation *per se* (Fahrig, 2003). Our studied system encompassed a range of small to intermediate proportions of woody cover, where the variation in possibilities of landscape configuration is highest (Villard & Metzger, 2014), possibly increasing the influence of

landscape configuration on species richness. The positive response of species richness and β_{nes} to landscape configuration (edge density) is also related to the processes of landscape complementation and landscape supplementation (*sensu* Dunning, Danielson, & Pulliam, 1992), which depend on landscape configuration (Fahrig, 2017). Species movement among land cover types is favored in patchy landscapes due to decreased distances between each land use type. Nonetheless, movement decisions also depend on vegetation structure similarity among natural vegetation and matrix (Russel, Swihar, & Craig, 2007; Berl, Jacob, Kenneth, Elizabeth, & Robert, 2018).

Within-habitat spatial heterogeneity matters

The relationship between spatial heterogeneity (sum entropy) and both α - and β diversity results from deterministic losses of the most sensitive species due to reduction in vegetation structural complexity within both native vegetation patches and anthropogenic matrices. Larger vegetation structural complexity within habitat patches increases niche availability, and consequently, patch capacity to host high species diversity (Brady, Mcalpine, Possingham, Miller, & Baxter, 2011). Furthermore, high similarity between patch and matrix vegetation structure favors species movement through the landscape (Kupfer, Malanson, & Franklin, 2006). By providing habitat breeding and food resources, the anthropogenic matrix can guarantee (re)colonization of habitat patches by species, increasing population size and reducing the risk of extinction (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013). For example, polyculture and agroforestry systems are wildlife-friendly matrices, as they are more structurally complex than pasturelands, intensive cereal cropping, and other annual monocultures, which in turn erode mammal diversity (Ferreira, Peres, Bogoni, & Cassano, 2018).

Previous studies have shown that within-habitat spatial heterogeneity, measured using image texture measures, explain bird species richness in ecosystems where vegetation heterogeneity is high and transitions between land-use classes are gradual (St-Louis et al. 2009; Wood, Pidgeon, Radeloff, & Keuler, 2013). Within-habitat spatial heterogeneity also drives compositional variation of tropical anuran communities (Sugai, Sugai, Ferreira, & Silva, 2019). In contrast, our study region comprises a set of landscapes that vary in the amount of woody cover and in the diversity of land uses, with sharp boundaries delineating the different land cover types. Therefore, even in a region characterized by less diversity of vegetation formations, spatial heterogeneity

played an important role in shaping the patterns of species diversity, possibly reflecting the availability of resources, shelters and structures that favor dispersal. Qualitative thematic mapping obscures differences in landscape structure that are potentially essential to species survival, and land cover mapping procedures are susceptible to subjective bias and errors in image segmentation (the delineation of boundaries of landscape units) and classification (St-Louis et al., 2009).

Concluding remarks

As far as we know, this is the first study that reports the role of landscape spatial heterogeneity as one of the main drivers on mammals assemblages. The effects of spatial heterogeneity on human-modified landscapes will be better understood by calculating texture metrics per land cover type. Thus, it will be possible to distinguish the effects of spatial heterogeneity by land cover types, i.e. "functional heterogeneity" framework proposed by Boscolo et al. (2016).

The effects of spatial heterogeneity and habitat configuration overcame the influence of habitat composition on alpha and beta mammal diversity in heterogeneous fragmented landscapes within western Brazil. Patch configuration may influence species movement and, consequently, habitat (re)colonization rates. Vegetation structural complexity in the anthropogenic matrix may also affect species movement, as it defines the matrix capacity to provide breeding and food resources. Therefore, landscape composition alone should not be used to support landscape management strategies aimed at mammalian conservation, that should also include strategies to preserve and improve vegetation structural complexity in both habitat patches and the matrix, enabling landscapes to harbor high species diversity by increasing niche availability.

Declarations

Permits - Data collection followed ASM guidelines (Sikes, 2016) and was authorized by the Brazilian biodiversity conservation institute (SISBIO License #1131-1, #1401-1, #2203-1, #2383 -8).

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Supplementary information

Spatial autocorrelation–We evaluated spatial autocorrelation between species assemblage composition and landscape geographic coordinates applying the Mantel test (Fortin and Dale 2009) using the 'mantel' function of the 'vegan' R package (Oksanen et al. 2017). Spatial correlation was weak (r=0.224; P-value=0.014), indicating a low level of spatial autocorrelation (Fig. S1).



Figure S1. Correlation between mammalian assemblage and landscapes locations. Spatial correlation was negligible (r=0.224; P-value=0.014).

Multicollinearity–We evaluated multicollinearity of predictive variables using Pearson's correlation, considering less correlated variables where absolute r < 0.7. We verified high correlation between the four sizes of moving windows for all the twelve NDVI texture measurements. Thus, we only used textures computed with the 3x3 window size for subsequent analysis, and performed a second round of correlation analysis among all textures calculated with this extent. As expected, we found that just three of the twelve texture measurements were poorly correlated: correlation, sum entropy, and difference entropy (Fig. S2). In a third round of correlation analysis, we compared the three non-correlated texture measurements with the four landscape

metrics and found no correlation between them (Fig. S3). Thus, we selected seven uncorrelated predictive variables, two representing landscape composition (woody cover and landscape heterogeneity) two representing landscape configuration (edge density, and patch density) and three representing spatial heterogeneity (texture measurements of correlation, sum entropy and difference entropy, Table 1).

	4.0 5.0 6.0 7.0)	0.38 0.41 0.44		0.86 0.90 0.94		0.75 -0.65		0.55 0.58		3.5 4.0 4.5	
Angular Second Mament	0.91	0.16	0.71	0.99	1.00	0.98	0.97	0.96	0.97	0.94	0.93	0.12 0.15
**************************************	Contrast		0.83	0.93	0.93	0.97	0.95	0.96	0.85	0.96	0.98	
• • • • • • • • • • • • • • • • • • •	**************************************	Correlation	0.58		0.16		0.21	0.19	0.37	0.21	2.5	0.00 0.10
0.38 0.42 • • • • • •	••••••••••••••••••••••••••••••••••••••			0.79	0.71	0.76	0.66	0.67	0.54	0.65	0.69	
o o partico o stati	·**•		°°°,°°°,°°,°°,°°,°°,°°,°°,°°,°°,°°,°°,°	Difference Variance	0.99	0.98	0.95	0.95	0.94	0.92	0.92	008 0.018
0.086 0.92		· • • • • • • • • • • • • • • • • • • •	· · · · · · · ·	·	Entropy	0.99	0.99	0.98	0.97	0.96	0.96	•
· · · · · · · · · · · · · · · · · · ·	··••••••••••••••••••••••••••••••••••••		°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°		· · · · · · · · · · · · · · · · · · ·	Inverse Difference Moment	0.99	0.99	0.94	0.98	0.98	30 0.40
9-0-0-0-0-0-0-0-0-0-0-0-0-0-0-0-0-0-0-0	···*• · · · · · · · · · · · · · · · · ·	• • • • • • •	°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°		*		rmation Measures of Correla	1.00	0.96	0.99	0.99	0
ب موجود م		**************************************		`` `**`		° •••••	° • • • • •	Sum Average	0.95	1.00	0.99	6.5 7.5
0.55 0.55 0.55 0.59 0.59	•••••••	******* ******	。 。 **** * * **** *	° •••• • • • •	Son and Son	° ••••••••••••••••••••••••••••••••••••	**************************************	,	Sum Entropy	0.93	0.91	
***. **.	°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°°	° °** ° 8°° ° ° °		° °*°°	et a contraction of the contract	° • •?»	°.,			Sum Variance	1.00	45 60
0.12 0.14 0.16	, , , , , , , , , , , , , , , , , , ,	0.00 0.10		008 0.014 0.020		.30 0.36 0.42	°*, ,	6.5 7.5	، سرم ای او او او	45 55 65	Variance	

Figure S2. Scatter plot matrices of correlation between twelve measurements of spatial heterogeneity. The diagonal panels present the frequency histograms of data distribution. The upper panels show the value of the Pearson correlations among metrics. Lower panels include the point plots with data for the pairs of metrics. Three of twelve texture measurements are not correlated: correlation, sum entropy and difference entropy.

		0.38 0.40 0.42 0.44		-2.6 -2.2 -1.8 -1.4		0.010 0.020		
	Correlation	0.58	0.37	0.25	0.65	0.23		0.00 0.10
0.38 0.41 0.44	· · · · · · · · · · · · · · · · · · ·	Difference Entropy	0.54	0.55	0.34	0.28	0.12	
-	**************************************	· · · · · · · · · · · · · · · · · · ·	Sum Entropy	0.34	0.29	0.54	0.19	00'N 60'N
-2.6 -2.0 -1.4	° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° °			Patch density (log10)	0.30	0.66	0.27	
	• • • • • • • • • • • • • • • • • • •				Woody cover	0.38	0.39	0.0 0.0 1.0
0.010 0.020	- °°° - °°° - °°°° - °°°°°		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° °	° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° ° °	Edge density	151	
	0.00 0.05 0.10		0.55 0.57 0.59		0.1 0.2 0.3 0.4 0.5		Landscape heterogeneity	4.1 0.1 0.0

Figure S3. Scatter plot and correlation between three measurements of spatial heterogeneity and four metrics of landscape structure. The diagonal panels present the frequency histograms of data distribution. The upper panels show the value of the Pearson correlations among paired metrics. Lower panels include the scatterplots with data for the pairs of metrics.

Mammalian species check list

Table S1. Check list of mammalian species detected in 20 heterogeneous fragmented landscapes in south west Brazil.

Order	Family	Genus	Species
Artiodactyla	Tayassuidae	Pecari	Pecari tajacu
		Tayassu	Tayassu pecari
	Cervidae	Blastocerus	Blastocerus dichotomus
		Mazama	Mazama americana
			Mazama gouazoubira
Carnivora	Felidae	Leopardus	Leopardus pardalis
		Panthera	Panthera onca
		Puma	Puma concolor
			Puma yagouaroundi
	Canidae	Cerdocyon	Cerdocyon thous
		Chrysocyon	Chrysocyon brachyurus
		Lycalopex	Lycalopex vetulus
	Mustelidae	Eira	Eira Barbara
		Pteronoura	Pteronura brasiliensis
		Lontra	Lontra longicaudis
	Procyonidae	Nasua	Nasua nasua
		Procyon	Procyon cancrivorus
	Dasypodidae	Dasypus	Dasypus novemcinctus
		Euphractus	Euphractus sexcinctus
		Cabassous	Cabassous tatouay
Didelphimorphia	Didelphidae	Didelphis	Didelphis albiventris
		Gracilinanus	Gracilinanus agilis
		Marmosa	Marmosa murina
		Marmosops	Marmosops ocelatus
		Micoreus	Micoreus constantiae
		Monodelphis	Monodelphis domestica
		Philander	Philander opossum
		Thylamys	Thylamys macrurus
Lagomorpha	Leporidae	Sylvilagus	Sylvilagus brasiliensis
Perissodactyla	Tapiridae	Tapirus	Tapirus terrestris
Pilosa	Myrmecophagidae	Myrmecophaga	Myrmecophaga tridactyla
		Tamandua	Tamandua tetradactyla

Order	Family	Genus	Species
Primates	Cebidae	Sapajus	Sapajus cay
	Atelidae	Alouatta	Alouatta caraya
	Pitheciidae	Callicebus	Callicebus pallescens
	Aotidae	Aotus	Aotus azarae
Rodentia	Caviidae	Hydrochoerus	Hydrochoerus hydrochaeris
	Dasyproctidae	Dasyprocta	Dasyprocta azarae
	Cuniculidae	Cuniculus	Cuniculus paca
	Echimyidae	Proechimys	Proechimys longicaudatus
		Thrichomys	Thrichomys pachyurus
	Sigmodontinae	Akodon	Akodon montensis
		Cerradomys	Cerradomys scotti
		Hylaeamys	Hylaeamys megacephalus
		Oecomys	Oecomys bicolor
		Rhipidomys	Rhipidomys macrurus
		Oligoryzomys	Oligoryzomys sp.
		Calomys	Calomys sp.

Reference

Fortin, M. J., & Dale, M. R. T. (2009). Spatial autocorrelation in ecological studies: A legacy of solutions and myths. Geographical Analysis, 41, 392–397. https://doi.org/10.1111/j.1538-4632.2009.00766.x

Capítulo 3

Less but better: interaction between the amount and quality of habitat drives mammalian habitat use in the Brazilian Pantanal [†]

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[†] Este capítulo encontra-se em processo de revisão na Landscape Ecology.

Abstract

Context An understanding of species-habitat relationships is required to assess the impacts of habitat fragmentation and degradation. To date, habitat modeling in fragmented landscapes has relied on landscape composition and configuration metrics and the importance of habitat quality in determining species distributions has not been sufficiently explored.

Objectives We evaluated how habitat use by herbivores and frugivorous mammals is shaped by an interaction of habitat amount and quality in the Brazilian Pantanal wetland. We also assessed if the contribution of habitat quality to species' habitat use varies according to the species sensitivity to habitat loss.

Methods We combined mammal detection data obtained from camera traps with thematic maps to estimate the amount of habitat and measured habitat quality using local environment variables and distance to waterbodies. We fitted univariate, additive, and interactive occupancy models to evaluate the relative support of each model and estimate species-specific occupancy and detection probabilities associated with various habitat features.

Results Habitat quality was more important than habitat amount in determining species habitat use (occupancy) in a naturally fragmented landscape. Habitat quality alone was the best predictor of habitat use for four of the six species, but no species' habitat use was explained solely by habitat amount. Habitat amount was influential only when considered in conjunction with habitat quality covariates and only for species that are more sensitive to habitat modification. The less sensitive species were better modeled by habitat quality covariates alone.

Conclusions Conservation programs should incorporate both habitat quality and amount when dealing with sensitive species and prioritize habitat quality management when focusing in less sensitive species.

Keywords

Artiodactyla, habitat modeling, habitat degradation, wetland, Perissodactyla, Rodentia
Introduction

The continual conversion of natural areas to anthropogenic land-use is a primary threat to biodiversity worldwide (Hansen et al. 2013). An understanding of species-habitat relationships is required to predict the impact of land-use change and inform species conservation and management actions (Fahrig 2003; Desbiez et al. 2009a; Lindenmayer and Fischer 2007). To date, habitat modeling in fragmented landscapes has relied on landscape composition and configuration metrics based on the patch-corridor-matrix and heterogeneous mosaic theoretical frameworks (Boscolo et al. 2016; Presley et al. 2019). Some authors have argued that the diversity of landscape effects on biodiversity can be explained simply by the amount of habitat in the landscape (Fahrig 2013). However, the importance of habitat quality and its relationship to habitat amount has not been sufficiently explored (Mortelliti et al. 2010). There is a growing interest in this topic because improving local habitat quality in remaining patches may be a promising solution in areas where increasing native vegetation cover is not viable (Baguette et al. 2013).

Species distributions in fragmented landscapes are driven by multiple, dependent ecological processes acting simultaneously (Lindenmayer and Fischer 2007; Fahrig 2017). Thus, a species' habitat use is shaped by a tradeoff between costs (e.g., energy spent to move, avoid predation and competition) and benefits (e.g., availability of food resources, water, salt, and breeding habitat) (Driscoll et al. 2013). Previous studies have shown positive effects of habitat amount on mammalian species occurrence and richness (Melo et al. 2017; Regolin et al. 2017). However, these results may be overly simplistic and/or biased, because habitat amount does not equate to habitat quality (Lindenmayer and Fischer 2007). Habitat amount is the total area covered by a specific habitat type within the landscape (Fahrig 2013; e.g., vegetative or land-cover types), and habitat quality is the ability of the environment to provide adequate resources and conditions for the survival of individuals and persistence of populations (Hall et al. 1997; e.g., food availability).

Measurements of landscape structure based on human perspectives of land-cover types are suitable to estimate the amount of habitat in a landscape (Fischer and Lindenmayer 2007; Fahrig 2013). However, this approach fails to clarify the role of habitat quality in species occurrence or persistence as it implies homogeneity within land-cover classes (St-Louis et al. 2009, 2014, Regolin et al. 2020). Natural

heterogeneity in vegetation structure and anthropogenic degradation lead to variation in biotic and abiotic habitat conditions that define habitat quality (Mortelliti et al. 2010), and its importance in predicting species distributions has been demonstrated for marsupials and rodents (Holland and Bennett 2007), primates (Willems et al. 2009), artiodactylans (Winnie-Jr et al. 2008), carnivores (Brady et al. 2011), xenarthrans (Santos et al. 2016), and birds (St-Louis et al. 2009, 2014; Wood et al. 2013). In patchy landscapes, habitat selection involves both the amount and the quality of habitat patches (Mortelliti and Boitani 2008; Gardiner et al. 2018; Costa-Araújo et al. *In press*) and varies among species (Kellner et al. 2019). An essential conservation challenge is to understand the interaction between these landscape features for species with different landscape perception (*sensu* Goheen et al. 2003; Hansbauer et al. 2010). Assessing the mechanisms driving habitat selection is important for designing effective conservation and management actions, particularly for endangered species that may be restricted in range due to habitat loss and/or degradation (Fischer and Lindenmayer 2007; Fahrig 2003).

Brazilian Pantanal is a naturally fragmented landscape covered mainly by native grasslands interspersed by patches of woody vegetation - forest and dense shrubland (Pott and Silva 2015). High vegetation productivity is driven by a seasonal flood regime, which allow for an abundance of wildlife, including stable populations of species that are threatened in other biomes (Alho 2008) such as, the lowland tapir, Tapirus terrestris (Trolle et al. 2008) and the white lipped peccary, Tayassu pecari (Keuroghlian and Eaton 2009). There are few protected areas in the Pantanal as most of the land (95%) is privately owned and operated as cattle ranches; the main economic activity in the region for the last two centuries (Harris et al. 2005). The cattle graze on natural grasslands and find complementary food sources in woody vegetation patches (e.g., fruits and leaves), which also provide relief from the hot temperatures found in the grasslands. Within woody vegetation patches, cattle also degrade the habitat of native mammal species by trampling plant seedlings and shrubs that are important food resources (Desbiez et al. 2009a). To improve cattle productivity, native vegetation has been recently replaced by pastures of exotic, invasive African grasses (*Brachiaria* spp.); however, the magnitude of the effects of habitat degradation and habitat loss on native species in Pantanal have not been well documented (but see Desbiez et al. 2009a; Dourado-Rodrigues et al. 2015; Eaton et al. 2017; Silveira et al. 2018). Although the sustainability agenda for the Pantanal proposed by a group of scientific experts recognizes that intensification of cattle production leads to habitat degradation, it does not include the improvement of habitat quality as a strategy for wildlife conservation (Tomas et al. 2019).



Figure 1. Expected interactive effects of the amount and quality of habitat on habitat use by six medium to large-bodied herbivores and frugivores mammalian species in the Brazilian Pantanal Wetland (A). Gradient of species sensitivity to habitat modifications: gray brocket deer, collared peccary, white lipped peccary, red brocket deer, agouti, and tapir (B).

In this study, we evaluate relative importance of habitat amount and quality on habitat use by six medium to large-bodied herbivores and frugivorous mammals in the Brazilian Pantanal wetland: lowland tapir (Tapirus terrestris, Perissodctyla: Tapiridae), agouti (Dasyprocyta azarae, Rodentia: Dasyproctidae), red brocket deer and the gray brocket deer (Mazama americana and Mazama gouazoubira, respectively, Artiodactyla: Cervidae), white lipped peccary and collared peccary (Tayassu pecari and Pecari tajacu, respectively, Artiodactyla: Tayassuidae). We aim to understand how species habitat use is shaped by a potential interaction between habitat amount and habitat quality in the region. We predict that in areas with little habitat, species use may be relatively invariant to changes in habitat quality (Figure 1A). However, at intermediate amounts of habitat, an increase in habitat quality will improve a species probability of use because quality can compensate for the amount of habitat (Figure 1A). Finally, in areas with high habitat amount, a decrease in quality habitat will reduce species use, but not as dramatically (Figure 1A). We also expect that the contribution of habitat quality to the habitat use will vary according to the species sensitivity to habitat modifications; habitat quality should be more important for the most sensitive species (Figure 1B).

Methods

Focal species

We selected six native mammalian herbivores and frugivores species because previous studies suggest that these species are adversely affected by habitat loss and degradation due to their narrow food resource requirements (Swihart et al. 2003; Kellner et al. 2019). We also choose these species because they differ in landscape perception and represent a gradient of sensitivity to habitat modifications from the less sensitive to the most: gray brocket deer, collared peccary, white lipped peccary, red brocket deer, agouti, and tapir, as described above (Figure 1B).

Gray brocket deer (*M. gouazoubira*) is widely distributed in a diversity of forest and cerrado cover types and occurs in patches of native vegetation in agricultural landscapes, which suggests it is tolerant to anthropogenic modifications (Black-Décima et al. 2009). In Pantanal, gray brocket deer occur primarily in edges between cerrado and forest habitats (Grotta-Neto et al. 2019). Collared peccary inhabits a great diversity of native vegetation types, including tropical rainforest, cerrado, semi-arid, and is tolerant to anthropogenic disturbances. White lipped peccary preferentially inhabits humid and dense pristine forests, but it is also found in dry forests near water bodies (Mayer and Wetzel 1987). Tapir and agouti mainly occupy native forests associated with perennial water bodies (Padilla and Dowler 1994; Desbiez et al. 2009a; Santos-Filho et al. 2012). Red brocket deer typically occur deep in the forest interior (Varela et al. 2009).

Study area

We conducted our study in the Pantanal biome, the world's largest wetland, in the *Nhecolândia* subregion, Mato Grosso do Sul State, Brazil (Figure 2). Vegetation is a mosaic of flooded and non-flooded grasslands, forest, and cerrado interspersed by seasonal and perennial lakes with freshwater or 'salines' – lakes with alkaline and brackish waters (Rodela et al. 2008). Floristic composition is mainly from the Cerrado biome, with influences of Atlantic Forest, Amazon, and Chaco (Pott and Silva 2015). The mean annual temperature is 26°C. Pantanal is a periodically flood wetland. The average annual rainfall is 1100 mm, but highly concentrated (60-80%) in the wet season (between December and May) when grasslands flood and lakes reach their highest water

level. The dry season occurs from June to November. Our study area consisted of five private ranches which raise cattle (*Bos taurus*, Bovidae) at low densities (0.25-0.35 head ha⁻¹). Native wildlife hunting is forbidden but hunting of feral pigs (*Sus scrofa*, Suidae), an exotic species introduced about 200 years ago, is permitted (Desbiez et al. 2009b).



Figure 2. (a) Land-use and land-cover thematic map of the study landscapes in Nhecolândia subregion within Brazilian Pantanal wetland (modified from Rodela et al. 2008), (b) Location of Pantanal wetland within Brazil, (c) Location of the study area within Pantanal wetland, and (d) aerial photograph of the study area (Rodela et al. 2008).

Camera trap sampling design

We sampled mammals from March to November 2008 using camera traps (Tigrinus®, Timbó, Santa Catarina State, Brazil) at 52 stations within the study area (Figure 2) chosen to represent a gradient of woody vegetation cover (forest or shrubland cover). We installed one un-baited camera trap 30-40 cm above the ground within each selected woody patch. We did not install devices in grasslands because previous experience revealed that camera traps failed to operate under extreme hot weather.

Stations were systematically placed 1–2 km apart (a systematic random sample) and cameras were programmed to operate 24 hours a day and recorded the date and time of each photograph. Each camera operated continuously during 30 days in dry and 30 days in wet seasons, totaling 3,120 camera-trap days (30 days*52 stations*2 seasons).

Habitat quality variables

We measured local habitat quality at each station using local environmental variables and recorded the distance to the nearest waterbodies (freshwater and saline lakes). At each station, we established two perpendicular 50-m transects centered on each camera. At 0.5-m intervals along each transect (50-m transect length/0.5-m interval x 2 transects = 200 points in each station), we counted the number of habitat quality variables that occurred at the point on the transect line: (i) acuri palm trees (*Attalea phalerata*, Aracaceae), (ii) shrubs at three heights (ground level < 0.1m, 0.1-0.5 m, and 0.5-1.0 m), (iii) bromeliads (*Bromelia antiacantha*, Bromeliaceae), and (iv) specified bare ground, when none of the previous variables touched the transect.

Attalea phalerata is a large-seed palm that dominates the understory and produces fruits year-round, which are consumed by the tapir and both peccaries, and it is the main food resource of the agouti (Desbiez et al. 2009b; Cid et al. 2013; Negrelle 2015). We considered shrub abundance as a proxy for the structural complexity of vegetation. Higher levels of structural complexity are associated with higher food resources for the herbivores and lower predation risk. *Bromelia antiacantha* is a thorny bromeliad that occurs in high-density on the forest floor in areas of high solar radiation. We hypothesized that bromeliads would affect the detectability of all six species at occupied stations because they can act as a barrier to movement for some species and facilitate escape routes for others (Antunes et al. 2010).

Distance to lakes and habitat amount

To estimate the distance-based metrics, we calculated the Euclidean distance from the camera to the nearest perennial or seasonal freshwater lake (distance to lake), and to the nearest saline (distance to saline) using the LSMetrics (see software details below). Habitat use (occupancy) by tapir and agouti is expected to be higher at camera stations hear freshwater lakes, and proximity to saline may increase habitat use by peccaries and deer, who seek mineral supplementation (Tobler et al. 2009).

We used the land-use and land cover map generated by Rodela et al. (2008), who interpreted and classified Landsat 7 images at a 1:20,000 cartographic ratio in 12 classes. Mapping was also supported by aerial photography interpretation (scale 1: 15,000) and field validation (Rodela et al. 2008). We converted land-use and land cover maps from vector (.shp) to 5-m matrix format (.tif) using QGIS (QGIS Development Team, 2019). We used the 'raster' R package (Hijmans et al., 2017) to reclassify the original 12 land-use and land cover classes into 5 categories (Figure 2; Table S1): (i) forest – *Cerradão* and seasonal forest and *carandá* tree patches), (ii) shrubland – cerrado shrubland, cerrado *stricto sensu*, (iii) grassland – grasslands, saline beach, saline field, and *vazante*, (iv) lakes – perennial or seasonal lakes, and (v) perennial saline lakes (Table S1).

We used LandScape Metrics (LSMetrics), an open-source free package (Niebuhr et al., *In prep.*, <u>https://github.com/LEEClab/LS_METRICS/wiki</u>), to calculate the following landscape structure metrics in relation to the amount of habitat within a specified spatial window: (i) forest cover – percentage of forest in the landscape, and (ii) cerrado cover – percentage of cerrado in the landscape. We calculated these composition-based metrics at 10 moving window extents: 4 ha (200x200m), 16 ha (400x400m), 36 ha (600x600m), 64 ha (800x800m), 100 ha (1000x1000m), 144 ha (1200x1200m), 196 ha (1400x1400m), 256 ha (1600x1600m), 324 ha (1800x1800m), and 400 ha (2000x2000m).

Multicollinearity analysis

We evaluated multicollinearity of our habitat amount and quality variables using Pearson's correlation (*r*). First, we verified weak correlation between local habitat quality variables (|r| < 0.40; Figure S1). Next, we calculated pairwise correlations for the 10 window extents for each landscape metric (habitat amount; Figures S2 and S3).

Not surprisingly, there was high correlation between moving window sizes, so we selected one extent of Forest cover (144 ha) and one extent of Cerrado cover (144 ha). When selecting an extent, we considered the range of values and the frequency of stations across this range, selecting the extent that resulted in as homogeneous frequency distribution as possible. We also avoided landscapes overlap as suggested by Holland and Fahrig (2004). Finally, we verified that there was low multicollinearity between the eight habitat quality variables and the two habitat amount extents (|r| < 0.55; Figure S4). The range, mean, and standard deviation of the final covariate set are presented in Table S2.

Species detection data and occupancy modelling

Our camera traps operated for 30 days per season (dry and wet) and we defined a survey as a 5-day period; accordingly, each camera station had 6 surveys (occasions) per season, totaling 12 surveys per station. We compiled detection histories for each of our native mammal species using the functions 'cameraOperation' and 'detectionHistory' of the camtrapR package (Niedballa et al. 2016). To organize detection and non-detection data along with the covariates, we used the function 'unmarkedFrameOccu' in the unmarked R package (Fiske and Chandler 2011).

We evaluated the influence of the amount and quality of habitat on speciesspecific occurrence using the static (single-season) occupancy model developed by MacKenzie et al. (2002) implemented in the unmarked R package (Fiske and Chandler 2011). This model includes two parameters: (1) occupancy (ψ) or the probability that the target species used a camera station during the season, and (2) detection probability (*p*), the probability of detecting the target species during a survey, given the station was used by the species. For each of our 6 mammalian species, we developed a candidate set of models based on each species' natural history (Table S3). We modelled occupancy probability (habitat use) as a function of habitat amount (forest or cerrado cover), habitat quality (local environmental variables, distance to lake, or distance to salines), or additive and interactive combinations of these standardized covariates (mean/standard deviation). We considered detection probability structures where detection varied: spatially according to the abundance of bromeliads, temporally among seasons (dry or wet), or was constant among all stations and seasons, *p*(.). We also included a null model where neither occupancy nor detection probability vary with our measured covariates (intercept only). Therefore, we fit 76 models to our tapir data, 67 models for agouti, 45 models for red brocket, 76 models for the white lipped peccary, 76 models for the collared peccary and 45 for the gray brocket. We compared models in each candidate set using the relative difference in Akaike's Information Criterion (Δ AIC), and report model weights (*w*), model fit (negative log-likelihood value), and the number of parameters (K; Burnham and Anderson 2002, Arnold 2010) using the 'modSel' function of the 'unmarked' R package. We report estimated coefficients for covariate effects (on the logit scale), and associated standard errors and confidence intervals using well-supported models.

Results

Tapir occupancy models

Our results show that tapir occupancy or habitat use was driven by an interaction between habitat amount (forest cover) and quality (abundance of medium shrubs) (Table S4). The best-supported model suggested that the species preferentially used landscapes with high forest cover and an abundance of medium shrubs (Figures 3A and S5A, w=0.07). The importance of vegetation structural complexity and high habitat cover was also indicated by the third most-supported model, which showed a negative effect of the interaction between bare ground and forest cover on tapir occurrence (Figures 3B and S5B, w=0.06). The detectability of the tapir was similar across stations and seasons ($\hat{p} = 0.25$; $\widehat{SE} = 0.03$).



Figure 3. Interactive effects of habitat amount and habitat quality when estimating mammal probability of use within Pantanal wetland, Brazil. Estimated habitat use (occupancy) for tapir was a function of the amount of forest cover and the local abundance of shrubs (A) or bare ground (B). Estimated habitat use for agouti (C) and white lipped peccary (D) were also interactive functions of forest cover and distance to freshwater and saline lakes, respectively.

Agouti occupancy models

The best-supported model demonstrated that agouti habitat use was driven by an interaction between habitat amount (forest cover) and quality (distance to lake) (Figures 3C and S5C; w=0.41, Table S4), and to a lesser extent by habitat quality alone (abundance of acuri palm trees) (Figure 4A, w=0.27, Table S4). The top model predicted divergent agouti responses to habitat quality conditional on the amount of

forest cover; in landscapes with high forest cover, agouti habitat use was high near lakes, but under low and medium habitat cover, habitat use was higher farther from lakes. The second-best model showed that agouti's habitat use was positively related to acuri palm abundance, it's main food resource. The agouti detectability was different between the two seasons, with higher detection probability during wet season ($\hat{p} = 0.53$; SE = 0.035) compared to the dry season ($\hat{p} = 0.25$; SE = 0.042).

Red brocket deer occupancy models

The habitat quality, measured by distance to saline, has the strongest influence on red brocket deer habitat use (Figure 4B, w=0.32, Table S4). Habitat use was higher at stations near salt water lakes (~0.90) and declined as distance to saline increased (Figure 4B). Although habitat amount (forest cover) was included in the second best supported model, the addition of this variable did not improve model fit and the confident interval associated with the estimated effect was centered near zero indicating that forest cover was a 'pretending variable' (Arnold 2010). The detectability of the red brocket deer did not differ across stations and seasons ($\hat{p} = 0.12$; $\widehat{SE} = 0.02$).

White lipped peccary occupancy models

Habitat use by white lipped peccaries was most influenced by a single habitat quality, but contrary to our predictions, peccary occurrence declined with the abundance of high shrubs (Table S4, Figure 4C, w=0.22). The second best supported model (w=0.10), suggested an interaction between habitat amount (forest cover) and quality (distance to salines). For low and medium forest cover landscapes, proximity to salines increased habitat use by white lipped peccary, but in high forest cover landscapes, proximity to salines decreased species use (Figure 3D and S5D). Local bromeliad abundance reduced detection probability for peccaries from 0.32 ($\widehat{SE} = 0.06$) at used stations with no bromeliads to 0.04 ($\widehat{SE} = 0.04$) for used stations with a high abundance of bromeliads.



Figure 4. Plots of predicted mammal species habitat use (occupancy) probability within Pantanal wetland, Brazil as a function of a single habitat quality covariate. Estimated habitat use for agouti was function of abundance of acuri palm tree (A). Estimated habitat use for red brocket der was function of distance to saline (B). Estimated habitat use for white lipped peccary was function of abundance of high shrubs (C). Estimated habitat use for collared peccary was function of distance to lake (D). The points represent the occupancy estimates for the 52 stations. Grey shading is the standard error.

Collared peccary occupancy models

Habitat use by collared peccaries was also influenced by a single habitat quality, but contrary to our predictions, collared peccary use increased with distance from freshwater lakes (Table S4, Figure 4D, w=0.23). Similar to our findings for white lipped

peccary, bromeliad abundance reduced detection probability for collared peccaries from 0.38 ($\widehat{SE} = 0.04$) to 0.25 ($\widehat{SE} = 0.04$) for used stations over the range of bromeliad abundances.

Gray brocket deer occupancy models

Gray brocket deer used most of the study area ($\hat{\psi} > 0.85$ for all stations) and accordingly, habitat use was not strongly influenced by any of our habitat covariates (Table S4). There was some evidence that habitat use was higher at stations further from salines or with fewer bromeliads, but the effects of these habitat quality covariates were imprecise (Table S4). The detection probability of gray brocket deer was similar across all used stations and seasons ($\hat{p} = 0.22$, $\widehat{SE} = 0.02$).

Discussion

In general, our results suggest that habitat quality is more important than habitat amount in determining species habitat use in a naturally fragmented landscape. We found that habitat quality alone was the best predictor of habitat use for four of the six species and habitat amount was influential only when considered in conjunction with habitat quality covariates and only for the most sensitive species (i.e., tapir, agouti, and white-lipped peccary). Habitat use by species that are more tolerant of habitat modification was better modeled by habitat quality covariates alone.

Only a subset of habitat quality covariates seemed important: those related to (1) distance to waterbodies (either freshwater or saline) and (2) abundance of shrub (medium and high) and bare ground. The influence of these habitat quality covariates on habitat use (positive, negligible, or negative) differed across species and sometimes interactively with habitat amount (tapir, agouti, and white-lipped peccary). The abundance of acuri palm tree was only important for the one species for which it is the main food source (agouti). Abundance of low shrubs and bromeliads did not affected on habitat use of any species. The only habitat amount covariate that was influential was forest cover and only when considered in conjunction with habitat quality covariates.

Interaction between habitat amount and quality in fragmented landscapes

Our results indicated that habitat quality and habitat amount interact to increase habitat use for the most sensitive species. This finding corroborates the importance of cost-benefits tradeoffs on species habitat selection. Contrary to our expectations, the contribution of habitat quality to species use was not highest at intermediate levels of habitat amount, but the influence of habitat quality depended on habitat amount (Figure 3). Our results demonstrated that habitat quality mattered even in landscapes with high habitat cover, i.e., species use probability could be low even in areas with high habitat cover when habitat quality is poor (e.g., tapir results). Surprisingly the effects of habitat quality on species-specific probability of use was divergent (negative, negligible, or positive) across a gradient of habitat amount.

The idea that habitat quality likely influences species' distribution in fragmented landscapes has been supported in some works that modeled biodiversity using only habitat quality measurements (e.g., Holland and Bennett 2007; Willems et al. 2009; Winnie-Jr et al. 2008; Brady et al. 2011; St-Louis et al. 2009; Wood et al. 2013). Other studies have compared the explanation power among metrics of habitat composition and quality, and found habitat quality can overcome habitat composition influences (e.g., St-Louis et al. 2014; Rocha et al. 2016; Santos et al. 2016; Regolin et al. 2020). Nonetheless, habitat loss and habitat degradation are dependent ecological processes acting simultaneously (Lindenmayer and Fischer 2007; Fahrig 2017) and few studies have shown the joint effects of habitat amount and quality on species distribution patterns in fragmented landscapes.

The pattern we found for the most sensitive species are in accordance with previous studies that suggest that species occurrence is determined by both the amount and the quality of remnant habitat patches. For instance, Mortelliti and Boitani (2008) found that patch use by carnivores (the badger *Meles meles* and the beech marten *Martes foina*) was driven by additive effects of landscape structure and food resources in the Province of Siena, Italy. Their results suggest that within certain structural limits, species occurrence probability increases in small and isolated habitat patches with relative high amounts of resources; however, these species were absence in the smallest and most isolated patches, despite availability of resources. Gardiner et al. (2018) assessed the occupancy pattern of a medium-sized marsupial (the eastern bettong *Bettongia gaimardi*) in an agricultural landscape of Tasmania, Australia. They found that species occurrence is determined by the amount of woodland cover and habitat quality, indicated by density of regenerating stems. Similarly, Costa-Araújo et al. (*In press*) revealed that the occurrence of the vulnerable titi monkey (*Callicebus*

melanochir) in mainly driven by patch area in the Brazilian Atlantic Forest, but improved habitat quality increases the species occurrence in small patches (<100 ha). Collectively, all three studies suggest that species' responses are driven mostly by habitat amount with additive effect of quality. To our knowledge, our study is the first to assess interactive effects of habitat quality and amount to predict species distributions in fragmented landscapes.

Understanding the underlying mechanisms of the role of habitat quality in habitat modeling is one of the main challenges of Landscape Ecology (Mortelliti et al. 2010). For example, it is unclear if habitat quality effects are species-trait dependent or whether habitat quality matters only within certain spatial arrangements (Mortelliti et al. 2010). The relationship between species sensitivity and the importance of habitat quality on species-specific habitat use contrasted our expectations. Habitat quality metrics were important to the habitat use by all six species, but in association with habitat amount for just the most sensitive species. The landscape we have evaluated is immersed in a relatively well preserved area, where habitat amount might not be a limiting resource for some of the studied species (e.g., the two deer and two peccary species). Thus the less sensitive species select areas associated with habitat quality, while the most sensitive do so by considering how it interacts with habitat cover gradient to include variegated landscapes and/or evaluate ecosystems that are not naturally fragmented (e.g., the Brazilian Atlantic Forest).

Sensitive species-specific findings: tapir, agouti, white-lipped peccary

As a forest dwelling specialist (Padilla and Dowler 1994), tapirs require forest patches to forage, breed, and move through the landscape. Additionally, our findings highlight the importance of habitat quality, indicated by the abundance of medium shrubs, which is proxy of food source availability. Tapirs can be affected by cattle presence within forest patches because cattle reduce the abundance of shrubs, as pointed out by Desbiez et al. (2009a). Nonetheless, Eaton et al. (2017) suggested that tapir is unaffected by cattle in the southwest Pantanal. To elucidate the disagreement among the results of Desbiez et al. (2009a), Eaton et al. (2017), and ours, future research could discriminate the effects of cattle-related habitat degradation and natural heterogeneity on vegetation structure complexity and how it affects tapir habitat use.

Our results differed from previous research in other regions. In the Brazilian Atlantic Forest, tapirs preferably use sites near water resources with high density of palms, in the southeast (Ferreguetti et al. 2018), and frequently used floodplains in the south (Vidolin et al. 2009). Tapirs occurred close to salt licks in the Chaco and Chiquitano dry forests of Bolivia (Noss et al. 2003) as well as in the Peruvian Amazon (Tobler et al. 2009). Recently, Paolucci et al. (2019) recorded tapirs using burned forests twice as often as undisturbed and closed canopy forests in the Amazon/Cerrado ecotone, in Brazil. It is possible that the varied findings in previous studies is due to differences in the limiting factors across regions. For example, while water bodies are very important resources to tapirs (Padilla and Dowler 1994) they are not limiting in our ecosystem. Many lakes occur throughout our study region that are easily accessed by tapirs and thus distance to lakes are not an important predictor of tapir habitat use in the region.

The predicted high habitat use by agouti in highly forested landscapes near water sources is in accordance with preceding works. Agouti habitat use was higher within forest patches in the Pantanal (Desbiez et al. 2009a). Santos-Filho et al. (2012) recorded agoutis exclusively in riparian forests in the Brazilian Cerrado. In the Atlantic Forest, red-rumped agouti (*Dasyprocta leporina*) occurrence was explained mainly by proximity to water (Ferreguetti et al. 2018). However, habitat use by agoutis has been poorly studied, which obscures interpretation of our interactive model. The second best model showed that agouti's occupancy was positively related to acuri palm abundance, as demonstrated by a previous work in the same site (Cid et al. 2013). Acuri palm fruits are the key food resources to agouti especially during the dry season (Cid et al. 2013).

White lipped peccaries are restricted to well-preserved forest across the species range (Altrichter et al. 2011). For instance, Reyna-Hurtado and Tanner (2005) found the species selecting medium subperennial forest and low-subperennial-flooded forest in Calakmul Forest, Campeche, Mexico. In the southern Atlantic Forest, Brazil, white lipped peccaries use mainly Araucaria forest and floodplains (Vidolin et al. 2009). The preservation of high quality forest patches is the main conservation strategy for the species persistence in the Pantanal (Keuroghlian et al. 2009) and in the Atlantic Forest (Keuroghlian and Eaton 2008). These studies define habitat quality in terms of fruit richness and availability, while we estimated food source abundance by counting acuri palm trees (including fruiting and non-fruiting individuals) and shrubs. Our results

suggested white-lipped peccary use was not influenced by acuri abundance, but was negative effected by the abundance of high shrubs. Peccary herds move mostly through trails within forest patches with abundance availability of fruits and rest in bare ground areas or low height vegetation (Mayer and Wetzel 1987). Thus, the species avoids areas with high concentration of bromeliads and high shrubs because they serve as barriers to movement or are inadequate for resting.

Our results also suggest an interaction between saline proximity and forest cover in the Pantanal. White lipped peccaries avoid flooded grasslands and intensively use forest areas because the high availability of food resources (Hofman et al. 2015). However, the species must visit these natural salt sources in medium and low forested areas because they are important for mineral supplementation. For example, whitelipped peccaries are often found using salt licks in the Peruvian Amazon (Tobler et al. 2009). It is possible that the species use forested areas far from salines when they are foraging and visit medium and low forested areas near salines when seeking for salt.

Conservation implications

Our study revealed that for sensitive species, habitat use is determined by the interaction of both the amount and the quality of habitat patches. That is, species response to habitat quality depends on the habitat amount. Landscape management for these sensitive species would benefit by identify the range of forest cover over which habitat quality improvements have the biggest effects. These forest cover thresholds are probably species-specific and vary among regions across the species distribution range. The observed patterns for the less sensitive species showed that habitat use is driven by habitat quality covariates, suggesting when habitat cover is not a limiting factor, species distributions can be predicted by habitat quality alone. We recommend that species conservation programs incorporate both habitat quality and amount when dealing with sensitive species; and prioritize habitat quality management when focusing in less sensitive species.

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Authors' contributions

All authors conceived study aim and hypothesis. ALR wrote the manuscript with inputs from LLB. LGOS designed data collection and carried out field work. ALR quantified landscape structure indices. ALR and LLB analyzed the data. All the authors revised the manuscript. Proof reading by LLB.

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Supplementary material

Additional supplementary material may be found online in the supporting information tab for this article.

Land-use and land cover classes	Description
Grassland	Low flood probability grassland
	Medium flood probability grassland
	High flood probability grassland
	Saline beach
	Vazante
	Saline field
Cerrado	Cerrado shrubland
	Cerrado stricto sensu
Forest	Cerradão plus seasonal forest
	Carandá tree patch
Lakes	Perennial or seasonal lakes
Saline	Perennial saline

Table S1. Description of land-use and land cover classes according to Rodela et al. (2008).



Figure S1. Scatter plot matrices and correlations between eight habitat quality variables collected at 52 sampled stations in the Brazilian Pantanal. The diagonal panels present frequency histograms for each habitat quality variable; variable ranges are given at the top or bottom of each column. The panels above and to the right of the diagonal show pairwise Pearson correlations among habitat quality variables. Lower panels include a scatterplot of paired habitat quality variables for each station.

	20 40 60 80		10 30 50		10 30 50		10 20 30 40 50		10 20 30 40	
Forest_cover_4ha	0.87	0.80	0.76	0.71	0.66	0.64	0.63	0.62	0.61	20 60 10
20 00 ••••••••••••••••••••••••••••••••••	Forest_cover_16ha	0.96	0.88	0.81	0.75	0.73	0.71	0.70	0.69	
		Forest_cover_36ha	0.95	0.86	0.80	0.76	0.73	0.72	0.70	10 40 70
			Forest_cover_64ha	0.96	0.91	0.87	0.84	0.82	0.80	
			and look and a second s	Forest_cover_100ha	0.98	0.94	0.92	0.90	0.87	10 30 50
0 30 20 0 0 0 0 0 0 0 0 0 0 0 0 0 0	· · · · · · · · · · · · · · · · · · ·				Forest_cover_144ha	0.99	0.96	0.93	0.91	
						Forest_cover_196ha	0.99	0.97	0.95	10 30 50
						. 19	Forest_cover_256ha	0.99	0.97	
								Forest_cover_324ha	0.99	10 30 50
		10 30 50 70		10 30 50		10 20 30 40 50		2.00 30 40 50	Forest_cover_400ha	

Figure S2. Scatter plot matrices and correlations between 10 extents of Forest cover around 52 sampled stations in the Brazilian Pantanal. The diagonal panels present frequency histograms for each extent; variable ranges are given at the top or bottom of each column. The panels above and to the right of the diagonal show Pearson correlation among extents pairs. Lower panels include a scatterplot of paired forest cover for each station.

		10 30 50		10 20 30 40		15 25 35		15 20 25 30 35		20 25 30 35	
C	errado_cover_4ha	0.74	0.61	0.49	0.44	0.40	0.36	0.33	0.34	0.38	0 20 50
10 30 50		Cerrado_cover_16ha	0.93	0.78	0.70	0.62	0.56	0.55	0.52	0.56	
			Cerrado_cover_36ha	0.92	0.83	0.74	0.67	0.65	0.60	0.61	10 30 50
10 25 40	* * * * * * *** * *** ***			Cerrado_cover_64ha	0.95	0.88	0.81	0.78	0.72	0.70	
° 8° 8° 8°					Cerrado_cover_100ha	0.97	0.92	0.89	0.84	0.81	15 30
15 25 35						Cerrado_cover_144ha	0.98	0.94	0.89	0.85	
° ° ° °							Cerrado_cover_196ha	0.98	0.93	0.89	15 25 35
15 25 35				**************************************			80°°°	Cerrado_cover_256ha	0.97	0.93	
8 8 8 8 8 8 8			**************************************	• • • • • • • • • • • • • • • • • • •			0 0	.8.88 ⁸⁸ .8° ⁶ .8°	Cerrado_cover_324ha	0.98	20 30
20 30										Cerrado_cover_400ha	
20 30			10 20 30 40 50				0.000 000 000 000 000 000 000 000 000 0			0.98	

Figure S3. Scatter plot matrices and correlations between 10 extents of cerrado cover around 52 sampled stations in the Brazilian Pantanal. The diagonal panels present frequency histograms for each extent; variable ranges are given at the top or bottom of each column. The panels above and to the right of the diagonal show Pearson correlation among extents pairs. Lower panels include a scatterplot of paired cerrado cover for each station.



Figure S4. Scatter plot matrices and correlations between eight habitat quality variables collected at 52 sampled stations in the Brazilian Pantanal and cover of forest and cerrado around each sampled station. The diagonal panels present frequency histograms for each variable of habitat quality and amount; variable ranges are given at the top or bottom of each column. The panels above and to the right of the diagonal show pairwise Pearson correlations among habitat quality and amount variables. Lower panels include a scatterplot of paired habitat quality and habitat amount for each station.

Covariate	Unit	Minimum	Maximum	Mean	Standard
					deviation
Acuri palm	count	2	66	32.74	15.69
Caraguata	count	0	93	26.79	24.43
bromeliad					
Low shrub	count	3	48	23.46	11.76
Medium shrub	count	0	55	18.22	13.76
High shrub	count	0	36	12.41	10.84
Bare ground	count	23	98	60.01	19.53
Distance to saline	meter	236	8893	3735.76	2273.59
Distance to lake	meter	21	589	239.01	122.11
Cerrado cover	percent	16	40	25.11	6.43
Forest cover	percent	7	57	23.62	12.01

Table S2. Range, mean, and standard deviation of covariates for occupancy models of mammalian species in Brazilian Pantanal.

Species		Acuri palm tree	Low shrub	Medium shrub	High shrub	Bromeliad	Bare ground	Cerrado cover	Forest cover	Distance to lakes	Distance to salines	Season
Tapir (Tapirus terrestris)	ψ	Χ	Х	Х	Х	Х	Х		Х	Х	Х	
	р					Х						Х
Agouti (Dazyprocta azarae)	ψ	Х	Х	Х	Х	Х	Х		Х	Х		
	р					Х						Х
Red brocket (Mazama	ψ		Х	X	Х	Х	Х		Х	Х	Х	
americana)	р					Х						
White lipped peccary	ψ	Х	Х	Х	Х	Х	Х		Х	Х	Х	
(Tayassu tajacu)	р					Х						Х
Collared peccary (Pecari	ψ	Х	Х	Х	Х	X	Х	Х		Х	Х	
tajacu)	р					Х						Х
Gray brocket (Mazama	ψ		Х	Х	Х	Х	Х	Х		Х	Х	
gouazoubira)	р					Х						

Table S3. Biologically meaningful covariates for each species occupancy (habitat use) are marked with an 'X' in the table. Ψ is occupancy and *p* in detection probability.

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Table S4. Summary of the best-supported occupancy models of mammalian species within Pantanal wetland, Brazil. Model selection statistics include: fit (-2log-likelihood value); K is the number of parameters, Δ AIC is the relative difference in AIC values compared with top-ranked model; *w* is the AIC model weight. The estimated effects (beta parameters) for model intercept and covariates and associated measures of precision including standard error (SE) and 95% confidence intervals (CI).

					Estimated effects for				
					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	w	(Beta Parameters)	Estimate	SE	CI	CI
Tapir (Tapirus terrestris)									
Ψ (forest_144ha*med_shrub) $p(.)$	220.62	5	0	0.07	Intercept	0.17	0.31	-0.42	0.77
					β(forest_144ha)	0.37	0.32	-0.26	1.01
					β (med_shrub)	-0.18	0.35	-0.86	0.5
					β (forest_144ha:med_shrub)	0.79	0.47	-0.13	1.70
Ψ (forest_144ha+high_shrub) $p(.)$	221.63	4	0.03	0.07	Intercept	0.31	0.32	-0.32	0.95
					β(forest_144ha)	0.64	0.30	0.06	1.22
					β(high_shrub)	-0.58	0.30	-1.16	0.01
Ψ (forest_144ha*bare_ground) $p(.)$	220.69	5	0.15	0.06	Intercept	0.15	0.30	-0.44	0.74
					β(forest_144ha)	0.41	0.32	-0.23	1.04
					β (bare_ground)	0.39	0.30	-0.19	0.98
					β (forest_144ha:bare_ground)	-0.49	0.34	-1.16	0.18
Ψ (forest_144ha+bare_ground) $p(.)$	221.76	4	0.29	0.06	Intercept	0.30	0.31	-0.32	0.91
					β(forest_144ha)	0.65	0.30	0.06	1.23

					Estimated effects for				
					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	w	(Beta Parameters)	Estimate	SE	CI	CI
					β (bare_ground)	0.55	0.29	-0.03	1.12
Ψ (forest_144ha*high_shrub) $p(.)$	220.99	5	0.75	0.05	Intercept	0.19	0.31	-0.41	0.8
					β(forest_144ha)	0.46	0.31	-0.16	1.05
					β(high_shrub)	-0.52	0.30	-1.11	0.07
					β (forest_144ha:high_shrub)	0.35	0.32	-0.28	0.97
Ψ(forest_144ha+high_shrub)	221.09	5	0.95	0.04	Intercept	0.36	0.33	-0.30	1.01
<i>p</i> (season)									
					β(forest_144ha)	0.64	0.30	0.06	1.23
					β(high_shrub)	-0.60	0.31	-1.19	0.00
$\Psi(\text{forest}_{144\text{ha}*\text{med}_{shrub}})$	220.28	6	1.33	0.03	Intercept	0.21	0.32	-0.41	0.82
<i>p</i> (season)									
					β(forest_144ha)	0.37	0.33	-0.27	1.02
					β(med_shrub)	-0.18	0.36	-0.88	0.51
					β (forest_144ha:med_shrub)	0.78	0.49	-0.18	1.73
Ψ(forest_144ha+bare_ground)	221.31	5	1.39	0.03	Intercept	0.32	0.32	-0.30	0.95
<i>p</i> (season)									
					β(forest_144ha)	0.65	0.30	0.06	1.23

					Estimated effects for				
					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	w	(Beta Parameters)	Estimate	SE	CI	CI
					β(bare_ground)	0.55	0.30	-0.03	1.13
$\Psi(\text{forest}_{144\text{ha}*\text{bare}}\text{ground})$	220.33	6	1.43	0.03	Intercept	0.17	0.31	-0.43	0.78
p(season)									
					β(forest_144ha)	0.40	0.33	-0.24	1.04
					β (bare_ground)	0.40	0.30	-0.20	0.99
					β (forest_144ha:bare_ground)	-0.47	0.34	-1.15	0.20
Ψ (forest_144ha+dist_lake) $p(.)$	222.41	4	1.59	0.03	Intercept	0.29	0.31	-0.31	0.89
					β(forest_144ha)	0.62	0.30	0.03	1.22
					β(dist_lake)	-0.49	0.32	-1.11	0.14
Ψ(forest_144ha*high_shrub)	220.55	6	1.85	0.03	Intercept	0.23	0.32	-0.36	0.86
p(season)									
					β(forest_144ha)	0.45	0.32	-0.17	1.07
					β(high_shrub)	-0.53	0.31	-1.13	0.06
					β(forest_144ha:high_shrub)	0.32	0.32	-0.3	0.94
Ψ(forest_144ha*med_shrub)	220.55	6	1.87	0.03	Intercept	0.18	0.30	-0.42	0.77
<i>p</i> (bromeliad)									
					β(forest_144ha)	0.37	0.32	-0.26	1.01

					Estimated effects for				
					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	W	(Beta Parameters)	Estimate	SE	CI	CI
					β (bare_ground)	-0.17	0.35	-0.84	0.51
					β (forest_144ha:bare_ground)	0.80	0.46	-0.11	1.71
Agouti (Dasyprocta azarae)									
Ψ(forest_144ha*dist_lake)	292.15	6	0.00	0.41	Intercept	1.51	0.52	0.48	2.53
p(season)									
					β(forest_144ha)	-0.62	0.37	-1.34	0.1
					β(dist_lake)	1.18	0.47	0.25	2.11
					β(forest_144ha:dist_lake)	-1.07	0.45	-1.95	-0.19
$\Psi(acuri) p(season)$	294.56	4	0.83	0.27	Intercept	0.76	0.31	0.14	1.37
					β(acuri)	0.72	0.32	0.09	1.35
Red brocket (Mazama americana))								
Ψ (dist_saline) $p(.)$	142.80	3	0	0.32	Intercept	0.33	0.50	-0.65	1.32
					β(dist_saline)	-1.12	0.50	-2.10	-0.15
Ψ (forest_144ha+dist_saline) $p(.)$	142.64	4	1.67	0.14	Intercept	0.34	0.51	-0.66	1.35
					β(forest_144ha)	-0.31	0.54	-1.36	0.75
					β(dist_saline)	-1.32	0.64	-2.58	-0.06
Ψ (dist_saline) <i>p</i> (bromeliad)	142.69	4	1.78	0.13	Intercept	0.28	0.49	-0.67	1.23

					Estimated effects for				
					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	w	(Beta Parameters)	Estimate	SE	CI	CI
					β(dist_saline)	-1.10	0.48	-2.05	-0.15
White lipped peccary (Tayassu pe	cari)								
$\Psi(high_shrub) p(bromeliad)$	123.76	4	0	0.22	Intercept	-0.85	0.37	-1.57	-0.14
					β(high_shrub)	-0.82	0.34	-1.50	-0.15
Ψ(forest_144ha*dist_saline)	122.55	6	1.59	0.10	Intercept	-0.10	0.43	-0.94	0.74
<i>p</i> (bromeliad)									
					β(forest_144ha)	0.41	0.48	-0.52	1.34
					β(dist_saline)	-0.22	0.41	-1.02	0.58
					β (forest_144ha:dist_saline)	1.42	0.61	0.23	2.60
Ψ(forest_144ha+high_shrub)	123.73	5	1.95	0.08	Intercept	-0.85	0.37	-1.56	-0.13
<i>p</i> (bromeliad)									
					β(forest_144ha)	-0.07	0.31	-0.69	0.55
					β(high_shrub)	-0.81	0.35	-1.49	-0.13
Colared peccary (Pecari tajacu)									
$\Psi(\text{dist_lake}) p(.)$	291.66	3	0	0.23	Intercept	0.97	0.35	0.28	1.66
					β(dist_lake)	1.12	0.41	0.32	1.92
$\Psi(dist_lake) p(bromeliad)$	290.71	4	0.11	0.21	Intercept	0.95	0.34	0.28	1.61
					Estimated effects for				
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					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	w	(Beta Parameters)	Estimate	SE	CI	CI
					β(dist_lake)	1.11	0.40	0.33	1.89
Ψ (dist_lake) p (season)	291.07	4	0.83	0.15	Intercept	0.99	0.35	0.30	1.69
					β(dist_lake)	1.12	0.40	0.33	1.91
Ψ (cerrado_144ha+dist_lake) $p(.)$	291.53	4	1.74	0.09	Intercept	0.98	0.36	0.28	1.68
					β(cerrado_144ha)	0.15	0.29	-0.42	0.71
					β(dist_lake)	1.13	0.42	0.31	1.95
$\Psi(cerrado_144ha+dist_lake)$	290.61	5	1.90	0.09	Intercept	0.96	0.35	0.28	1.63
<i>p</i> (bromeliad)									
					β(cerrado_144ha)	0.13	0.28	-0.42	0.68
					β (dist_lake)	1.12	0.41	0.32	1.91
Gray brocket (Mazama gouazoub	ira)								
Ψ (dist_saline) $p(.)$	274.43	3	0	0.13	Intercept	2.01	0.64	0.76	3.27
					β(dist_saline)	0.87	0.62	-0.34	2.09
$\Psi(.) p(.)$	275.84	2	0.81	0.09	Intercept	1.80	0.49	0.83	2.76
Ψ (bromeliad) $p(.)$	274.89	3	0.91	0.08	Intercept	1.87	0.53	0.84	2.93
					β(bromeliad)	-0.56	0.40	-1.34	0.23
Ψ (dist_saline) <i>p</i> (bromeliad)	274.33	4	1.81	0.05	Intercept	2.09	0.72	0.68	3.51

					Estimated effects for				
					occupancy			Lower	Upper
Model description	fit	K	ΔΑΙΟ	w	(Beta Parameters)	Estimate	SE	CI	CI
					β(dist_saline)	0.93	0.68	-0.40	2.27
Ψ (cerrado_144ha+dist_saline) $p(.)$	274.39	4	1.91	0.05	Intercept	2.04	0.66	0.73	3.34
					β(cerrado_144ha)	-0.13	0.45	-1.01	0.75
					β(dist_saline)	0.91	0.65	-0.36	2.18



Figure S5. Interactive effects of habitat amount and habitat quality when estimating mammal species occupancy probability within Pantanal wetland, Brazil. Tapir occurrence (habitat use) was a function of the amount of forest cover and the local abundance of shrubs (A) or bare ground (B). Habitat use estimates for agouti (C) and white lipped peccary (D) were also interactive functions of forest cover and distance to freshwater and saline lakes, respectively. All covariate values are standardized. Colors represent occupancy probability, presented with a blue-to-red gradient (low-to-high habitat use). The points and topographic lines represent the occupancy estimates for the 52 stations.



Figure S6. Additive effects of habitat amount and habitat quality when estimating mammal species occupancy probability within Pantanal wetland, Brazil. Tapir occurrence was a function of the amount of forest cover and the local abundance of shrubs (A) or bare ground (B). All covariate values are normalized. Lines represent occupancy probability, presented with a blue-to-red gradient (low-to-high occupancy). The points represent the occupancy estimates for the 52 stations.

Conclusão

Capítulo 1

Incentivamos que estudos futuros avaliem redes de interação entre morcegos e plantas em paisagens antrópicas com um nível variável de heterogeneidade da composição, consistindo de unidades com diferentes níveis de complexidade estrutural e em gradientes de quantidade de habitat. Um entendimento abrangente dessas redes pode trazer uma visão sobre a dinâmica das redes de morcegos em paisagens fragmentadas. Com o desenvolvimento desses estudos, entenderemos melhor o processo de dispersão de sementes modulado por morcegos, apoiando programas de regeneração e restauração que se beneficiam de funções desempenhadas por morcegos.

Capítulo 2

Este é o primeiro estudo que relata o papel da heterogeneidade espacial como um dos principais fatores determinantes da estruturação de assembléias de mamíferos em paisagens fragmentadas. Os efeitos da heterogeneidade espacial em paisagens modificadas pelo homem serão melhor compreendidos quando o cálculo das métricas de textura forem realizados por tipo de cobertura do solo. Os efeitos da heterogeneidade espacial e da configuração do habitat superaram a influência da composição do habitat na diversidade alfa e beta de mamíferos. A dos fragmentos pode influenciar o movimento configuração das espécies e, consequentemente, as taxas de (re)colonização do habitat. A complexidade estrutural da vegetação na matriz antropogênica também pode afetar o movimento das espécies, pois define a capacidade da matriz de fornecer recursos, incluindo alimentação e abrigos. Portanto, a composição da paisagem por si só não deve ser usada para apoiar estratégias de manejo de paisagens voltadas para a conservação de mamíferos não-voadores. Estas estratégias também devem buscar a preservação e melhoraria da complexidade estrutural da vegetação nos fragmentos de habitat e na matriz, permitindo que as paisagens abriguem alta diversidade de espécies ao aumentar a disponibilidade de nichos.

Capítulo 3

Em geral, nossos resultados sugerem que a qualidade do habitat é mais importante do que a quantidade de habitat na determinação do uso de habitat em uma paisagem naturalmente fragmentada. Para espécies sensíveis, o uso do habitat é determinado pela interação entre a quantidade e a qualidade das manchas de habitat. Os padrões observados para as espécies menos sensíveis mostraram que o uso do habitat é impulsionado pelas covariáveis da qualidade do habitat, sugerindo que quando a cobertura do habitat não é um fator limitante, a distribuição das espécies pode ser prevista apenas pela qualidade do habitat. Recomendamos que os programas de conservação de espécies incorporem tanto a qualidade quanto a quantidade do habitat ao lidar com espécies sensíveis; e priorizar o manejo da qualidade do habitat ao focar em espécies menos sensíveis.



Our new heros' Bansky 7 de maio de 2020