Universidade de Aveiro Departamento de Biologia
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Ana Catarina Neves Ferreira Lino

Heterogeneidade de habitats e morcegos neotropicais: processos e padrões ecológicos e evolutivos

Habitat heterogeneity and neotropical bats: ecological and evolutionary processes and patterns

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia e Ecologia das Alterações Globais, realizada sob a orientação científica do Professor Doutor Carlos Manuel Martins Santos Fonseca, Professor Associado com Agregação do Departamento de Biologia da Universidade de Aveiro e coorientação científica da Professora Doutora Maria João Ramos Pereira, Professora Adjunta do Departamento de Zoologia do Instituto de Biociências da Universidade Federal do Rio Grande do Sul e do Professor Doutor Erich Fischer, Professor Titular do Instituto de Biociências da Universidade Federal de Mato Grosso do Sul.

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A toda a minha família
Aos meus pais
Ao Rui
Sempre lá

o júri

presidente

Prof. Doutor Carlos Manuel Martins da Costa
professor catedrático da Universidade de Aveiro

Prof. Doutor Carlos Manuel Martins Santos Fonseca
professor associado com agregação da Universidade de Aveiro
orientador

Doutor João Tiago Sabino Lino Marques
investigador auxiliar da Universidade de Évora

Doutora Rita Gomes Rocha
investigadora de pós-doutoramento da Faculdade de Ciências da Universidade do Porto

Prof. Doutora Maria Da Luz Da Costa Pereira Mathias
professora catedrática da Faculdade de Ciências da Universidade de Lisboa

Doutor Eduardo Manuel Silva Loureiro Alves Ferreira
professor auxiliar convidado da Universidade de Aveiro

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palavras-chave

diversidade genética, ecologia de comunidades, heterogeneidade de habitats, mamíferos, morcegos, neotrópicos.

resumo

A perda e a fragmentação dos habitats representam as maiores ameaças à diversidade em todo o mundo, afetando pelo menos 40% das espécies de mamíferos. Mudanças antropogénicas na paisagem têm consequências para as espécies e, portanto, para todo o ecossistema, uma vez que os mamíferos fornecem vários bens e serviços importantes para o funcionamento ecossistémico. Assim, o foco desta tese é avaliar as consequências da perda e fragmentação do habitat em várias dimensões da biodiversidade. Inicialmente foi realizada uma meta-análise sobre as consequências genéticas da perda e fragmentação de habitat em mamíferos. Em segundo lugar, tendo os morcegos Neotropicais como grupo modelo, avaliou-se o efeito das variáveis da paisagem na diversidade beta e nas diversidades taxonómica, funcional e filogenética. Para isso, foram estudadas as comunidades de morcegos da região da Serra da Bodoquena (Mato Grosso do Sul, Brasil). Por fim, avaliou-se a existência de correlações entre a diversidade de espécies e diversidade genética de duas espécies de morcegos e também se explorou quais as variáveis que afetam essas correlações. Os resultados deste trabalho sugerem uma perda global da diversidade genética em populações de mamíferos que vivem em situações de alta fragmentação de habitat. A meta-análise revela que as espécies de mamíferos com grande massa corporal são as mais afetadas pela fragmentação; os mamíferos terrestres e arbóreos são mais afetados comparativamente às espécies voadoras; todas as medidas genéticas estudadas são negativamente afetadas pela fragmentação em mamíferos herbívoros; e as espécies dependentes das florestas são as mais suscetíveis à fragmentação. Relativamente às comunidades de morcegos da Serra da Bodoquena, verificou-se que as respostas das espécies às variáveis da paisagem mudam de acordo com a escala estudada. Na escala menor, apenas a distância à área pristina de maior dimensão (o parque nacional) afeta negativamente as diversidades; na escala intermédia, tanto a distância ao parque nacional como as bordas florestais afetam negativamente as diversidades; e na escala maior, além da distância ao parque nacional e das bordas florestais, também a área florestal afeta negativamente as três dimensões da biodiversidade. A diversidade genética em *Artibeus planirostris* não foi afetada por nenhuma das variáveis estudadas, mas a riqueza alélica e a heterozigotia esperada de *Carollia perspicillata* foram negativamente relacionadas à distância ao parque nacional e à área florestal. As correlações entre diversidade de espécies e genéticas foram principalmente negativas para *A. planirostris* e positivas para *C. perspicillata* indicando que esta última é ecologicamente mais semelhante às outras espécies das comunidades. Foi detetado isolamento por distância para *C. perspicillata*. Os resultados obtidos nesta tese mostram que unidades de conservação com áreas de habitat contínuo e pouco modificadas são fundamentais na preservação das várias dimensões da diversidade; pelo menos algumas espécies são sensíveis às bordas florestais e, mesmo áreas com menor cobertura florestal, são importantes para a manutenção das dimensões de biodiversidade avaliadas. Possivelmente, um mosaico de florestas contínuas e áreas não-florestadas aumenta a diversidade de morcegos porque fornece mais recursos para os morcegos explorarem.

keywords bats, community ecology, genetic diversity, habitat heterogeneity, mammals, neotropics.

abstract

Habitat loss and fragmentation pose the greatest threats to biodiversity worldwide, affecting at least 40% of mammalian species. Anthropogenic landscape changes have severe consequences for species and, therefore, for entire ecosystems because mammals provide several goods and services important for ecosystem function. Thus, the focus of this thesis is to evaluate the consequences of habitat loss and fragmentation on several dimensions of biodiversity. Firstly, meta-analysis on the genetic consequences of habitat loss and fragmentation on mammals was done. Secondly, taking Neotropical bats as models, the effect of the landscape variables on total beta diversity and on taxonomic, functional and phylogenetic diversities was evaluated. For this, bat assemblages of Serra da Bodoquena (Mato Grosso do Sul, Brazil) were sampled. Lastly, correlations between species and genetic diversity of two bat species in this region and variables affecting these correlations were evaluated. The outcomes of this thesis suggest an overall loss of genetic diversity in mammalian populations within highly fragmented habitats. The meta-analysis shows that mammalian species with large body mass are the most negatively affected by fragmentation; terrestrial and arboreal mammals are more affected than flying species; herbivores suffer consistent negative effect of fragmentation in all genetic parameters analysed; and forest-dependent species are the most susceptible to fragmentation. Concerning the bat assemblages of Serra da Bodoquena, responses to landscape variables vary according to the scale of analysis. At the smallest scale, only the distance to the nearest border of the largest continuous pristine area (the Serra da Bodoquena National Park) negatively affects diversities; at the intermediate scale both the distance to the national park and the forest borders negatively affects bat diversities; and at large scale, beyond the distance to the national park and forest border, forest area also negatively affects the three studied dimensions of biodiversity. The genetic diversity of *Artibeus planirostris* was not affected by any of the studied variables but the allelic richness and the expected heterozygosity of *Carollia perspicillata* were negatively related to the distance to the national park and forest area. Species-genetic diversity correlations were mainly negative for *A. planirostris* and positive for *C. perspicillata* indicating that *A. planirostris* could be considered an outlier species and that *C. perspicillata* is ecologically more similar to other species in communities. Isolation by distance was found in *C. perspicillata* populations. The results of this thesis show that conservation units with areas of continuous and unmodified habitats are fundamental in preserving the various dimensions of diversity; at least some species are sensitive to forest borders and, even areas with less forest cover are important for the dimensions of diversity evaluated. Possibly a mosaic of continuous forests and non-forests enhance diversity because it provides more resources for bats to exploit.

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CHAPTER 1

GENERAL INTRODUCTION

General introduction

1.1 Habitat loss and fragmentation worldwide: consequences for mammals

The rapid increase of human population size has led to severe changes in land use worldwide. The main drivers of these changes are the creation and expansion of urban areas, the intensification of cattle and agricultural activities for food supplementation, and timber extraction. However, the importance of each of these drivers is different across the world (Foley et al., 2005). These human activities bring a myriad of negative effects like the loss of biodiversity because they profoundly alter natural landscapes through fragmentation, degradation, and loss of habitats (Brooks et al., 2002). The compositional characteristics of landscapes are profoundly altered through the substitution of natural vegetation by other land uses and the configuration of landscapes suffer drastic changes as the decrease of natural habitat available for species, the increase of the number of patches of favourable habitat within an unfavourable matrix, the decrease of patch size and the increase in isolation between them (Fahrig, 2003). Such changes affect species, populations and communities, particularly shifts in species richness (Püttker et al., 2008; Murphy and Romanuk, 2014), population size (Koskimäki et al., 2014), geographical distribution (Sanderson et al., 2002; Morrison et al., 2007) and genetic diversity (Gibbs, 2001). However, sometimes these consequences are not so evident or immediately noticeable because some species experience an "extinction dept", i.e. a time delay to respond to landscape changes that is not immediately noticeable but may lead to species extinction (Kuussaari et al., 2009). For these reasons, it is extremely important to understand the effect of habitat loss and fragmentation on species and, whenever possible, understand if general patterns emerge, or if these threats affect species in a specific way.

The class Mammalia is composed by 6,495 species (Burgin et al., 2018) widely distributed throughout the Earth's habitats (Schipper et al., 2008). Mammals are ecologically diverse, showing high plasticity in eco-morphology, diverse life-history traits, and diverse behavioural patterns. Furthermore, mammals provide several goods and services important for human well-being and they play key roles in ecosystem functioning. In some countries, wild mammals have a direct nutritional and economic value because they are important sources of meat, both for subsistence of local populations or for commercial proposes, imposing threats all around the world (Milner-Gulland et al., 2003). Mammals also have an intrinsic value associated to ecotourism (Durrheim and Leggat, 1999). Furthermore, mammalian species have important roles in the food webs by comprising species that feed at various levels of the food chain, as herbivores, insectivores, carnivores and omnivores. Thus, they have an important

regulatory function as predators or preys (Kolb and Hewson, 1980), they are important to regulate insect populations (Kunz et al., 2011), they provide seed dispersal (Willson, 1993) and pollination of several species (Carthew and Goldingay, 1997; Kunz et al., 2011) and they also act as indicators of ecosystem health (Leis et al., 2008). Still, our knowledge on them remains relatively scarce, patchy and geographical biased (Reeder et al., 2007). Nowadays, mammals face several threats due to human activities and it is estimated that at least 40% of the species worldwide are being affected by loss and degradation of habitats (Schipper et al., 2008). The response of mammals to these threats heavily depends on species characteristics and how they perceived the changed habitat. So, it is crucial to understand how habitat loss and fragmentation affect not only the distribution of species and composition of communities but also the genetic diversity of populations, as these modifications can constrain species to small areas and reduce gene flow between populations. Additionally, these threats are not uniformly distributed across the globe, with tropical and neotropical regions being the most affected (Schipper et al., 2008). Thus, in a world in constant change, remains crucial to understand how species and populations respond to emergent threats.

1.2 The Cerrado: a neglected but rich domain

Brazil, with more than 5.8 million km^2, is the fifth largest country of the world comprising six major phytophysiognomic domains – Amazon, Cerrado, Atlantic forest, Caatinga, Pantanal and Pampa (Fig. 1.1). The Cerrado occupies a large area in South America and it comprises 22% of the Brazilian territory with 2 million km^2. This domain has a central position in Brazil, being bordered in the north by Amazonia, in the south by the Atlantic Forest, in the northeast by the Caatinga and in the southwest by the Pantanal. Its latitude and longitude vary between 5º to 20º and between 45º to 60º, respectively, which promotes gradual changes in climate along all domain. This fact, is amplified by the range of altitudes present in Cerrado that vary from 100 meters near Pantanal to around 1500 meters in some areas of the Central Plateau (Oliveira and Marquis, 2002). Generally, the climate is classified as seasonal tropical. The annual mean temperature is 22-23 ºC with a maximum of 40 ºC and a minimum that can reach zero degrees during winter. The mean precipitation is 1200 to 2800 mm per year and occurs mainly during the rainy season, i.e. between October to March that corresponds to the austral spring and summer months (Coutinho, 2000).

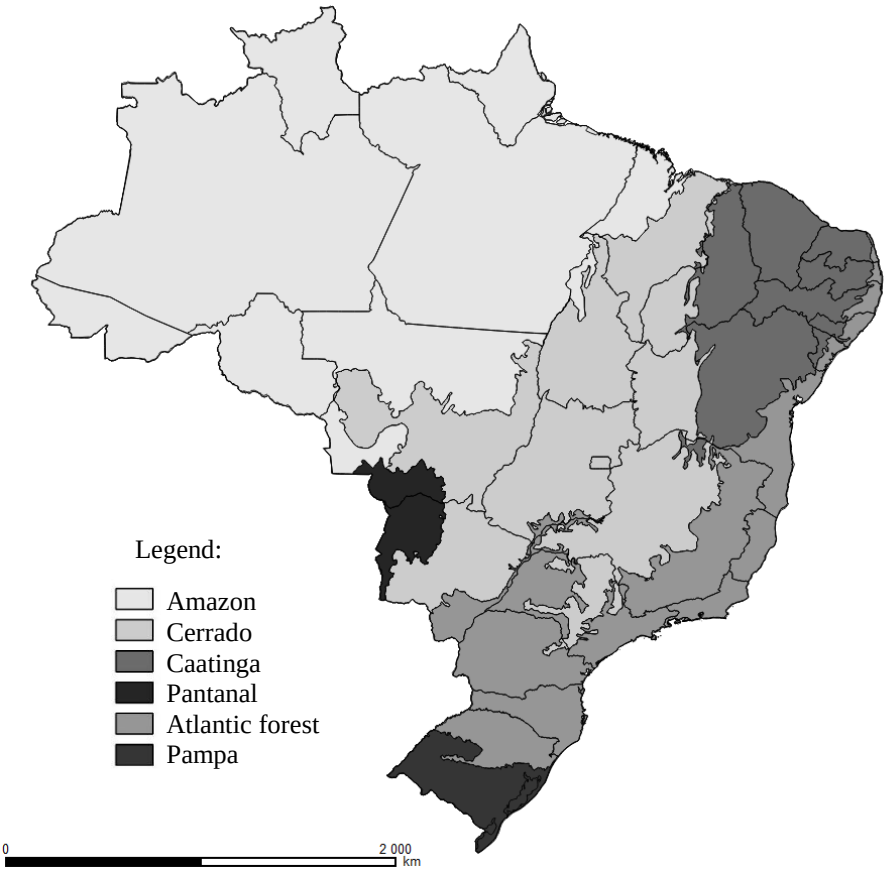

Fig. 1.1 – Brazilian phytophysiognomic domains

The strategic location of the Cerrado makes it an important connection point for biodiversity, which enhances its importance from the conservation viewpoint. Besides being the richest savanna of the world (Silva and Bates, 2002), the Cerrado is also considered one of the 25 most important biodiversity hotspots due to its high rate of endemism, both in fauna and flora, and because it retains less than 20% of its natural vegetation (Myers et al., 2000). Additionally, studies estimate that 30% of the Brazilian biodiversity is present in Cerrado. Until now, at least 1,268 vertebrate species and 10,000 plant species have been recorded, of which 117 and 4,400 are endemic, respectively. Nonetheless, inventories of fauna and flora are considered unsatisfactory (Myers et al., 2000).

The Cerrado is characterized by a heterogeneous mosaic of physiognomies comprising forests formations, savannas and grasslands. The five main structural types described for Cerrado are: the cerradão – a dense forest of closed canopy with 8 to 15 meters height; the cerrado *sensu stricto* – a savanna with a predominance of scrubs with 5 to 8 meters; the campo Cerrado – a savanna with small scrubs of 3 to 6 meters tall and with trees scarcely distributed;

the campo sujo - a grassland with some scattered scrubs and small trees; and the campo limpo - a grassland without trees and scrubs (Silva and Bates, 2002).

The diversity of Cerrado has been neglected for decades and, during this time, conservation priorities focused mostly the Atlantic Forest and the Amazonia. Initially, it was thought that the Cerrado had a poor fauna and flora, neglecting its importance from a conservation viewpoint. For these reasons, it was severely devastated for decades without effective restrictions. The change of the Cerrado started in the 18th century with activities related with mining exploration for gold and diamonds that involved deforestation, water and air pollution but also the subsidence of the soils. The first large urban centres were also created in strategic locations to facilitate mining activities.

The soils of Cerrado are poor in organic matter and nutrients, are very acid and, due to their high porosity and good drainage, are also leached (Coutinho, 2000). These characteristics prevented their use for agriculture for decades, but not for livestock activities that soon began to modify the landscape. Thus, the native vegetation was clear-cut, burned and substituted by African grasses to feed the cattle. The exponential growth of bovines in Cerrado is a direct consequence of the increase of planted pastures. It was only in the 1950's, with the increasing demand of agriculture products, that agriculture activities in Cerrado increased at a large scale. However, the use of the Cerrado soils was only possible due to technological advances in agronomic sciences. As such, extensive areas of Cerrado have been deforested and contaminated through the combined application of fertilizers and lime (Oliveira and Marquis, 2002). With the development of modern agriculture, the Cerrado has become an important producer of cotton, rice and corn, but mainly the largest source of soybeans and livestock of the whole of Brazil, with negative direct consequences for its native vegetation and fauna. Due to the extensive growth of deforestation of the Cerrado, only 20% of its original vegetation persists (Myers et al., 2000; Oliveira and Marquis, 2002). The importance of the Cerrado has been perceived too late when large areas were already devastated. The Cerrado remains the least protected domain of Brazil with only 8.3% of its territory subjected to some kind of protection – and, if considering only areas with native vegetation, this number drops to 6.5% (Françoso et al., 2015). The most important protected areas in the Cerrado are the Emas National Park (131,832 ha), the Grande Sertão Veredas National Park (84,000 ha), the Serra da Bodoquena National Park (77,000 ha), the Serra da Canastra National Park (71,525 ha), the Chapada dos Veadeiros National Park (60,000 ha), the Chapada dos Guimarães National Park (33,000 ha) and the Brasilia National Park (28,000 ha).

The conversion of natural landscapes has several negative consequences that act in cascade. Those immediately noticeable are habitat loss and fragmentation where patches of native vegetation are surrounded by extensive areas of modified habitat. This could lead to the loss of species both plant - due to the direct cut of natural vegetation - and animal - due to the

loss of habitats on which those species depend. Coupled with these processes often the intrusion of exotic species occurs; these will compete with native species for space and resources. Due to deforestation and to the use of fertilizers, soils become eroded and groundwater polluted (Silva and Bates, 2002).

Currently, the importance of the Cerrado has already been recognized and accepted so, it becomes imperative to revert or at least minimize the impact of human activities in this domain. Such measures include for example the protection and restoration of its natural vegetation, through the connection between remnants and through the implementation of more sustainable agriculture and livestock activities.

1.3 Diversity and importance of the order Chiroptera: The New World bats

Biodiversity is heterogeneously distributed in the globe and it is in the tropics that it reaches its highest values. High productivity, high energy availability and climatic stability (Gaston, 2000) are potentially some of the factors underneath such diversity values. Although several hypotheses have been raised to try to explain the latitudinal diversity gradient, a single answer is difficult to obtain (Brown, 2014). But, in fact, this pattern has been demonstrated for a wide range of taxonomic groups (e.g. for passerine birds - Kennedy et al., 2014) and this is also true for bats (Ramos Pereira and Palmeirim, 2013). The Chiroptera constitutes the second largest order of mammals, with more than 1400 recognised bat species (Mammal Diversity Database, 2018), being overcome only by Rodentia. Due to its high functional diversity, bats play key ecological functions in ecosystems. Frugivorous bat species help forest regeneration through seed dispersal, while nectarivorous bats help forest maintenance by changing pollen from male stamens and female pistils within a plant or among plants, promoting pollination. Around 70% of all bat species are insect feeders and, for this reason, important controllers of insect populations that constitute agricultural pests (Kunz et al., 2011). Finally, there are also bats that feed on small vertebrates or even blood, playing regulatory functions as predators or prey (Kunz et al., 2011).

Taxonomic, functional and phylogenetic diversities of bats in Brazil is high. The last Brazilian checklist of bats recorded 178 species distributed in nine families (Phyllostomidae – 92 species; Molossidae – 29 species; Vespertilionidae – 28 species; Emballonuridae – 17 species; Thyropteridae – 5 species; Mormoopidae – 3 species; Noctilionidae – 2 species; Furipteridae – 1 species; Natalidae – 1 species) and 68 genera (Nogueira et al., 2014). In terms of feeding habits, there are in Brazil species that feed on insects, fruits, nectar, pollen, leaves, fishes, small vertebrates and even blood. In fact, here occur simultaneously the three

sanguinivorous species present in the entirely world (*Desmodus rotundus*, *Diphylla ecaudata* and *Diaemus youngi*). Such trophic diversity is unparalleled in the Mammalia.

1.4 Neotropical bats and habitat fragmentation

Habitat loss and fragmentation are ubiquitous threats and constitute serious problems for biodiversity. These widespread human-induced changes are responsible for the drastic reduction of original vegetation with consequent isolation of remnant fragments, changing communities in landscapes. Consequently, it is essential to understand how communities respond to these changes. Although, bats have been pointed as good indicators of landscape changes due to their high local abundance, species richness and ecological diversity (Jones et al., 2009), their responses to landscape changes are still not clear. Based on principles of Island Biogeography Theory (IBT - MacArthur and Wilson, 1967) it is expected that habitat loss and fragmentation lead to the decrease in abundance and species richness, once smaller fragments have less foraging and roosting resources. For bats, general patterns are difficult to obtain because larger fragments or even continuous habitats do not necessarily support more species and individuals than smaller fragments. While some studies found that species richness and abundance are higher in more continuous habitats (Cosson et al., 1999), others found the opposite, i.e. higher species richness and abundance in moderately fragmented forest than in continuous forests (Klingbeil and Willig, 2009), or did not find any significant differences between continuous habitats and forest fragments (Bernard and Fenton, 2007). However, beyond the area size other compositional and configurational characteristics of the landscape may strongly affect bat responses to habitat changes, such as quantity of each cover type, forest patch density, spatial configuration, connectivity of fragments, edge density and structure of the surrounding matrix (Avila-Cabadilla et al., 2012; Cisneros et al., 2015). Additionally, bat responses to these landscape characteristics are generally ensemble- and species-specific. Frugivorous bats are considered the most resilient to landscape changes due to their generalist behaviour and large home-ranges. In fact, abundance of several frugivores bats seems to have a negative relation with forest cover. Species of the genera *Carollia* and *Sturnira* are some of the most abundant frugivores in the neotropics and they feed on plant species highly abundant in early- or mid-successional stages such as *Cecropia*, *Piper* and *Solanum*, which could explain the observed general patterns of higher densities of frugivores in areas with less vegetation (Klingbeil and Willig, 2009). Even so, canopy and understory frugivores have different traits promoting different vulnerability to fragmentation. Canopy frugivores, e.g. *Artibeus* spp., feed on tree species that produce high quantity of fruits in short periods and, because these trees are usually patchily distributed (Milton et al., 1982), canopy frugivores need to travel long distances

to satisfy their feeding requirements. On the other hand, understory frugivores eat fruits of shrubs and small trees with a localized distribution. These scrubs produce few fruits per night but present a fruit production that is extended over weeks or months. For this reason, understory frugivores have shorter flights and smaller home-ranges (Henry and Kalko, 2007) and are found in open and cluttered areas (Marciente et al., 2015). Nectarivore bats, especially those with smaller home-ranges are negatively affected by habitat disruption except in cases where the matrix provides more foraging resources with higher quality than forests, as may occur in some agricultural areas (Quesada et al., 2003; Estrada et al., 2006; Cleary et al., 2016). Gleaning animalivorous (Phyllostomidae, Phyllostominae) are associated with complex vegetation structures. They prefer mature forests or late successional forests and are sensitive to open and non-forested areas due to the limited prey availability, low natural abundance and small home-range sizes (Meyer et al., 2008). Despite this, in Iquitos (Peru), researchers reported that gleaning animalivorous are associated with edge density probably because their prey species are abundant in edges in this area. These results are not in concordance with others that report that gleaning animalivorous are edge-sensitive, responding negatively to disturbance and fragmentation (e.g. Fenton et al., 1992; Medellín et al., 2000). Aerial insectivorous are affected in different ways depending on their preferred foraging habitat and feeding mode, traits which are related to wing loading and aspect ratio of the species. The wing loading is obtained dividing the mass by body area and the aspect ratio is obtained dividing the square of the wingspan by the area (Norberg and Rayner, 1987). Aerial insectivorous with low wing loading and low aspect ratio forage mainly in cluttered spaces and are generally associated with greater forest cover present in mature forests, because these areas support high vegetation diversity and, consequently high diversity of insects (Wilson et al., 1996). On the other hand, aerial insectivores with high wing loading and aspect ratio feed mainly in open areas or above canopy and have an energetically cheap flight. For these reasons, they can fly long distances in uncluttered space and they can easily transpose the obstacles imposed by fragmentation (Gonçalves et al., 2017).

1.5 Genetic consequences of habitat loss and fragmentation on bats

Beyond changing assemblage structure, habitat loss and fragmentation also affect genetic structure of populations putting the long-term viability of populations at risk (Struebig et al., 2011). Migratory species have the ability to perform long distance dispersal and, for this reason, generally have lower genetic structure (Moussy et al., 2013). On the other hand, sedentary species have limited dispersal ability so, tendentially have higher genetic structure (Moussy et al., 2013). However, exceptions to these patterns are observed. For example, the

migratory species *Myotis myotis*, can fly several hundreds of kilometres annually. Even so, it seems to avoid crossing the Strait of Gibraltar, with only 14 km width. The strait seems to act as a barrier to gene flow between European and North African colonies of *M. myotis*, as confirmed by the presence of two genetically distinct clades in each side of the Mediterranean (Castella et al., 2000).

In general, bats have been considered highly mobile to be affected by habitat loss and fragmentation. For many years, it was expected for bats to be able to overcome the barriers imposed by fragmentation, maintaining gene flow between populations. In fact, evidence suggests that some species are not particularly affected by fragmentation at least, at certain scales. For example, the fragmentation of the Alto Paraná Atlantic Forest has not affected gene flow between populations of *A. lituratus*, the largest Neotropical seed-dispersing bat that feeds mainly on *Ficus* (McCulloch et al., 2013). Additionally, at shorter scales, the small understory frugivorous bat *Carollia castanea*, can also maintain gene flow in agricultural landscapes in northeast Costa Rica (Ripperger et al., 2014). Other studies, however, have showed that genetic structure of bat populations can be shaped by landscape changes. Thus, to the extent that landscape modifies and becomes fragmented, genetic diversity of populations tends to decrease and differentiation between population tends to increase. Such changes may occur even at small scales (e.g. Meyer et al., 2009; Ripperger et al., 2012); for example, *Dermanura watsoni* from the same agricultural landscapes of *C. castanea* referred above, are unable to maintain healthy levels of gene flow, presenting high genetic differentiation between populations (Ripperger et al., 2012). Similar results were also found in two other phyllostomid bats, *Uroderma bilobatum* and *Carollia perspicillata*, in an island system in Panama. Although both species present significant genetic differentiation between populations, genetic differentiation was higher in the less vagile species, *C. perspicillata*, which emphasizes the importance of species traits when evaluating the response to fragmentation (Meyer et al., 2009).

Specialization degree is considered a good predictor of species sensibility to habitat loss and fragmentation, with more specialist species potentially more susceptible to the negative effects of these processes. For example, *Myotis macropus*, a highly specialised species that feeds mainly on aquatic insects over permanent waterway shows low levels of gene flow between its populations, although it is a highly vagile species; such pattern is probably due the degradation and destruction of the riparian vegetation along its distribution range (Campbell et al., 2009). So, species traits seem to, at least partially, determine species response to fragmentation. However, other factors directly linked with landscape may also work concurrently. Patch area for example, is associated with levels of genetic diversity in fragments but its effects are not transversal for all species. Using three bat species Struebig et al. (2011) evaluated if patch area was responsible for the patterns of genetic diversity in tropical forest fragments. In their study, they found that *Kerivoula papillosa* and *Rhinolophus trifoliatus*

exhibit a decline in allelic richness in fragments compared to continuous forest; however, this pattern was correlated with patch area only for the first species. The allelic richness of the third species, *Rhinolophus lepidus*, was similar in continuous habitat and fragments (Struebig et al., 2011) probably because this species is the least dispersal-limited.

Contrary to predictions that genetic structure of bats was not affected by habitat loss and fragmentation, bat responses to these factors are not straightforward. There are several factors directly linked with species traits or landscape characteristics affecting this relation. Thus, more genetic studies are required to help to understand which factors are affecting the genetic response of bats to landscape changes.

1.6 Aims and structure of the thesis

The general objective of this thesis is to evaluate the consequences of habitat loss and fragmentation on several dimensions of biodiversity – taxonomic, functional, and phylogenetic diversities of assemblages and genetic diversities of populations. To respond to this aim, I firstly conducted a meta-analysis to review the genetic consequences of habitat loss and fragmentation on mammals all around the world. Then, taking bats as a model group, I studied the effects of landscape variables under bat assemblages of the Serra da Bodoquena, a region characterized by a landscape forest gradient.

The specific aims of each chapter are the follow:

In **Chapter one** I present a general introduction with the topics covered by this thesis.

In **Chapter two** I present a brief description of several aspects of the studied area – the Serra da Bodoquena region, a karstic region that belongs to Cerrado.

In **Chapter three**, by using a meta-analysis, we describe general trends of the effects of habitat loss and fragmentation on several genetic measures – allelic diversity, allelic richness, observed and expected heterozygosity and inbreeding coefficient – and we evaluate which traits – body mass, reproductive rate, home range, locomotion mode, trophic guild and forest dependency – increase or decrease the susceptibility of mammalian species to habitat loss and fragmentation. We predict a general loss of genetic diversity on populations living in fragments compared to those living in continuous habitats, but the magnitude of this loss depends on species characteristics. So, we predict that large-bodied species, species with low reproductive

rate, wide home-ranges, those species with terrestrial and arboreal locomotion and more specialized species can be the most negatively affected by fragmentation.

In **Chapter four** we evaluate which landscape variables affect bat assemblages in the Serra da Bodoquena. Firstly, we quantify metrics related to bat assemblages, i.e. taxonomic, functional and phylogenetic diversities and beta diversity. Then, we evaluate which landscape characteristics (distance to nearest border of Serra da Bodoquena National Park, forest cover, forest border length and number of forest fragments) affect bat assemblages at three different scales (buffers of 300, 1000 and 2500 meters). We expect that assemblages living in more impacted areas are a subset of species from those living in well preserved areas and that bat species richness and taxonomic, functional and phylogenetic diversities decrease in more fragmented areas, with less vegetation cover and larger borders.

In **Chapter five** we test which landscape variables affect species diversity and genetic diversity of two co-occurring bat species, *Artibeus planirostris* and *Carollia perspicillata*, living in the Serra da Bodoquena region and we test if species and genetic diversity are correlated across the studied sites. Additionally, we also evaluate if species and genetic dissimilarity change in similar ways. In this chapter we predict that studied species respond differently to landscape characteristics because they have different ecological characteristics and different vagilities. Additionally, we predict a pattern of isolation by distance in the least vagile species, *C. perspicillata*, and that species with similar landscape characteristics should retain similar species and genetic diversities.

Finally, I provide a general discussion of the main outcomes of the previous chapters in **Chapter six** along with conservation implications of our main results. I also dissertate about the weakness and gaps of my thesis, present perspectives for future work, and summarize our main major conclusions.

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CHAPTER 2

STUDY AREA

Study Area

2.1 Location

Mato Grosso do Sul (MS) State is located at Central-West Brazil (Fig. 2.1a). It has an area of 357,146 km^2 and 2,619,657 inhabitants. During the last decades, human activities have altered the natural vegetation of Mato Grosso do Sul. However, some remnants of natural vegetation persist, as is the case of the Serra da Bodoquena National Park (SBNP; Fig. 2.1b). This well-preserved park and its adjacent areas are the focus of this research. The SBNP was created in 2000 with the main aim to protect natural ecosystems with high ecological importance, such as the most well-preserved area of Atlantic Forest of the state. The SBNP encompasses almost 77,000 ha distributed in two distinct geomorphological units, the norther and southern borders. The northern part has 27,793 ha and the southern sector has 48,688 ha that are incorporated in territories of 4 municipalities: Bonito, Bodoquena, Jardim and Porto Murtinho.

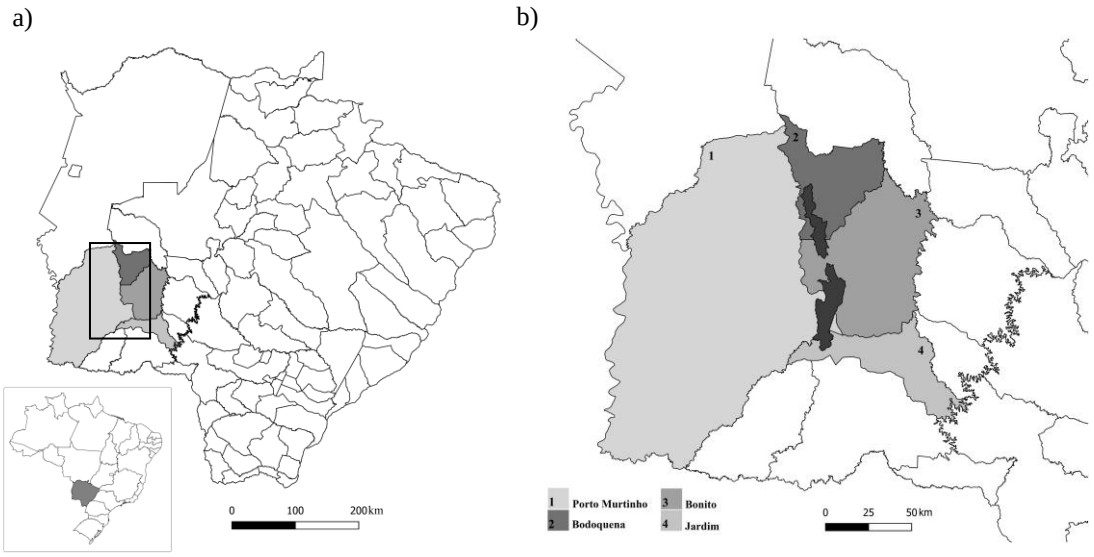

Fig. 2.1 – a) Location of Mato Grosso do Sul State in Brazil and the approximated location of Serra da Bodoquena National Park (SBNP); b) Limits of the municipalities that integrate the SBNP (approximate area that encompasses SBNP is represented by dark grey).

2.2 Land Cover

Mato Grosso do Sul is characterized by high biodiversity levels promoted by its strategic location in the transition between three Brazilian domains: Pantanal, Cerrado and Atlantic Forest (Fig. 2.2). Although inserted in the Cerrado, the Serra da Bodoquena National Park is greatly influenced by other adjacent domains and has a central role in their connection. In fact, Serra da Bodoquena corresponds only to 0.2% of the surface of Mato Grosso do Sul but nonetheless it includes 16% of all the remnants of Atlantic Forest in the state, with a predominance of decidual seasonal forest ecosystems (Campanili and Prochnow, 2006). Semi-deciduous seasonal forest, an Atlantic forest physiognomy, and Cerrado vegetation types are also found here.

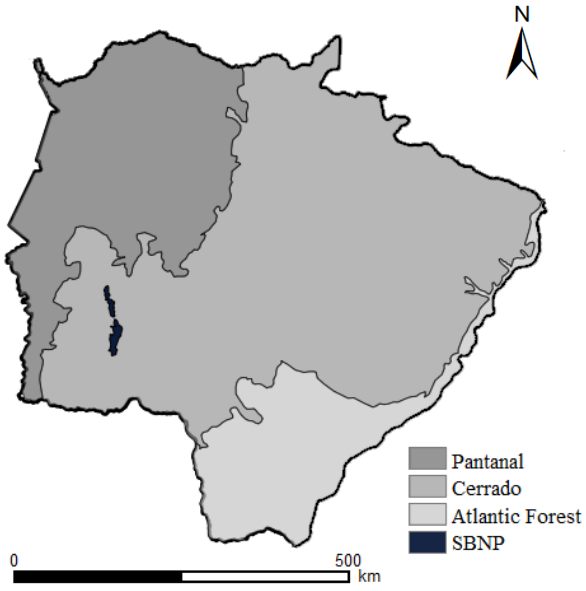

Fig. 2.2 – Domains present in Mato Grosso do Sul State.

2.3 Hydrography

The Serra da Bodoquena region is integrated in the hydrographic basin of the Paraguay River and in the sub-basins of Miranda and Apa River (Fig. 2.3). Within SBNP and in adjacent areas are located headwaters of very important rivers for the region. At the west side of the park, in the Municipality of Porto Murtinho, there are the Aquidabã and Branco Rivers that flow directly to the Paraguay River. At the northern border of the Serra da Bodoquena, the Salobra River represents the main watercourse flooding into the Miranda River within the municipality of Bodoquena. In adjacent areas of the SBNP there are other two rivers, the Formoso at the east and the Prata at the southeast, both tributaries of the Miranda River. Perdido River is the main watercourse at the southern border of the Serra da Bodoquena and it is a tributary of the Apa River (Salzo, 2006). Due to geology of region the norther part of the Serra da Bodoquena has fluvial features whereas the southern sector has karst landforms (Sallun Filho et al., 2004).

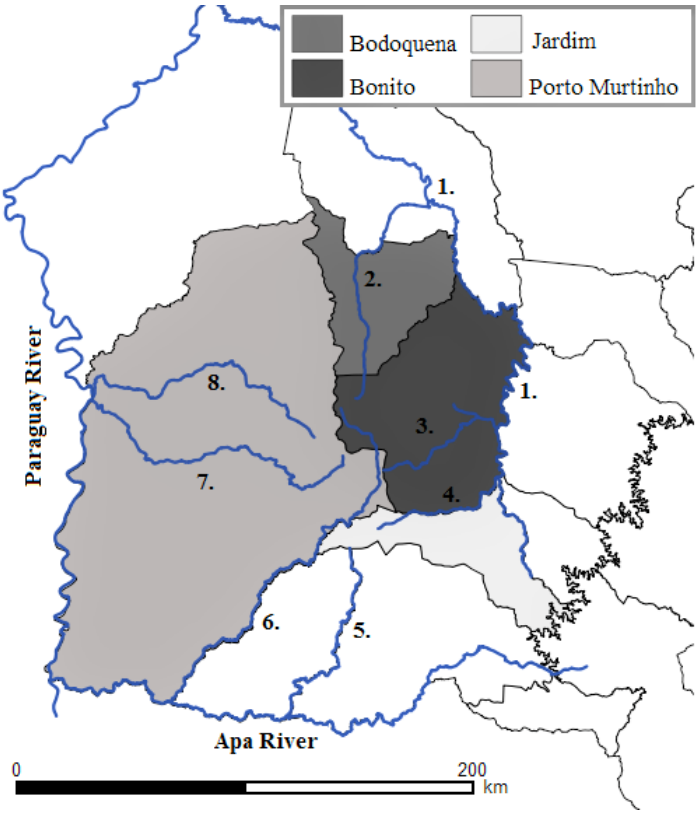

Fig. 2.3 – Main watercourses in the Serra da Bodoquena region. Legend: 1. Miranda River; 2. Salobra River; 3. Formoso River; 4. Prata River; 5. Caracol River; 6. Perdido River; 7. Branco River; 8. Aquidabã River.

2.4 Geological origin and geomorphology

Serra da Bodoquena belongs to a set of plateaus that border the Pantanal basin. This karstic region is integrated in the Paraguay Folded Belt, a Neoproterozoic unit developed under the Corumbá group, whose origin is dated between 550 to 570 million years ago (Boggiani, 1999). This region results from the break of a supercontinent called Rodinia, which formed a large ocean among continental platforms. Due to the deposition of the calcareous shells of marine dead organisms, the limestones rocks were formed. Then, 20 million years later, the continental plates approximated again, collided and formed a set of mountain ranges, which after a series of erosion processes formed the Serra da Bodoquena (Boggiani, 1999).

As referred the plateau of the Serra da Bodoquena has a carbonate origin of the Corumbá Group, but the plains are composed by carbonate rocks and flyschoid sediments, which were folded and metamorphosed and they belong to the Corumbá and Guiabá group (Almeida et al., 1976; Sallun Filho et al., 2004). The altitude of the plateau varies from 350 to 800 meters and is composed by calcitic limestone of the Bocaina formation, as well as carbonate and terrigenous rocks of the Cerradinho formations, both belonging to Corumbá group. The highest point of the plateau is characterized by intrusive granites (Sallun Filho et al., 2004). The plains around the plateau are quite diverse. The west border has a rugged relief that marks the transition to the Paraguay River with an altitude that varies between 150 to 450 meters and it is composed by granite-gneiss rocks. On the other hand, the east border has a soft slope as the transition to the floodplain of the Miranda River. This border with altitudes that vary between 100 to 300 meters, is composed by terrigenous and carbonated rocks of the Corumbá Group and by marbles of the Cuiabá Group. At the south of the plateau, the border is formed by lowlands with altitudes varying between 200 to 400 meters, developed under the Cerradinho formation, marbles of the Cuiabá Group or sandstones of the Aquidauana formation. The north of the Serra da Bodoquena plateau ends with alluvial plains at low altitudes, between 80 to 250 meters (Sallun Filho et al., 2004).

The presence of soluble rocks, i.e. limestones, in the Serra da Bodoquena promotes the formation of a typical karst topography and the presence of several caves and waterfalls that further increase the value of the region.

2.5 Climate

Serra da Bodoquena region is classified as Aw by the Köppen-Geiger climatic classification (Kottek et al., 2006), which means that it has tropical climate with wet summer (October to April) and dry winter season (May to September). The four municipalities (Bodoquena, Bonito, Jardim and Porto Murtinho) that enclose the area of the Serra da Bodoquena have identical patterns of temperature and precipitation (Fig. 2.4) with the lower values occurring between June and September.

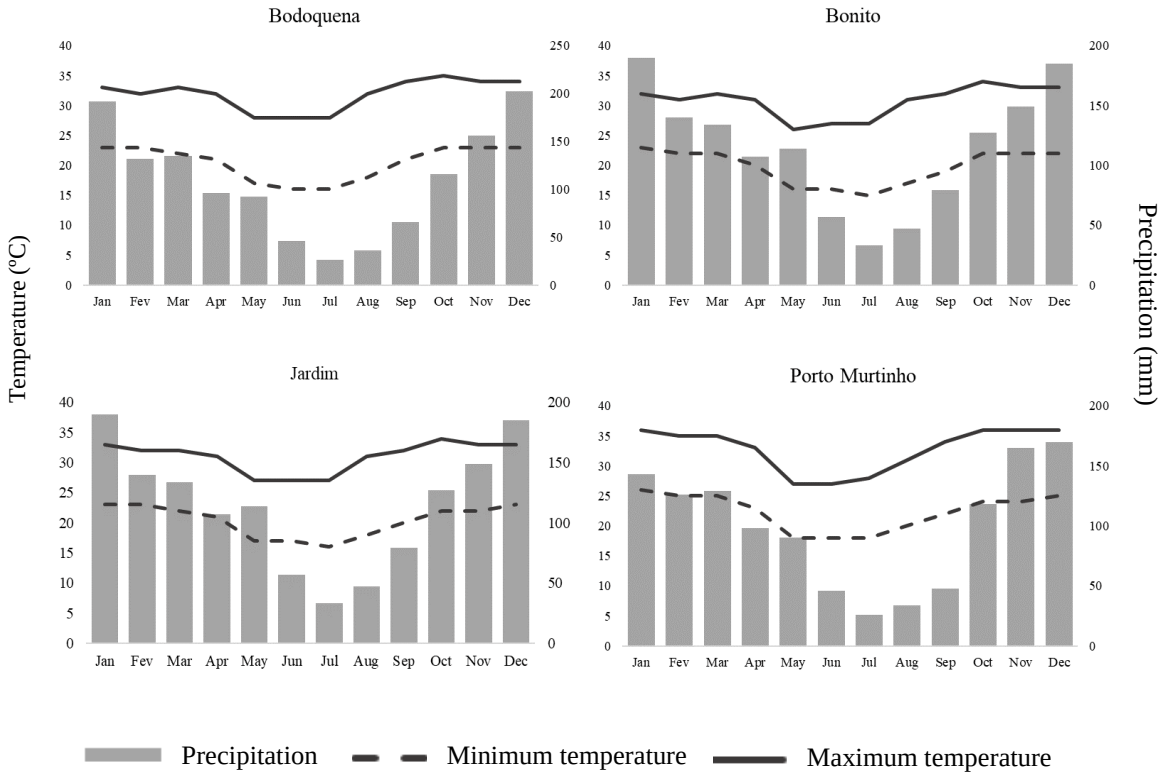

Fig. 2.4 – Mean meteorological data of the last 30 years in 4 municipalities that encompasses the Serra da Bodoquena National Park, namely Bodoquena, Bonito, Jardim and Porto Murtinho (http://www.climatempo.com.br/).

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CHAPTER 3

A META-ANALYSIS OF THE EFFECTS OF HABITAT LOSS AND FRAGMENTATION ON GENETIC DIVERSITY IN MAMMALS

A meta-analysis of the effects of habitat loss and fragmentation on genetic diversity in mammals

Ana Lino[a], Carlos Fonseca[a], Danny Rojas[a,b,c], Erich Fischer[d], Maria João Ramos Pereira[a,e]

[a]Department of Biology & Centre for Environmental and Marine Studies (CESAM), University of Aveiro, Campus Universitário de Santiago 3810-193 Aveiro, Portugal.

[b]Department of Ecology and Evolution, Stony Brook University, 650 Life Sciences Building Stony Brook, NY 11794, USA.

[c]Department of Natural Sciences and Mathematics, Pontificia Universidad Javeriana Cali, Colombia.

[d]Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brazil.

[e]Department of Zoology, Institute of Biosciences, Universidade Federal do Rio Grande do Sul, Av. Bento Goncalves 9500, Porto Alegre RS 91540-000, Brazil.

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3.1 Abstract

Human activities have led to global changes with direct consequences for biodiversity. For this reason, special concerns have arisen, particularly in respect to global threats such as habitat loss and fragmentation, because they decrease population size, promote the loss of species genetic diversity, contract species geographical distribution and facilitate species loss. Interest in the genetic consequences related to habitat changes has increased in the last decades, so it became crucial to understand how genetic diversity changes due to habitat loss and fragmentation and if the degree of genetic losses is related with species traits. Thus, we conduct a meta-analysis to test if genetic diversity of mammalian populations that live in fragments is lower than those living in continuous habitats and we also explore which species traits could be related with the observed patterns. Through this meta-analysis we detected an overall decrease in allelic diversity, allelic richness, observed heterozygosity and expected heterozygosity in mammalian species that live in situations of high habitat fragmentation. However, not all species are affected the same way. We found that species with larger body mass are the most negatively affected by fragmentation; terrestrial and arboreal mammals are more negatively affected than flying species; herbivores suffer consistent negative effect of fragmentation in the four genetic measures analysed; and forest-dependent species are the most susceptible to the negative effects of fragmentation. We expected to detect an increase in inbreeding coefficients in fragments when compared to continuous habitats; however, this pattern did not arise, probably because time since fragmentation was not enough and/or species have ways to avoid inbreeding. The patterns here described allow a better understanding of which mammalian species are more susceptible to the negative effects of habitat loss and fragmentation, potentially giving support for the conservation and management of their populations.

Keywords: Allelic diversity; Habitat loss; Heterozygosity; Inbreeding, Mammals.

3.2 Introduction

Among the many factors that can negatively impact mammalian species, habitat loss and fragmentation are the most worrying. The term fragmentation has been widely used in the literature as an umbrella describing changes that occur in landscapes, including the loss of habitat area (Lindenmayer and Fischer, 2006). Nonetheless, fragmentation and habitat loss represent different processes (Fahrig, 2003), as the former is the transformation of continuous areas into discontinued patches of a given habitat, and habitat loss means the reduction of the available habitat area. Despite being recognized as two different processes, habitat loss and fragmentation are interdependent and occur simultaneously in most cases (Didham et al., 2012; Villard and Metzger, 2014; Hanski, 2015). The main consequences of the combined effects of habitat loss and fragmentation are substantial decreases in population size (Koskimäki et al., 2014) and species richness (Püttker et al., 2008; Murphy and Romanuk, 2014), contraction of original geographical distribution (Sanderson et al., 2002; Morrison et al., 2007), and loss of genetic diversity (Gibbs, 2001). Additionally, these processes put at risk species that are intolerant to edge conditions or that suffer high predation at edges (e.g. Batáry and Báldi, 2004). Habitat loss and fragmentation may also reduce the availability of resources for mammalian species, precluding the occurrence of species that require high resource abundance, especially if individuals are unable to encompass sufficient patches in their home ranges (Thornton et al., 2011).

Principles of the island biogeography theory (IBT) of MacArthur and Wilson (1967) were initially applied to understand how species would be affected by habitat loss and fragmentation. The IBT proposes that as island size decreases and isolation increases, insular communities become less diverse because small and isolated islands tend to show high extinction and low colonization rates. The application of IBT to mainland landscapes with fragmented habitats considers habitat patches as islands surrounded by an inhospitable matrix. However, over the years, ecologists have found that the IBT is a generally weak model when applied to fragmented habitats in mainland, as isolation and area *per se* proved to be poor predictors of fragment occupation by the species (Prugh et al., 2008). Furthermore, the matrix is not equally inhospitable for different species; actually, it can allow or preclude movement and dispersal of individuals depending on species' characteristics, and certain species can even take benefits from the matrix for breeding or food supplementation (Ewers and Didham, 2006; Driscoll et al., 2013). Furthermore, the IBT does not consider species traits (Didham et al., 2012), which adds inadequacy for its application under the mainland habitat fragmentation context.

In the last decades, the growing interest in assessing the genetic consequences of habitat loss and fragmentation has led to the development of several studies in plants (Honnay and

Jacquemyn, 2007), invertebrates (Williams et al., 2003), birds (Athrey et al., 2012), mammals (Lancaster et al., 2016) and reviews by some authors (e.g. Keyghobadi, 2007; Aguilar et al., 2008). Many of these studies have reported that habitat loss and fragmentation affect the genetic structure of populations by eroding genetic diversity and increasing genetic differentiation. As fragmentation and habitat loss increase, remnant fragments become more isolated and gene flow between populations tends to decrease unless species are able to overcome the distance between fragments and/or the unsuitable habitat. Reduction and disconnection of suitable natural habitats are often followed by sharp demographic declines, and the resultant smaller populations are more prone to the effects of genetic drift and inbreeding. However, in addition to landscape characteristics, the effects of habitat loss and fragmentation also depend on species traits. Body size is closely linked to other ecological attributes such as dispersal ability and habitat requirements (Swihart et al., 2003; Henle et al., 2004). Generally, larger species have higher dispersal abilities (Tucker et al., 2018), but despite this fact they are considered susceptible to the negative effects of fragmentation (Ewers and Didham, 2006). Locomotion mode is another important trait; flying species are considered less affected because flight ability enables them to easily cross gaps between fragments (Harris and Reed, 2002). Life history traits such as sexual maturity, litter size, number of reproduction events, growth rate and lifespan determine the persistence of species in fragments (Henle et al., 2004) as short sexual maturity, higher litter sizes, higher number of litters per year, high growth rates and high lifespans favour population recovery. Feeding guilds have also been identified as a predictor of vulnerability to forest fragmentation for neotropical vertebrates (Vetter et al., 2011). Finally, species that are not entirely dependent on forest and also use open habitats are expected to be the least affected by fragmentation and loss of forest habitats (Vetter et al., 2011).

Mammals have high importance for conservation and the effects of fragmentation and habitat loss on their genetic structure have been widely addressed. Thus, combining the results of these studies is relevant firstly to understand general patterns of species responses; secondly, as mammals include an array of species with quite different traits, it is important to understand which species traits influence the observed patterns, and how. For these reasons, we present here a meta-analysis to evaluate how the combined processes of habitat loss and fragmentation affect mammal genetic structure, and to explore the species' traits influencing their responses. We do not disassociate habitat loss and habitat fragmentation; instead we focus on the joined effect of these simultaneous processes. Specifically, we describe general trends of the effect of habitat loss and fragmentation on several genetic measures – allelic diversity, allelic richness, observed and expected heterozygosity and inbreeding coefficient –, and evaluated which traits – body mass, reproductive rate, home range, locomotion mode, trophic guild and forest dependency – increase or decrease susceptibility to fragmentation.

3.3 Methods

Literature search

To assess the trends of genetic responses of mammals to habitat loss and fragmentation we searched for papers in the Web of Science database using a combination of the keywords: 'habitat loss' or 'fragmentation' and 'genetic diversity' or 'inbreeding' with 'mammal*' and the names of the terrestrial mammalian orders. Retrieved studies were checked for meeting the defined criteria, and their references inspected to include further studies. We performed similar searches in the OATD (https://oatd.org/) and Openthesis (http://www.openthesis.org/) databases for theses and dissertations that met the criteria. We selected original articles, theses and dissertations published until January 2018 that evaluated effects of habitat loss and fragmentation in mammals and included contrasting situations of "low fragmentation" and "high fragmentation". The "low fragmentation" class, hereafter named "control", included large continuous areas of native habitats as well as fragmented areas representing the larger habitat patches within each study. In its turn, the "high fragmentation" class, hereafter named "fragmented", included the most disturbed areas, with less availability of natural habitat. Thus, low and high fragmentation are contrasting classes relatively to each study. In addition, we considered the natural habitat ascribed by the authors to their study species (Table S3.1). We also considered as controls the studies that used samples from zoological collections representing the genetic diversity before fragmentation. For studies based on codominant markers (microsatellites) we considered allelic diversity (Ad – mean number of alleles per locus), allelic richness (Ar – allelic diversity standardised for sample size), observed heterozygosity (Ho – the average observed heterozygosity of individuals at the population level), expected heterozygosity (He – the expected heterozygosity of individuals within populations under the assumptions of Hardy-Weinberg equilibrium) and the coefficient of inbreeding (Fis – reflects an increase in homozygosity relative to Hardy–Weinberg expectation). For studies based on dominant markers (mtDNA) we considered haplotype diversity (Hd – the probability that two randomly chosen haplotypes are different). This parameter was analysed together with expected heterozygosity (Aguilar et al., 2008). When inbreeding coefficients were not provided in the original articles, we calculated them as Fis = (He – Ho)/He (Höglund, 2009). For all studies, we also recorded the number of sampled individuals as a measure of sampling size. Finally, we collected information on species traits to use as continuous or categorical covariates in subsequent analyses (Table S3.2). Continuous variables were body mass, reproductive rate and home range size. We estimated reproductive rate as the mean litter or clutch size multiplied by the mean number of litters or clutches per year (Quesnelle et al., 2014). Categorical variables were locomotion mode, trophic guild and forest dependency. For

locomotion mode, we categorized the species as terrestrial (species that spend most of their lives on the ground and use it to move), arboreal (species that spend most of their lives in trees and move through branches at the canopy or subcanopy) and aerial (corresponding to bat species because they are the only flying mammals). We considered five trophic guilds in the analyses: omnivore (species that eat a variety of plant and animal items), insectivore (species that feed mainly on invertebrates), herbivore (species that feed on any plant structure as leaves, fruits, nectar, pollen or seeds), carnivore (species that feed mainly on vertebrates) and mycophage (species that mostly eat fungus). Information on body mass, reproductive rate, home range, locomotion mode, trophic guild and forest dependency were collected from the literature (e.g. Strahan, 1983; Reis et al., 2006; Quin et al., 2010; IUCN, 2017). We followed Vetter et al. (2011) to classify species according to forest dependency: species that only use forest habitats (forest habitats), species that also use intermediate habitats as shrubs, bushes and parks (intermediate habitats), species that also use open habitats as fields and grasslands (open habitats), and species that mostly occur in open areas with short grasses (e.g. steppes and grasslands). The last category was excluded from this analysis because species usually do not use forests (n = 4; Vetter et al., 2011). Data regarding habitat preferences was extracted from IUCN Red List (IUCN, 2017).

Data analysis

With the genetic metrics collected from the original studies, we computed means and standard deviations in each of the two conditions, continuous and fragmented habitats, to perform the meta-analysis. The analyses were performed individually for each of the metrics – Ad (n = 14), Ar (n = 24), Ho (n = 28), He (n = 32) and Fis (n = 27). For each study, the extent of the effect of fragmentation, i.e. the difference between the mean value of each of the genetic measures in continuous and fragmented habitats, was quantified through the standardized mean difference (Hedge's d) a measure of effect size (Gurevitch and Hedges, 2001). Negative values of effect size (d) for Ad, Ar, Ho and He indicate that fragmentation acts to decrease these parameters. On the other hand, negative values of effect size for Fis suggest positive effects of habitat loss and fragmentation for mammal populations, thus lower inbreeding (Aguilar et al., 2008). To combine estimates of the effect sizes of different studies, we used random-effect models. This statistical model encompasses both the variance within and between studies, due to sampling errors and random variation and, for these reasons, are the most used in ecological studies (Joricheva et al., 2013). Heterogeneity among effect sizes was evaluated with sub-group analysis based on Q-statistics. If heterogeneity was detected, i.e. if studies were significantly different from each other, we assessed which variables were responsible for those differences.

When $Q_{between}$ is significantly greater than Q_{within}, the categorical variable explains heterogeneity (Harrison, 2011). For continuous variables, we performed meta-regression analysis with log-transformed values. Information on quantitative species traits present in the literature showed high variability. So, it is important to understand if different results arise depending on the used data in analyses. For this, we perform several meta-regressions with lower, higher and medium values for body mass, home range and reproductive rate, and with all possible combinations between them. Before computing meta-regression analysis, we tested for correlations between continuous variables (body mass, home-range, and reproductive rate) with the Spearman rank correlation. Different correlation tests were done for each set of species included in each of the genetic metrics analysed (results of Spearman correlation tests are present in table S3.3). By this way, meta-regression analyses were done with the body mass and home range size for Ad and Ar and only with body mass for observed and expected heterozygosity. Analyses were performed in RevMan 5.3 (Cochrane, 2014), in OpenMEE (Dietz et al., 2014) and in R (R Core Team, 2013).

Potential publication bias

The most common publication bias is the tendency of authors and journals to publish studies with statistically significant results. We examined possible publication bias related with studies included in our meta-analysis in two ways. Firstly, we used funnel plots to graphically examine the occurrence of symmetry around the mean effect size when plotting the effect size versus the standard error (Egger et al., 1997). Secondly, publication bias was examined by fail-safe number calculation that determines how many nonsignificant studies would have to be added to the meta-analysis for the overall mean effect size to turn non-significant, enabling to estimate if publication biases may be safely ignored. The original approach developed by Rosenthal (1979) is an unweighted method that overestimates the number of studies needed to reduce a meta-analysis to nonsignificant. For this reason, we estimate publication bias based on a later revised fail-safe n developed by Rosenberg (2005) that is a weighted version of the Rosenthal´s fail-safe n. A fail-safe number is considered robust, i.e. publication bias may be safely ignored, if it is greater than 5n + 10, where n is the number of studies in the meta-analysis (Rosenthal, 1979).

3.4 Results

Searches in the Web of Science database returned 533 studies, of which 133 were initially selected based on their titles and abstracts. After complete inspection, only 21 met the criteria for inclusion in our meta-analysis. Through inspection of studies quoted in these articles, we added eight other articles meeting our criteria. Searches in OATD and Openthesis databases retrieved 1969 documents but only five followed our criteria. Two of them matched with articles already included in our meta-data, thus only three were added. In total, we included 32 studies in the analysis (Fig. 3.1; Table S3.1; Table S3.2). As some authors studied more than one species we ended up with 38 input data distributed in Rodentia (n = 11), Primates (n = 9), Chiroptera (n = 8), Diprotodontia (n = 4), Carnivora (n = 3) and Dasyuromorphia, Didelphimorphia and Artiodactyla (n = 1, each). The studies were distributed across 6 biogeographic regions: Australian (n = 12), Neotropics (n = 10), Paleartic (n = 5), Afrotropics (n = 5), Oriental and Nearctic (n = 3, each).

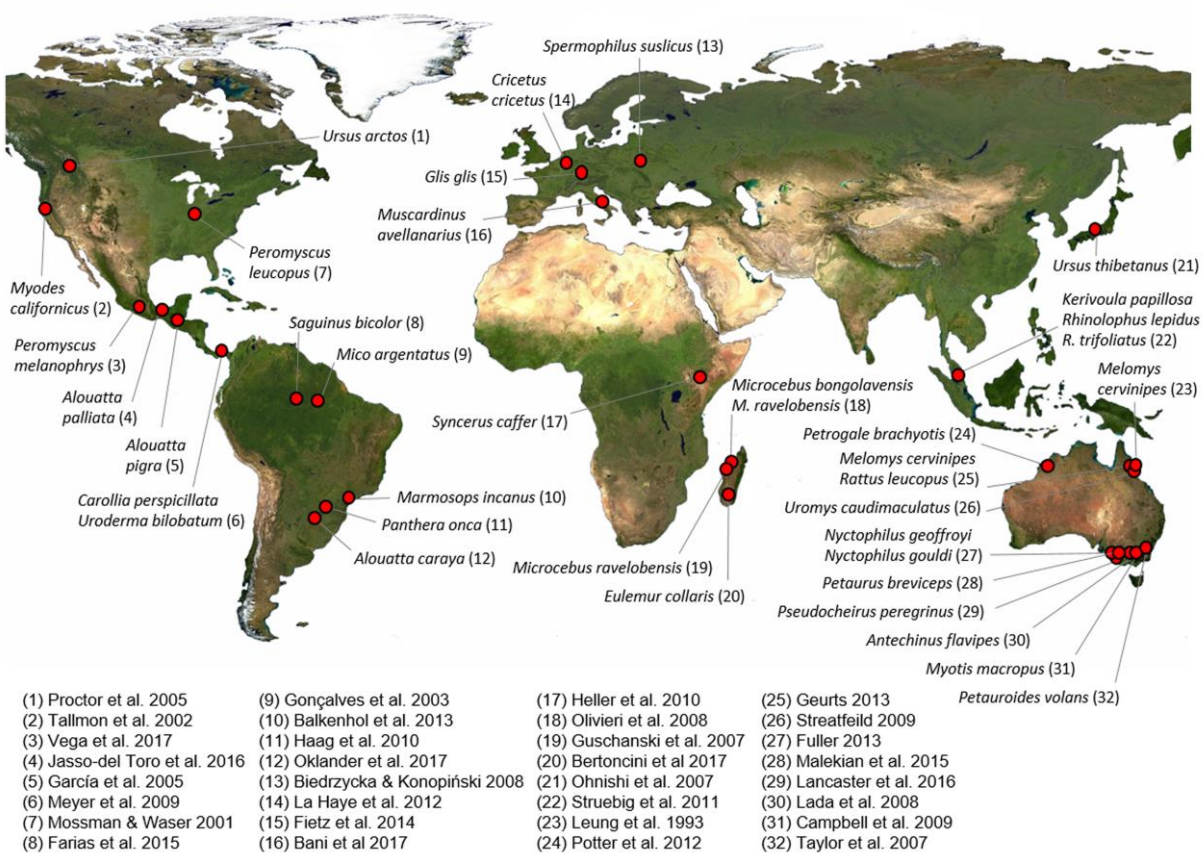

Fig. 3.1 – Distribution of mammal species studied for effects of habitat loss and fragmentation on population genetic diversity, which were included in the present meta-analysis.

Funnel plots revealed a slight publication bias while the calculated weighted fail-safe numbers only revealed publication bias for Fis [Ad: 300 > (5 * 14) + 10 = 80; Ar: 864 > (5 * 24) + 10 = 130; Ho: 803 > (5 * 28) + 10 = 150; He: 959 > (5 * 32) + 10 = 170; Fis: 0 < (5 * 27) + 10 = 145]. Heterogeneity tests show variation between studies for all diversity measures [Ad: $Q_{between}$ = 258.86 $p < 0.001$, I^2 = 95%; Ar: $Q_{between}$ = 329.15, $p < 0.001$, I^2 = 93%; Ho: $Q_{between}$ = 222.73, $p < 0.001$, I^2 = 88%; He: $Q_{between}$ = 429.01, $p < 0.001$, I^2 = 93%; Fis: $Q_{between}$ = 493.15, $p < 0.001$, I^2 = 95%]. Results of Hedge's *d* were negative and significantly different from zero ($p < 0.05$) for Ad, Ar, Ho and He (Fig. 3.2), indicating that fragmentation brings negative consequences to these parameters. On the other hand, despite a slightly negative Hedges' *d* for Fis, fragmentation showed non-significant overall effect on this measure ($p = 0.440$).

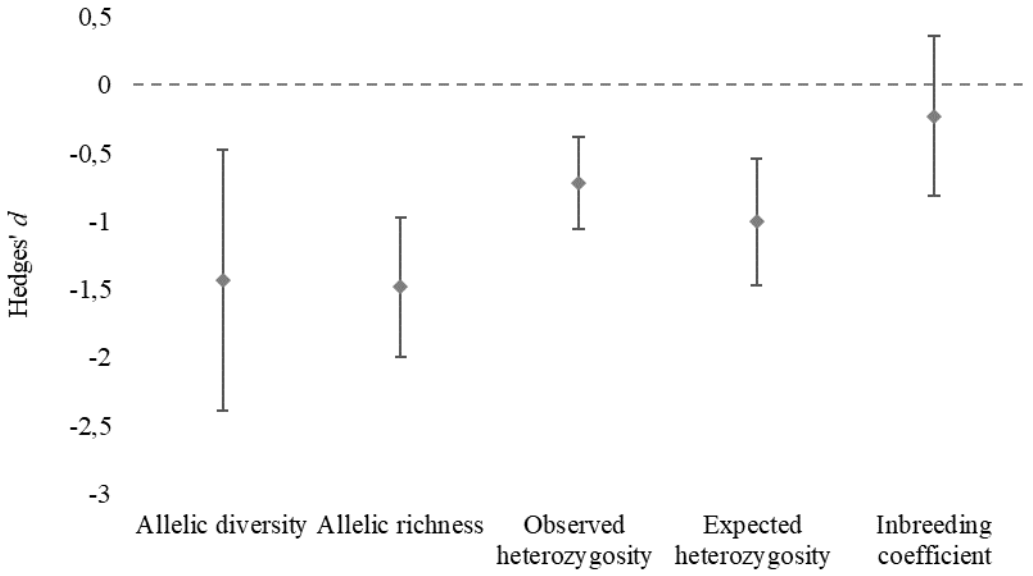

Fig. 3.2 – Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat loss and fragmentation on different measures of genetic diversity.

Results of meta-regression analyses are the same regardless of the values that were used (i.e. lower, higher and mean values; Table S3.4) and they show a negative correlation between body mass and the effect size for allelic richness and expected heterozygosity. The Hedges' *d* for both measures decreased as body mass of mammal species increased, meaning that species of higher body mass are the most negatively affected by fragmentation (Fig. 3.3).

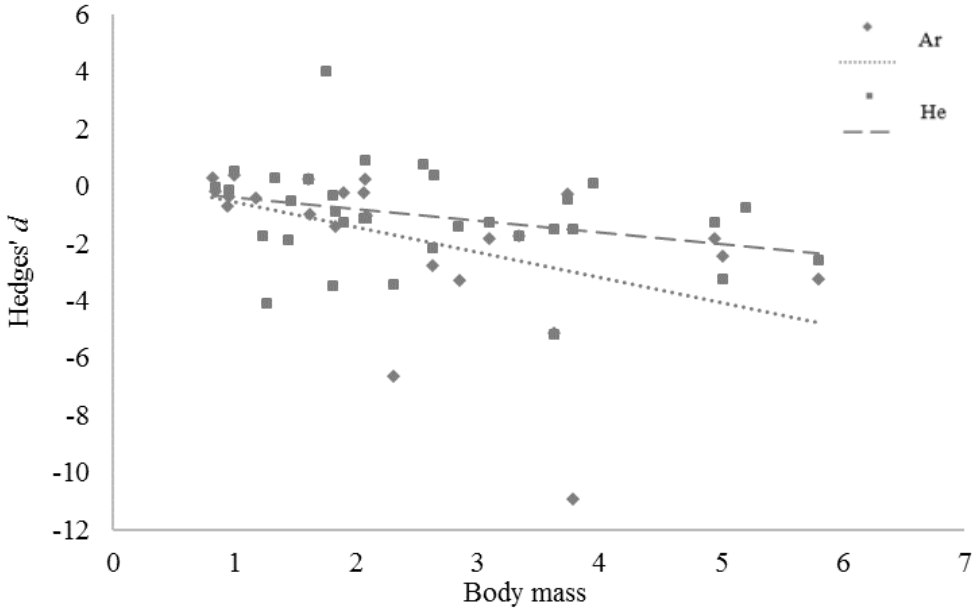

Fig. 3.3 – Hedges' *d* values for allelic richness (Ar) and expected heterozygosity (He) as a function of log-transformed values of body mass (mean values) of mammalian species included in this study. Linear relationships between Ar and He and log-transformed values of body mass are represented by the dotted lines. (Meta-regression model equation for allelic richness = 0.301 + 0.212HRm - 0.833Mm; $r^2 = 0.32$, $p < 0.01$ and for expected heterozygosity = -0.066 - 0.359Mm, $r^2 = 0.12$, $p = 0.04$).

Tests for subgroup differences do not report significant differences for allelic diversity and observed heterozygosity in respect to species locomotion mode ($\chi^2_{Ad} = 1.97$, $p = 0.370$; $\chi^2_{Ho} = 0.44$, $p = 0.800$) and for observed and expected heterozygosity in respect to forest dependency ($\chi^2_{Ho} = 0.85$, $p = 0.650$; $\chi^2_{He} = 0.45$; $p = 0.800$). On the other hand, tests of heterogeneity showed that locomotion mode affects how allelic richness and expected heterozygosity of species respond to fragmentation ($\chi^2_{Ar} = 27.56$, $p < 0.001$; $\chi^2_{He} = 11.57$; $p = 0.003$; Fig. 3.4). Terrestrial and arboreal mammals showed the strongest negative effect of fragmentation on Ar ($d_{terrestrial} = -2.68$, $p < 0.001$; $d_{arboreal} = -1.49$; $p = 0.001$). Additionally, for expected heterozygosity those species with terrestrial locomotion are the most negatively affected by fragmentation ($d_{terrestrial} = -1.94$, $p < 0.001$). While flying mammals were negatively affected, the value is only marginally statistically significant ($d_{Aerial} = -0.83$; $p = 0.080$).

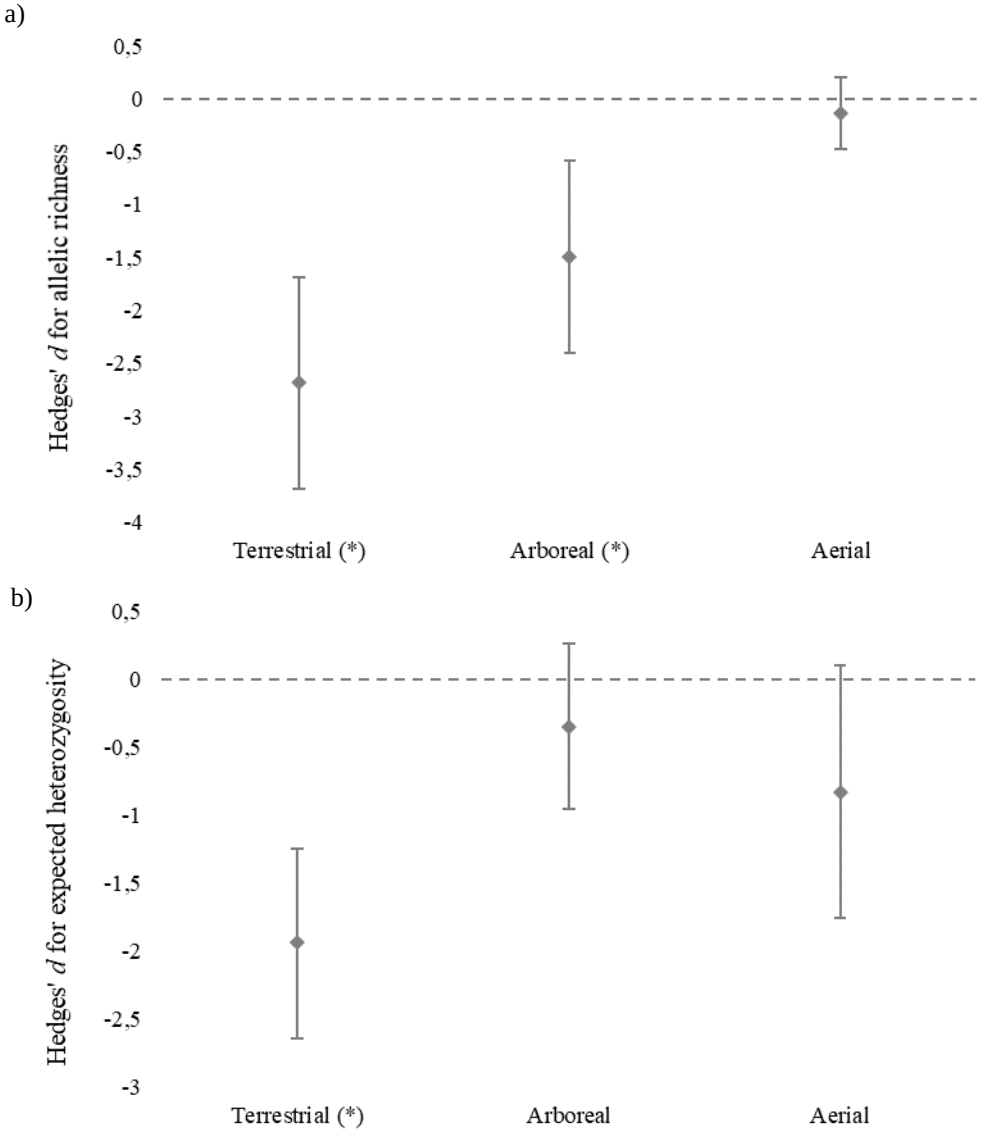

Fig. 3.4 – Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on a) allelic richness and b) expected heterozygosity of mammalian species with different types of locomotion. (*) indicates Hedges' *d* with significant p-values (i.e., $p < 0.05$).

Fragmentation differently affected mammals' genetic diversity – Ad, Ar, Ho and He – according to species trophic guild ($\chi^2_{Ad} = 41.76$, $p < 0.001$; $\chi^2_{Ar} = 18.59$, $p < 0.001$; $\chi^2_{Ho} = 16.53$, $p = 0.002$; and $\chi^2_{He} = 22.73$, $p < 0.001$; Fig. 3.5). Allelic diversity of herbivores and mycophages are negatively affected by fragmentation ($d_{herbivore} = -1.84$, $p = 0.020$; $d_{mycophage} = -3.13$, $p < 0.001$; Fig. 3.5a). The same occurs with allelic richness for herbivores and carnivores ($d_{herbivore} = -2.61$, $p < 0.001$; and $d_{carnivores} = -1.83$, $p < 0.001$; Fig. 3.5b). The observed heterozygosity of omnivores and herbivores decreased in fragments ($d_{omnivores} = -1.13$, $p = 0.008$; and $d_{herbivores} = -0.83$, $p < 0.001$; Fig. 3.5c) and the expected heterozygosity was negatively affected for herbivores, mycophages and carnivores ($d_{herbivores} = -1.26$, $p < 0.001$; $d_{mycophages} = -1.88$, $p <$

0.001; $d_{carnivores}$ = -1.27, p = 0.001; Fig. 3.5d). It is important to note that carnivores and mycophages included only one species each (*Panthera onca* and *Myodes californicus*, respectively) so these categories are highly underrepresented.

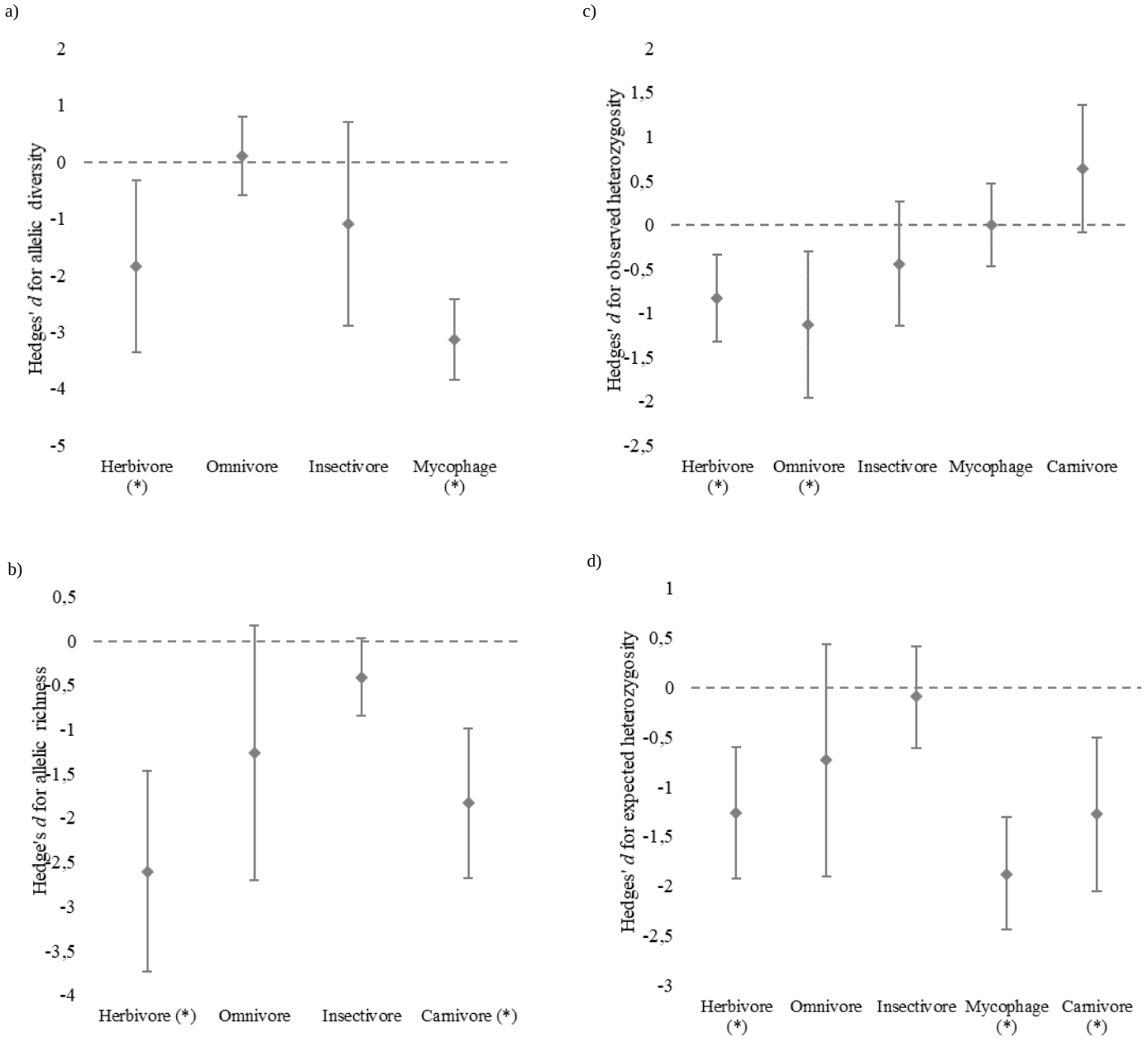

Fig. 3.5 – Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation effects on a) allelic diversity, b) allelic richness, c) observed heterozygosity and d) expected heterozygosity of mammalian species belonging to different trophic guilds. (*) indicates Hedges' *d* with significant p-values (i.e., $p < 0.05$).

Regarding forest dependency, we found that effects of fragmentation for forest specialists are severe, as fragmentation acts to decrease allelic diversity ($d_{\text{forest habitats}}$ = -1.53, p = 0.020) and allelic richness ($d_{\text{forest habitats}}$ = -1.21, p < 0.001; Fig. 3.6). Those species that also use intermediate habitat also lost allelic diversity ($d_{\text{intermediate habitats}}$ = -0.65, p = 0.040) and allelic richness ($d_{\text{intermediate habitats}}$ = -0.83, p = 0.030) due to fragmentation, although with less intensity. Allelic richness of species that also use open habitats was also affected by fragmentation ($d_{\text{open habitats}}$ = -3.25, p < 0.001). However, this category was underrepresented due to the inclusion of a single species (*S. caffer*).

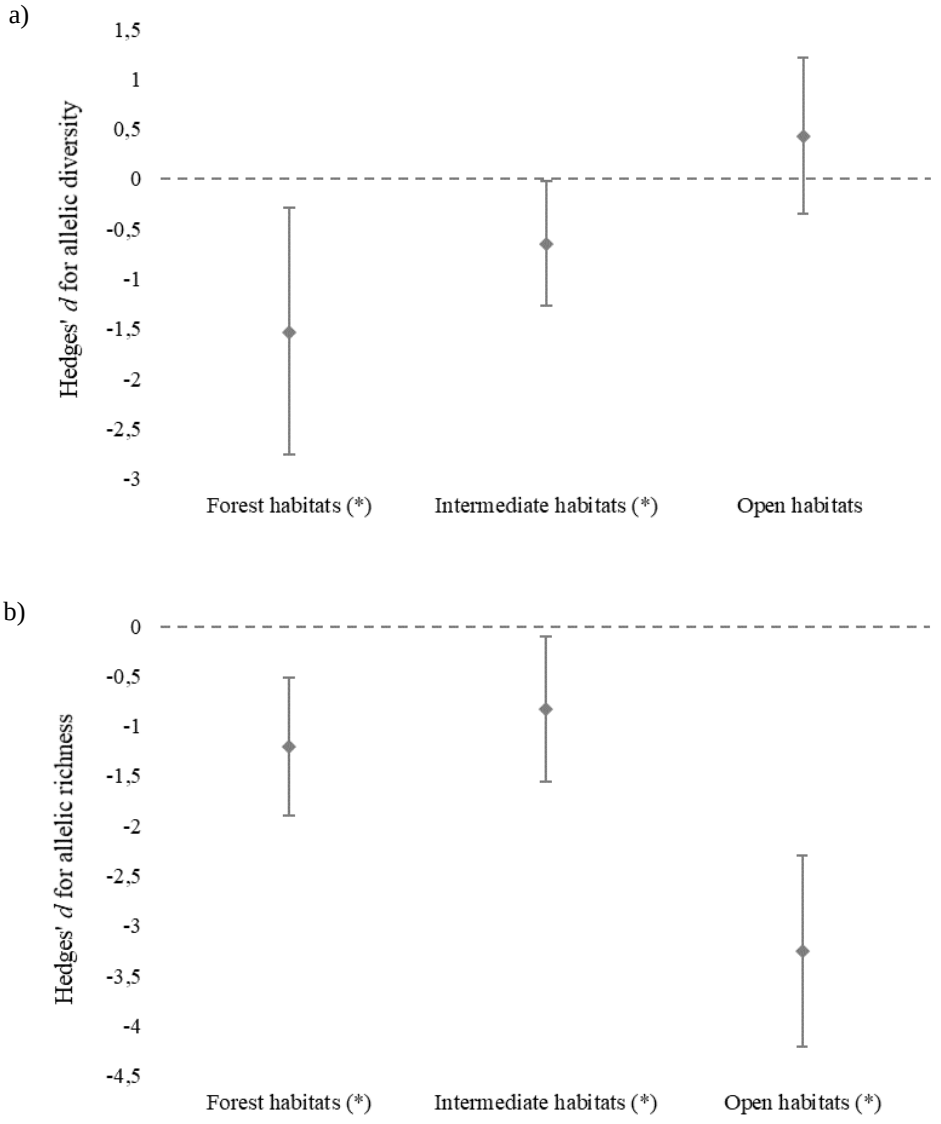

Fig. 3.6 – Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on a) allelic diversity and b) allelic richness of mammalian species with different forest dependencies. (*) indicates Hedges' *d* with significant p-values (i.e., p < 0.05).

3.5 Discussion

With this meta-analysis we detected overall negative genetic consequences in mammalian species that result from habitat loss and fragmentation. Decreases in allelic diversity, allelic richness, expected heterozygosity and observed heterozygosity are widespread in the face of these threats but, as expected, not all species are affected similarly. Briefly, we found that i) consequences of fragmentation are higher for mammals with larger body mass, ii) terrestrial and arboreal mammals are more negatively affected by habitat loss and fragmentation than flying species; iii) herbivores are those that suffer consistent negative effects of fragmentation in the four genetic measures analysed; and iv) forest-dependent species are more affected by fragmentation than species that also use other habitat types. We expected to detect an increase in homozygosity compared to Hardy–Weinberg expectations due to deviation of random mating in fragments; however, we did not find this trend. A possible explanation is that the time since fragmentation may still not be enough to detect significant changes in inbreeding coefficient (Potter et al., 2012). Also, species may possess mechanisms for inbreeding avoidance such as sex-biased dispersal and kin recognition (Cockburn et al., 1985; Rendall et al., 1996; Parr et al., 2010); indeed, this may explain why a decrease in the diversity metrics is generally evident but does not necessarily impacts the levels of heterozygosity.

The negative effect of habitat loss and fragmentation on allelic richness is more pronounced for species with larger body mass. Although evidence indicates that larger species are, on average, more vagile and can move longer distances between fragments than small-bodied ones (Swihart et al., 2003; Tucker et al., 2018), larger individuals generally require wider areas and increased resource availability to survive (Biedermann, 2003), so they tend – necessarily – to occupy larger home-ranges. However, habitat loss tends to reduce resource availability and smaller and fragmented areas are unable to support the same population densities as continuous habitats. Thus, the density of large-bodied mammalian species tends to decrease in fragmented habitats, which potentially increases their susceptibility to the negative effects of fragmentation (Purvis et al., 2000; Crooks, 2002), like the losses of alleles demonstrated in our analysis. Overall, small mammals require less food and territory per capita and thus can present denser patchy-populations than large mammals (Blackburn and Gaston, 1999). After the fragmentation event, the number of individuals in populations may be reduced but small mammal densities certainly tend to be higher than those of large mammals, and thus the differences we found in terms of the impact of habitat loss and fragmentation on the genetic diversity between these groups. Additionally, small mammals tend to present small home ranges (with the exception of some species of the Chiroptera), which precludes their incorporating numerous patches in fragmented areas, so potentially decreasing inter-patch gene flow (Pabijan et al., 2012). However, small mammals generally show fast growth, early maturity, large litters,

and short gestation and interbirth interval, enabling them to more easily recover after population declines (Quesnelle et al., 2014). Additionally, as population size and genetic diversity are positively correlated (Frankham, 1996), an increase in population size should lead to a recovery in genetic diversity.

Gene flow, the ability to exchange genetic variation between population, is of prime importance because it can prevent genetic drift, inbreeding, local genetic structure and genetic isolation of populations living in fragments (Peakall et al., 2003; Dutta et al., 2013). Our results show that locomotion mode influences the intensity of the negative effect of fragmentation on allelic richness of mammals, with terrestrial and arboreal species more affected than aerial ones. Certainly, aerial species present higher potential ability for transposing the unfavourable matrix and maintaining inter-patch gene flow. However, from the eight bat species included in the meta-analysis, only two showed positive effect sizes. So, bats can also suffer negative effects of fragmentation as occur for example for *Kerivoula papillosa* and *Rhinolophus trifoliatus* in Southeast Asia (Struebig et al., 2011).

Habitat loss and fragmentation change the quantity and quality of resources available in the landscape. So, mammals of different guilds should be affected differently by landscape changes. In our meta-analysis, all mammalian guilds were negatively affected at least with respect to one genetic measure. Allelic diversity and expected heterozygosity of mycophagous species and allelic richness and expected heterozygosity of carnivorous species show significant negative effects due to fragmentation. However, the results concerning these two guilds should be taken with caution, as only one species of each was analysed – *Myodes californicus* (Rodentia) and *Panthera onca* (Carnivora). Mills (1995) found a strong negative effect of habitat edges for *M. californicus* and for mycorrhizal fungi, its main food. The reluctance of this species to use the matrix and the unavailability of its main food type in changed habitats could justify the change in the genetic structure of its populations, resulting in low allelic richness and low expected heterozygosity in fragments. Carnivorous species have tendentially larger body mass, larger home ranges, lower population densities and lower reproductive rates; traits that make them more vulnerable to the negative effects of habitat loss and fragmentation (Vetter et al., 2011). Herbivores were consistently negatively affected by fragmentation in all genetic measures. The higher negative effect of habitat loss and fragmentation on herbivores indicates that these species may be less prone to use and/or traverse the matrix among fragments. Habitat fragmentation acts to decrease not only the quantity but also the quality of food available (Arroyo-Rodríguez and Mandujano, 2006; Vetter et al., 2011), thus smaller fragments present lower carrying capacity. Consequently, as populations reduce, further alleles and heterozygosity are lost. The negative effects of fragmentation are more severe if species are unable to use the matrix as secondary habitat, unable to cross the matrix between fragments, or when the matrix

becomes increasingly more different from fragments, and potentially unfavourable (Ewers and Didham, 2006; Prevedello and Vieira, 2010).

Forest-dependency was reported as a predictor of species sensitivity to fragmentation in neotropical vertebrates (Vetter et al., 2011). Vetter et al. (2011) found that those species that also use intermediate habitats showed the highest percentage of negative effects due to fragmentation, followed by species that only use forest habitats. In contrast, our results support that the loss of genetic diversity due to habitat loss and fragmentation is more intense in forest-dependent species than in species that also use intermediate habitats. However, we failed to detect the higher resilience of species that also use open habitats probably due to the low number of species included in this category. A stronger negative effect of fragmentation on allelic richness and diversity is expected for forest dependent species as they are the most reluctant to go beyond the limits of forested areas. This reluctance to cross intermediate or non-forested areas tends to reduce – or even to completely hinder – gene flow between populations of different fragments, so populations are unable to overcome the negative effects imposed by habitat loss and fragmentation. Under this situation, corridors linking fragments are of high importance for maintenance of gene flow and population genetic diversity (Montgelard et al., 2014; Waits et al., 2016).

Although our meta-analysis provides valuable information on how habitat loss and fragmentation affect genetic diversity of mammalian species and contributes to the understanding of characteristics promoting higher sensitivity to environmental changes, we are aware that our sample size is relatively small for some groups because we faced limitations to include additional studies. Several studies focus on fragments without a continuous area representative of a pre-fragmentation situation, or the descriptions done by original authors are not sufficiently clear to consider some areas as adequate controls. In addition, some studies do not provide the genetic measures for fragments and controls, which precluded us to use them in this meta-analysis. Finally, although numerous studies have been published on this topic, available data is relatively small for comparisons between fragmented and continuous habitats. Therefore, future studies should address contrasting conditions of habitat loss and fragmentation, and more clearly describe these situations, to enable their inclusion in synthetic analyses.

3.6 Acknowledgements

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CHAPTER 4

BAT DIVERSITY IN A GRADIENT OF FOREST LOSS AND FRAGMENTATION

Bat diversity in a gradient of forest loss and fragmentation

Ana Lino[1], Maria João Ramos Pereira[1,2], Maurício Silveira[3], Alan Eriksson[3,4], Carolina Ferreira Santos[5], Jose Manuel Ochoa Quintero[3,6], Clarissa de Araújo Martins[3,7], Gustavo Graciolli[5], Carlos Fonseca[1], Erich Fischer[5]

[1]Department of Biology & Centre for Environmental and Marine Studies (CESAM), University of Aveiro, Campus Universitário de Santiago 3810-193 Aveiro, Portugal.

[2]Department of Zoology, Institute of Biosciences, Universidade Federal do Rio Grande do Sul, Av. Bento Goncalves 9500, Porto Alegre RS 91540-000, Brazil.

[3]Programa de Pós-Graduação em Ecologia e Conservação, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil

[4]Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand

[5]Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil

[6]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogota, Colômbia

[7]Unité Mixte de Recherche, Centre National de la Recherche Scientifique, Université d'Angers, 49045 Angers, France

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4.1 Abstract

Habitat loss and fragmentation have caused a myriad of negative consequences for biodiversity conservation worldwide. Human-induced effects on nature vary according to taxa, geographic locations, and intensity of the land use changes. In the Neotropics, bats represent a useful model group to study such effects, as they are highly abundant and taxonomically and ecologically diverse. Here we address how bat diversity responds to a gradient of forest loss and fragmentation in the karstic region of Serra da Bodoquena, Brazil. We evaluate the effects of landscape variables on different biodiversity dimensions – alpha taxonomic, functional and phylogenetic diversities and in beta diversity. Considering presence-absence data, species turnover more than species nestedness determined total beta diversity, whereas, accounting for abundance data, turnover and nestedness had similar weights on beta diversity. Based on abundance data, turnover and total beta diversity responded to the distance to the pristine Serra da Bodoquena National Park, and the length of forest borders additionally affected total beta diversity. The responses of the three studied dimensions of alpha diversity to landscape metrics depended on the geographical scale considered. No effects were detected at small scale (300 m buffer zone) on taxonomic, functional and phylogenetic diversities, which only negatively responded to the distance to the national park. At intermediate scale (1000 m buffer zone) the length of forest borders additively affected the three diversity dimensions negatively, and area of forest cover was the third explanatory variable at large scale (2500 m buffer zone). The results indicate that proximity to the national park and short extension of forest border – thus less habitat fragmentation – are important to maintain high alpha taxonomic, functional and phylogenetic diversities of bats in the Serra da Bodoquena, although species turnover across the gradient of forest fragmentation increases taxonomic beta diversity.

Keywords: Beta diversity; Chiroptera, Functional diversity; Habitat loss; phylogenetic diversity; Serra da Bodoquena.

4.2 Introduction

Human activities such as agriculture, livestock production, logging and urbanization are the main contemporary sources of landscape changes, reducing and degrading natural habitats around the world (Tilman et al., 2001; Foley et al., 2005; Ellis and Ramankutty, 2008). These changes result in direct and indirect effects on biodiversity and on ecosystem functions, with a myriad of negative consequences for the quality of human life (Warren-Thomas et al., 2015; Emmerson et al., 2016). Therefore, addressing the effects of landscape changes is crucial for developing ways of restoration of natural systems and, ultimately, for biodiversity conservation. The magnitude of the effects of habitat loss and fragmentation depends on the rate of land use conversion, on landscape composition and configuration, and upon the traits of the species occupying the landscape, which can determine their ability to use the modified environments (Ewers and Didham, 2006; Klingbeil and Willig, 2010).

The number of species in communities and its closest related measure, species diversity, are basic measures of diversity, which are highly used in the literature and easy to interpret (Gotelli and Colwell, 2001). For these reasons, these are the most common metrics used when trying to evaluate the effects of habitat loss and fragmentation. However, biological diversity goes beyond taxonomic diversity since it also includes the variation of the species' ecological functions and the phylogenetic distances among them. Therefore, indices of functional and phylogenetic diversity have been recognized as important components of biodiversity. Functional diversity measures the extent of functional differences among the species in a community (Tilman, 2001), while phylogenetic diversity measures phylogenetic differences between species (Vane-Wright et al., 1991; Faith, 1992; Webb et al., 2013). Another way to evaluate how much disturbance modifies the local assemblages is by analysing the species substitution or loss, i.e., how much species turnover or nestedness influence beta diversity throughout temporal or spatial gradients of disturbance intensity. Species turnover refers to the replacement of some species by others along a gradient, including simultaneous gains and losses of species resulting from environmental sorting, competition and/or history constraints. In its turn, nestedness occurs when sites with few species represent subsets of richer sites, with a non-random pattern driven by environmental conditions or resources (Legendre et al., 2005; Baselga, 2010; Leprieur et al., 2011).

Bats have been pointed out as a useful group to assess the effect of landscape changes because they are taxonomic, functional and phylogenetically diverse (Patterson et al., 2003; Simmons and Conway, 2003). Chiroptera is the second-most speciose mammalian order with more than 1400 recognized species (Mammal Diversity Database, 2018). Additionally, bats show highly diverse functional traits related to the differential use of the environment, including diet, dispersal ability, wing morphology, foraging habitat, foraging strata, and foraging mode.

Mainly due to their diverse feeding habits, bats have a crucial importance for ecosystem functioning (Kunz et al., 2011). Around 70% of bat species feed on insects and other arthropods, being important arthropod population controllers (Cleveland et al., 2006); others that feed on fruits are very important seed dispersers, helping the maintenance of forest diversity and recovery (Muscarella and Fleming, 2007), and those feeding on nectar and/or pollen promote plant pollination (Muchhala and Jarrín-V, 2002; Kunz et al., 2011). In addition, several species also feed on small vertebrates and three on blood, playing important regulatory functions as predators (Kunz et al., 2011). Another important bat trait is wing morphology, which relates to species' flight manoeuvrability, agility, speed, and, consequently, the strata of foraging (Norberg and Rayner, 1987; Kalko et al., 1996). Species with high aspect ratio and high relative wing loading are fast flyers with poor manoeuvrability, and forage in open areas, above forest canopy or over water (e.g. *Myotis nigricans*; Kalko et al., 1996, Marinello and Bernard, 2014, Fischer et al., 2018). On the other hand, species with low aspect ratio and low relative wing loading have slower and highly manoeuvrable flights, foraging in spatially complex environments (e.g. *Carollia perspicillata*; Marinello and Bernard, 2014).

Available studies evaluating the effect of habitat loss and fragmentation on bats do not point to a single direction, possibly because the response to landscape characteristics is species-specific and scale-dependent (Bernard and Fenton, 2007; Meyer and Kalko, 2008; Pinto and Keitt, 2008; Klingbeil and Willig, 2010; Farneda et al., 2015). Some studies found species richness positively related to forest cover (García-Morales et al., 2016), while others did not detect differences between continuous and fragmented forests (Bernard and Fenton, 2007) or showed higher species richness in moderately fragmented habitats (Klingbeil and Willig, 2009) or reported that some species are tolerant to or benefited from land alterations (Gonçalves et al., 2017). Thus, studies that take a multidimensional approach, including taxonomic, functional and phylogenetic diversities, can more accurately evaluate the effects of habitat loss and fragmentation on bats. In general, taxonomic, functional and phylogenetic diversities tend to decrease in response to these changes (Frank et al., 2017; Wordley et al., 2017; Ramos Pereira et al., 2018). Taxonomic diversity is affected due to the loss of more sensitive and rare species, such as some Phyllostominae bats (Fenton et al., 1992). Landscape changes affect functional diversity because environments may lose available functional spaces and become unsuitable for some specialized species (Gonçalves et al., 2017; Ramos Pereira et al., 2018). Finally, habitat loss and fragmentation may decrease phylogenetic diversity because some clades are lost and assemblages become more phylogenetically correlated (Frishkoff et al., 2014; Frank et al., 2017). Thus, old-growth forests or landscapes with increased forest cover are expected to show high phylogenetic and functional diversities (Cisneros et al., 2015, Gonçalves et al., 2017, but see Fischer et al., 2018) while land-use intensification is expected to decrease them (Ramos Pereira et al., 2018).

Karst systems, landscapes formed by the dissolution of soluble rocks, are important formations for biodiversity conservation because they tend to harbour a distinct and rich biodiversity (Clements et al., 2006; Chape et al., 2008). Beyond cliffs and alluvial terraces, the topographic features of karst regions also include caves and sinkholes that are important refuges for many cave–dwelling species (Hamilton-Smith, 2001; Clements et al., 2006; Cunha et al., 2009;). Karsts cover 10 to 15% of the world's continental area but their distribution is not uniform around the world, as the northern hemisphere is richer on these formations (Ford and Williams, 2007). Karsts are scattered distributed in South America, representing less than 2% of the total continental area. Some are found in Andean countries, but a significant part is located in the plateaus of central Brazil (Auler, 2004) with 19 recognized karst regions (CECAV, 2009). The karst formation of Serra da Bodoquena is singular within the Cerrado domain, as it harbours the largest continuous area of floristic elements of the Atlantic Forest in the state and is located in the zone of transition to the Pantanal floodplain. Such ecotonal zones tend to show high species richness because they present higher levels of habitat complexity and heterogeneity than adjacent areas (Fahr and Kalko, 2011) and could assemble many species from the bordering different formations, as reported for bats in the Mato Grosso do Sul State (Fischer et al., 2015, 2018). Here we evaluate factors affecting bat assemblages in this highly complex region, which ranges in terms of vegetation cover from areas with well-preserved forests to more degraded and fragmented landscapes. We intend to understand the processes behind assembly patterns in Serra da Bodoquena, i.e. understand if turnover or nestedness are shaping assemblies across the studied landscapes. We expect more impacted areas will present a subset of species from those well-preserved areas as some species, particularly from the Phyllostominae, are sensible to fragmentation and habitat disturbance and tend to be excluded from more impacted areas (Fenton et al., 1992; Medellín et al., 2000), and we explore if turnover or nestedness are mediated by landscape characteristics. Additionally, we evaluate species richness and taxonomic, functional and phylogenetic dimensions of bat diversity across sampling sites in the Serra da Bodoquena region to understand whether habitat loss and fragmentation affect, and in which direction, these dimensions of diversity. We hypothesise that bat richness and taxonomic, functional and phylogenetic diversities tend to decrease in more fragmented areas, with less vegetation cover and larger borders, and with increasing distance to the national park, the largest area of continuous and less disturbed forest in the Serra da Bodoquena region.

4.3 Methods

Study region and site selection

This study focused the karstic region of the Serra da Bodoquena, a north-south oriented plateau (150 to 800 m.a.s.l.) with approximately 18,000 km^2 surrounded by the Pantanal floodplain (< 100 m.a.s.l.), in the Mato Grosso do Sul State, southwestern Brazil (Fig. 4.1). Regional water springs and rivers drain to the Pantanal through the Miranda and Apa basins, which are sub-basins of the Paraguay river. Climate is tropical wet, Aw of Köppen-Geiger, with wet summers and dry winters (Kottek et al., 2006). Mean annual rainfall ranges from 1300 to 1700 mm and mean annual temperature from 22 to 26 ºC. The highly diverse vegetation is mostly composed of deciduous and semideciduous forests, woodland and arboreal savannas (cerradão and cerrado *sensu stricto*, respectively) and grasslands (Furtado et al., 1982, Baptista-Maria et al., 2009). About 4% of the Bodoquena region is under protection by the Serra da Bodoquena National Park, a conservation unit with almost 77,000 ha mainly covered by pristine habitats. Bordering the park, natural areas have been widely converted into livestock pastures and corn and soybean croplands and explored for ecotourism and adventure tourism, like rafting and cave diving.

To select sampling sites representing the gradient of forest loss and fragmentation in the Serra da Bodoquena, we initially graded the entire region (18,000 km^2) in 360 hexagons of 5,000 ha each over satellite images. Then, in each hexagon, we quantified the area modified for human use and the area covered by deciduous and semideciduous forests, and ranked the 360 hexagons according to this. Based on this information, we selected 17 hexagons representing a gradient from 0 to 100% of forest cover. Additional criteria of selection were accessibility, presence of watercourses, and avoidance of closely-located hexagons representing similar positions in the forest cover gradient. We surveyed bats four times in the 17 sites, during the dry season (June to September) in 2015 and 2016 and the wet season (January to March) in 2016 and 2017. We set 343.2 m^2 (132 x 2.6 m) mist-nets for 6 h after dusk, with net area equally distributed between deciduous and adjacent semideciduous forest understories; where deciduous forest was absent all nets were placed in semideciduous forest (n = 7). The netting effort per site was 8,236.8 m^{2}h, and the total effort was 140,025.6 m^{2}h. We measured forearm length (to ± 1 mm), body mass (to ± 1 g), recorded sex and reproductive state, and pre-identified in the field all the captured individuals. Bats were then marked with collar bands to recognize recaptures and released at the same site of capture, except for some specimens collected for confirmation of identifications and inclusion as vouchers in the Zoological Collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS). Captures were conducted under legal authorization of Brazilian Ministry of the Environment MMA/ ICMBio number 41652-1.

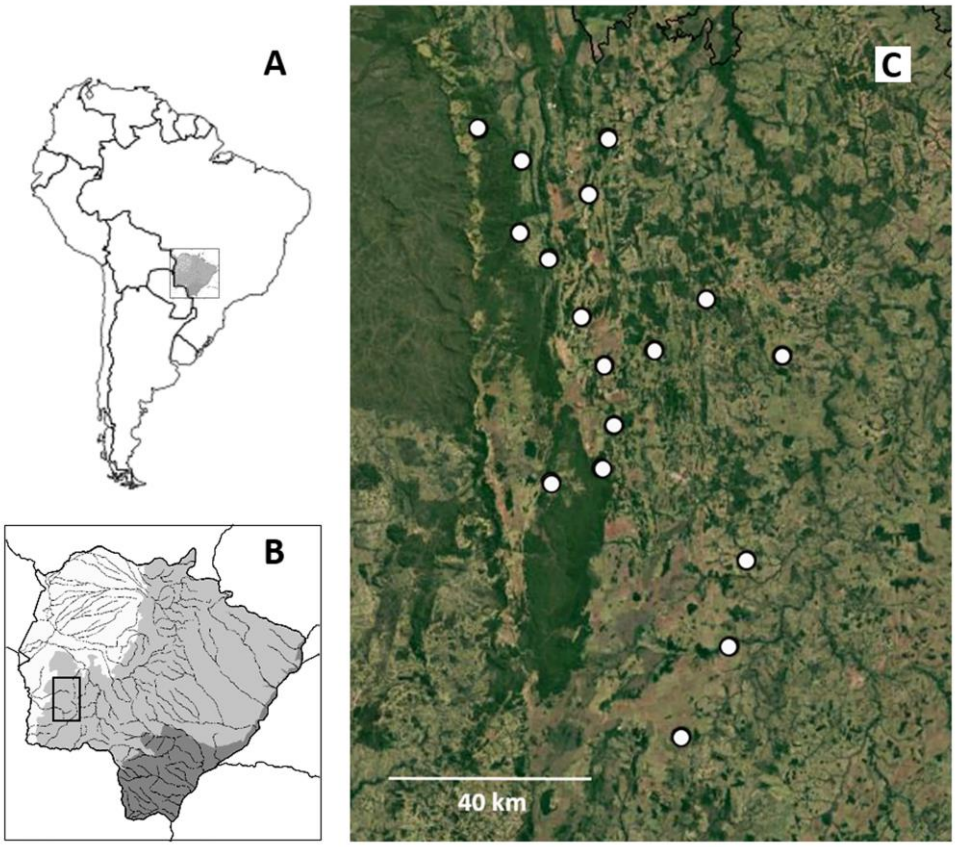

Fig. 4.1 – (A) Location of Mato Grosso do Sul State in South America; (B) location of the Serra da Bodoquena study region (rectangle) in Mato Grosso do Sul, with light, middle and dark grey indicating the Pantanal, Cerrado and Atlantic Forest domains, respectively; and (C) distribution of sample sites in the landscape (Landsat 2018, Google; image limits: 20º19' to 21º44' S; and 55º58' to 57º06' W). Darker green is deciduous or semideciduous forest patches, and the long and large vertical patches at left correspond to the Serra da Bodoquena National Park's area.

Landscape variables

For landscape metrics, we defined circular concentric buffers with radius of 300 m (28.27 ha), 1000 m (314.16 ha) and 2500 m (1963.50 ha) encircling the survey places. Landsat 2012 images were transformed into raster files and processed using Fragstagts (McGarigal et al., 2012). We recorded distance from each sampling site to nearest border of the Serra da Bodoquena National Park (meters, DIST) and the forest cover (squared meters, FORE), forest border length (meters, BORD) and number of forest fragments (FRAG) in each of the three buffer sizes, used to evaluate whether bat responses to landscape attributes are scale-dependent. Although data on home range size are unavailable for several Neotropical bat species, these

three scales can encompass a variety of home range sizes and behaviours of species present in our study areas. For example, mean home range size of *Carollia perspicillata* in Ecuador was estimated to be 5.5 ha (Bonaccorso et al., 2006), while home range of *Artibeus planirostris* in Pantanal averages 72.25 ± 102,05 ha (Martins, 2016). Additionally, *A. jamaicensis* bats can forage within 10 to 15 km radius (Morrison, 1979) and the largest neotropical fruit-bat *A. lituratus* is reported to move up to 113 km over a period of 14 months (Esbérard et al., 2011, Arnone et al., 2016).

Description and quantifications of dimensions of biodiversity

Taxonomic diversity (TD) was evaluated using the abundance of each species by sampling site. Functional diversity (FD) was estimated based on species abundance and on species-specific traits, which were selected following Cisneros et al. (2015). Thus, we used ecologically relevant response traits to build a table including categorical (0,1) and quantitative data. Based on literature data (Table S4.1), we classified bat species according to feeding guild (omnivores, frugivores, nectarivores, insectivores, carnivores, sanguivores and piscivores), foraging location (above canopy, canopy and understory), foraging strategy (gleaning, trawling, hover and aerial) and annual breeding pattern (univoltine, bivoltine and multivoltine). Quantitative variables included body mass (g), forearm length (mm), relative wing loading (N m^{-2}), aspect ratio and skull measures (greatest length of skull, condylobasal length, length of maxillary toothrow, breadth across upper molars, width across postorbital constriction and breadth of braincase; all measured in mm). For body mass and forearm length, we used average values from our data on the bats captured, except for species with less than 10 captures, for which we used data from previous studies in the Mato Grosso do Sul or as near as possible to our study location (Table S4.1). Relative wing loading, aspect ratio and skull measures were obtained from the literature (Table S4.1). Phylogenetic distances (PD) were estimated based on species abundance and a nearly all extant mammalian supertree (Bininda-Emonds et al., 2007). When a species was absent in the supertree (n = 3) we used the closest known congener. Phylogenetic distances between species were computed based on the 'cophenetic' function implemented in the 'picante' R package (Kembel et al., 2010). Functional and phylogenetic diversities were computed based on Rao's quadratic entropy (Rao, 1982) and taxonomic diversity was computed based on Gini-Simpson index, an equivalent measure of Rao's quadratic entropy. The three dimensions of biodiversity were computed with the function 'rao.diversity' in SYNCSA R package (Debastiani and Pillar, 2012).

Data analysis

All analyses were done in the R statistical environment (R Core Team, 2013). We used a non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity to assess differences in bat assemblage composition among sampling sites. NMDS was performed using packages vegan (Oksanen et al., 2018) and MASS (Venables and Ripley, 2002).

Beta diversity analyses were conducted according to Legendre (2014) and Legendre and De Cáceres (2013). We used presence-absence data to account for species composition, and abundance data, to account for differences in abundance. Total beta diversity was partitioned into its replacement and richness differences components using the Baselga family coefficient with Sorensen dissimilarity in the 'beta.div.comp' function, which provides three dissimilarity matrixes: (1) a replacement matrix, which accounts for the spatial turnover, i.e. the gradual change of species from site to site; (2) a richness/abundance matrix, which corresponds to the nestedness; and (3) a total dissimilarity matrix. Using this function, we calculated indices of total beta diversity, total replacement diversity, total nestedness and the relative importance of replacement and nestedness for total beta diversity. Each dissimilarity matrix was used to perform a Principal Coordinate Analysis (PCoA) with Lingoes correction for negative eigenvalues. The resulting coordinates, along with landscape variables, were subject to a forward selection, with the 'forward.sel' function of R package adespatial (Dray et al., 2018), to select the significant landscape variables to include in a distance-based redundancy analysis, with the 'capscale' function. The significance of variables included in 'capscale' were evaluated with an F-test ($p < 0.05$; 999 permutations).

We examined whether ordination of bat assemblage composition (NMDS performed at one dimension), species richness, taxonomic diversity, functional diversity and phylogenetic diversity vary with landscape metrics at the three studied scales (28.27 ha, 314.16 ha and 1963.50 ha) using generalized linear models (GLM). Previously to the analyses, continuous variables were standardized, i.e. transformed to standard scores, which sets data from different sources onto the same scale. We used Poisson error distribution with log link-function for species richness and normal error distribution with identity link-function for NMDS axis and for the three studied diversities. Previously, we tested for multicollinearity between predictor variables using the Variance Inflation Factor (VIF) in 'car' R package (Fox, 2007). Higher values represent higher collinearity; here we considered $VIF < 5$ as negligible collinearity. For each buffer, we produced all combinations of explanatory variables to construct a set of possible models. For each model we calculated Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) in 'AICcmodavg' package (Mazerolle, 2017). Candidate models were then compared and ranked, and the best models were those that

present lower values of AICc. Models whose ΔAIC < 2 are considered to have substantial support and equally best models (Burnham and Anderson, 2002).

We performed all analyses at two levels, firstly including all bat species surveyed in the study sites and secondly including only species of the Phyllostomidae as using ground-level mist nets likely underestimates aerial insectivores from the Vespertilionidae, Molossidae and Emballonuridae (Kalko et al., 1996). On the other hand, even with this limitation, species of these families were captured through standard protocols and we considered reasonable to assume that netting bias is similarly distributed among sites.

4.4 Results

We captured 1901 bat individuals belonging to 23 species in four families – Phyllostomidae (19 species), Vespertilionidae (2), Molossidae (1) and Noctilionidae (1) (Table 4.1). Total abundance ranged from 1 (*Anoura geoffroyi*, *Dermanura cinerea*, *Pygoderma bilabiatum*, *Molossops temminckii* and *Noctilio leporinus*) to 907 (*Artibeus planirostris*). Four species constituted 88% of the captures (*A. planirostris* – 48%, *Sturnira lilium* – 16%, *Carollia perspicillata* – 13%, *Platyrrhinus lineatus* – 11%). The NMDS analysis does not show subgroups neither when analysed all bat species captured (Fig. S4.1) nor when analysed phyllostomid species alone (Fig. S4.2). Additionally, GLM analyses with values of NMDS projected in one dimension showed that DIST justify the ordination when all bat species were included (Table S4.2; Fig. S4.3), and BORD was significant at large scale when only phyllostomids were included (Table S4.3; Fig. S4.4).

Table 4.1 – Number of bat individuals recorded per species in the Serra da Bodoquena region, Mato Grosso do Sul, Brazil

Phyllostomidae	
Stenodermatinae	
Artibeus planirostris	907
Sturnira lilium	295
Platyrrhinus lineatus	215
Artibeus lituratus	32
Platyrrhinus helleri	7
Chiroderma doriae	4
Dermanura cinerea	1
Pygoderma bilabiatum	1
Carolliinae	
Carollia perspicillata	253
Glossophaginae	
Glossophaga soricina	97
Anoura caudifer	26
Lonchophylla dekeyseri	4
Anoura geoffroyi	1
Desmodontinae	
Desmodus rotundus	28
Phyllostominae	
Lophostoma silvicolum	6
Chrotopterus auritus	5
Phyllostomus hastatus	3
Phyllostomus discolor	2
Lophostoma brasiliense	2
Vespertilionidae	
Myotis nigricans	7
Eptesicus furinalis	1
Molossidae	
Molossops temminckii	3
Noctilionidae	
Noctilio leporinus	1

Partitioning total beta diversity – the impact of landscape variables

For presence-absence data, total beta diversity was 0.14 and 0.13, when all species and only phyllostomids are included respectively. Species turnover accounted for 77% (all species) and 73% (phyllostomid species) and species nestedness accounted for 23% (all species) and 27% (phyllostomid species). For abundance data, total beta diversity was 0.22 when included all

species or only phyllostomids. Species turnover accounted for 52% (all species) and 50% (phyllostomid species) and species nestedness accounted for 48% (all species) and 50% (phyllostomid species). None of the predictor variables (DIST, FORE, BORD, FRAG) were selected through forward selection when using presence-absence data, but DIST was an explanatory variable of species turnover, and DIST and BORD of total beta diversity, in models based on abundance data (Table 4.2). DIST was the only statistically significant variable for species turnover at the three scales (28.27 ha, 314.16 ha and 1963.50 ha) and for total beta diversity at small and intermediate scales. At our large scale (1963.50 ha), BORD along with DIST entered in the models for total beta diversity (Table 4.2). None of the studied variables was selected for species nestedness.

Table 4.2 – Results of the distance-based redundancy analysis (dbRDA) computed with the results of the forward selection, showing the significant environmental variables ($p < 0.05$) affecting species turnover and total beta diversity when abundance of all bat species and only phyllostomid species where analysed. Independent variables are: distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG).

	All species			**Only phyllostomid species**		
	Selected variables	Sig. variables	$R^2\|R^2_{adj}$	Selected variables	Sig. variables	$R^2\|R^2_{adj}$
Species turnover						
28.27 ha	DIST	$P < 0.05$	0.12|0.07	DIST	$P < 0.05$	0.12|0.07
314.16 ha	DIST	$P < 0.05$	0.12|0.07	DIST	$P < 0.05$	0.12|0.07
1963.50 ha	DIST	$P < 0.05$	0.12|0.07	DIST	$P < 0.05$	0.12|0.07
Total beta diversity						
28.27 ha	DIST	$P < 0.05$	0.15|0.09	DIST	$P < 0.05$	0.15|0.09
314.16 ha	DIST	$P < 0.05$	0.15|0.09	DIST	$P < 0.05$	0.15|0.09
1963.50 ha	DIST	$P < 0.05$	0.24|0.14	DIST	$P < 0.05$	0.25|0.15
	BORD	$P = 0.06$		BORD	$P < 0.05$	

Impact of landscape variables on bat assemblages

Multicollinearity tests showed no correlations between the studied landscape variables at small and intermediate scales, but number of forest fragments was correlated with other variables at the large scale. Thus, we removed it in the subsequent analyses at that scale and used all four explanatory variables at small and intermediate scales. GLM including all species (Table 4.3) or phyllostomids only (Table 4.4) showed similar results, but different explanatory variables affected taxonomic, functional and phylogenetic diversities at different scales, while

none of the included variables at three studied buffers explained species richness (Fig. 4.2). At the small scale, only distance to the national park explained the variation in taxonomic, functional and phylogenetic diversities across sites. Areas nearer to the park showed higher values of the three diversity dimensions. At the intermediate scale, the best model included the distance to the national park and forest border length as explanatory, negatively related variables for taxonomic, functional and phylogenetic diversities. At the large scale the best model for the three dimensions of diversity included the distance to the national park, forest border length and forest cover, all them negatively related with the three diversity measures.

Table 4.3 – Best models explaining taxonomic, functional and phylogenetic diversities considering all bat species captured. Values are present in unstandardized (unstand) and standardized (stand) forms. Independent variables: distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG). Akaike's Information Criterion for small samples (AICc), and variation between the AICc (ΔAICc) and weight for each model are presented. Standard error (SE), t-value and p-value are presented for each variable.

Model	Estimate (unstand| stand)	SE (unstand| stand)	t-value (unstand| stand)	p-value	R^2	K	AICc	Weight
Buffer 300 meters (28.27 ha)								
Taxonomic diversity								
Model					0.50	3	-20.07	0.60
Intercept	0.74| 0.63	0.04| 0.03	18.86| 23.09	< 0.05				
DIST	-0.000008| -0.11	0.000002| 0.03	-3.85| -3.85	< 0.05				
Functional diversity								
Model					0.28	3	-44.04	0.46
Intercept	0.29| 0.26	0.02| 0.01	15.03| 19.08	< 0.05				
DIST	-0.000003| -0.03	0.000001| 0.01	-2.40| -2.40	< 0.05				
Phylogenetic diversity								
Model					0.26	3	-43.32	0.42
Intercept	0.26| 0.23	0.02| 0.01	13.06| 16.36	< 0.05				
DIST	-0.000002| -0.03	0.000001| 0.01	-2.30| -2.30	< 0.05				
Buffer 1000 meters (314.16 ha)								
Taxonomic diversity								
Model					0.69	4	-24.69	0.69
Intercept	-0.91| 0.63	0.07| 0.02	13.89| 28.32	< 0.05				
BORD	-0.00002| -0.07	0.000007| 0.02	-2.93| -2.93	< 0.05				
DIST	-0.000009|- 0.11	0.000002| 0.02	-5.03| -5.03	< 0.05				
Functional diversity								
Model					0.54	4	-48.24	0.58
Intercept	0.37| 0.26	0.03| 0.01	11.39| 23.11	< 0.05				
BORD	-0.000009|	0.000003|	-2.83|	< 0.05				

	-0.03	0.01	-2.83				
DIST	-0.000003| -0.04	0.0000009| 0.01	-3.21| -3.21	< 0.05			
Phylogenetic diversity							
Model					0.51	4	-46.85	0.54
Intercept	0.34| 0.23	0.03| 0.01	9.93| 19.43	< 0.05			
BORD	-0.000009| -0.03	0.000003| 0.01	-2.68| -2.68	< 0.05			
DIST	-0.000003| -0.04	0.0000009| 0.01	-3.03| -3.03	< 0.05			
Buffer 2500 meters (1963.50 ha)							
Taxonomic diversity							
Model					0.75	5	-24.49	0.70
Intercept	1.06| 0.63	0.09| 0.02	11.53| 30.62	< 0.05			
FORE	-0.00000001| -0.07	0.000000005| 0.03	-2.66| -2.66	< 0.05			
BORD	-0.000004| -0.06	0.000001| 0.02	-2.87| -2.89	< 0.05			
DIST	-0.00001| -0.15	0.000002| 0.03	-5.64| -5.64	< 0.05			
Functional diversity							
Model					0.71	5	-52.06	0.90
Intercept	0.46| 0.26	0.04| 0.01	11.36| 28.13	< 0.05			
FORE	-0.000000008| -0.04	0.000000002|0.01	-3.46| -3.46	< 0.05			
BORD	-0.000002| -0.03	0.0000006| 0.01	-3.25| -3.25	< 0.05			
DIST	-0.000005| -0.06	0.0000009| 0.01	-4.93| -4.93	< 0.05			
Phylogenetic diversity							
Model					0.70	5	-51.05	0.89
Intercept	0.43| 0.23	0.04| 0.01	10.29| 23.91	< 0.05			
FORE	-0.000000008| -0.04	0.000000002| 0.01	-3.31| -3.31	< 0.05			
BORD	-0.000002| -0.03	0.0000006| 0.01	-3.31| -3.31	< 0.05			
DIST	-0.000004| -0.06	0.0000009| 0.01	-4.70| -4.70	< 0.05			

Table 4.4 – Best models for each buffer explaining taxonomic, functional and phylogenetic diversities when including only phyllostomid species. Independent variables are distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG). Akaike's Information Criterion for small samples (AICc), and variation between the AICc (ΔAICc) and weight for each model are presented. Standard error (SE), t-value and p-value are presented for each variable.

Model	Estimate (unstand| stand)	SE (unstand| stand)	t-value (unstand| stand)	p-value	R^2	K	AICc	Weight
Buffer 300 meters (28.27 ha)								
Taxonomic diversity								
Model					0.49	3	-19.57	0.60
Intercept	0.74| 0.63	0.04| 0.03	18.46| 22.54	< 0.05				
DIST	-0.000008| -0.11	0.000002| 0.03	-3.82| -3.82	< 0.05				
Functional diversity								
Model					0.29	3	-44.03	0.48
Intercept	0.30| 0.26	0.02| 0.01	15.19| 19.24	< 0.05				
DIST	-0.000003| -0.03	0.000001| 0.01	-2.48| -2.48	< 0.05				
Phylogenetic diversity								
Model					0.28	3	-24.64	0.46
Intercept	0.47| 0.41	0.03| 0.02	13.76| 17.23	< 0.05				
Distance	-0.000005| -0.06	0.000002| 0.02	-2.44| -2.44	< 0.05				
Buffer 1000 meters (314.16 ha)								
Taxonomic diversity								
Model					0.67	4	-23.44	0.66
Intercept	0.9| 0.63	0.07| 0.02	13.25| 27.03	< 0.05				
BORD	-0.00002| -0.06	0.000007| 0.02	-2.75| -2.75	< 0.05				
DIST	-0.000009| -0.11	0.000002| 0.02	-4.87| -4.87	< 0.05				
Functional diversity								
Model					0.54	4	-47.91	0.60
Intercept	0.38| 0.26	0.03| 0.01	11.34| 23.08	< 0.05				
BORD	-0.000009| -0.03	0.000003| 0.01	-2.76| -2.76	< 0.05				
DIST	-0.000003| -0.04	0.0000009| 0.01	-3.28| -3.28	< 0.05				
Phylogenetic diversity								
Model					0.54	4	-28.66	0.62
Intercept	0.62| 0.41	0.06| 0.02	10.56| 20.76	< 0.05				
BORD	-0.00002| -0.06	0.000006| 0.02	-2.79| -2.79	< 0.05				
DIST	-0.000005| -0.07	0.000002| 0.02	-3.24| -3.24	< 0.05				

Buffer 2500 meters (1963.50 ha)								
Taxonomic diversity								
Model 1					0.73	5	-22.51	0.56
Intercept	1.04| 0.63	0.10| 0.02	10.71| 28.62	< 0.05				
FORE	-0.00000001| -0.07	0.000000006| 0.03	-2.37| -2.37	< 0.05				
BORD	-0.000004| -0.06	0.000001| 0.02	-2.69| -2.69	< 0.05				
DIST	-0.00001| -0.15	0.000002| 0.03	-5.26| -5.26	< 0.05				
Model 2					0.61	4	-20.54	0.21
Intercept	0.86| 0.63	0.07| 0.03	12.35| 24.83	< 0.05				
BORD	-0.000003| -0.05	0.000002| 0.03	-2.05| -2.05	0.06				
DIST	-0.000008| -0.11	0.000002| 0.03	-4.22| -4.22	< 0.05				
Functional diversity								
Model					0.67	5	-49.38	0.75
Intercept	0.46| 0.26	0.04| 0.01	10.33| 26.22	< 0.05				
FORE	-0.000000007| -0.04	0.000000003| 0.01	-2.85| -2.85	< 0.05				
BORD	-0.000002| -0.03	0.0000006| 0.01	-3.00| -3.00	< 0.05				
DIST	-0.000004| -0.06	0.000001| 0.01	-4.43| -4.43	< 0.05				
Phylogenetic diversity								
Model					0.68	5	-30.49	0.74
Intercept	0.75| 0.41	0.08| 0.02	9.81| 23.83	< 0.05				
FORE	-0.00000001| -0.06	0.000000004| 0.02	-2.63| -2.63	< 0.05				
BORD	-0.000004| -0.06	0.000001| 0.02	-3.33| -3.33	< 0.05				
DIST	-0.000007| -0.10	0.000002| 0.02	-4.28| -4.28	< 0.05				

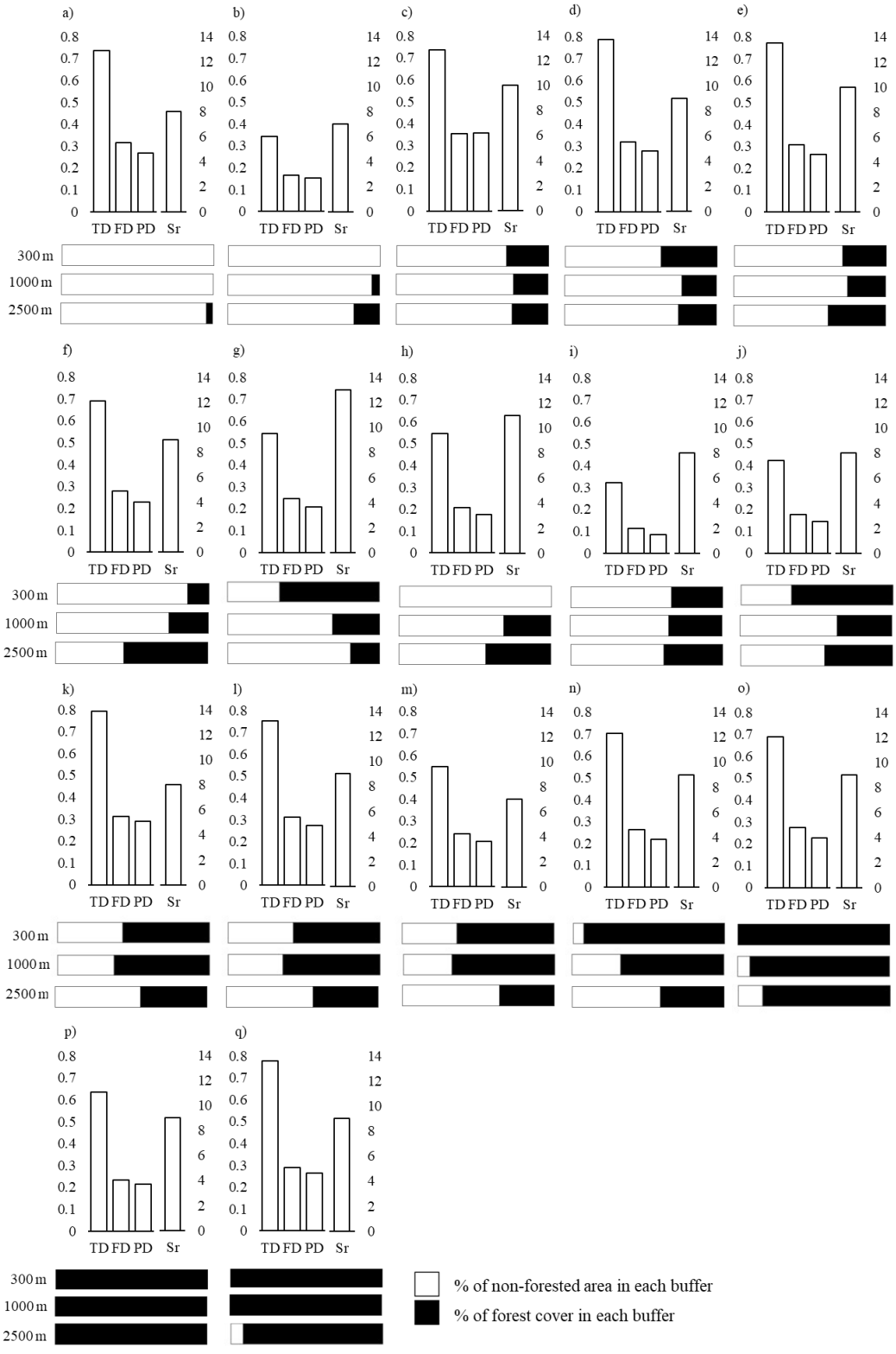

Fig. 4.2 – Taxonomic (TD), functional (FD) and phylogenetic (FD) diversities (left Y-axes), number of species captured (Sr) (right Y-axes), and percentages of forest and non-forest cover (horizontal bars) measured in three concentric buffer zones of 300, 1000, and 2500 m radius for the 17 studied landscapes in the Serra da Bodoquena, Brazil.

4.5 Discussion

Taxonomic, functional and phylogenetic diversity of bats similarly respond to the gradient of forest loss and fragmentation in the Serra da Bodoquena region. The three diversities decrease as the distance to the national park increases, and negatively respond to length of forest borders at intermediate and large scales and additionally to forest cover at large scale, indicating that effects of forest loss and fragmentation are best detected at our large scale (2500 m buffer; 1963.5 ha). Beta diversity of Serra da Bodoquena bats (0.22 using abundance data) is comparable to quite different groups elsewhere, like Atlantic Forest odonates (0.21) or Amazonian anurans (0.20) (Bitar et al., 2015; Pires et al., 2018), but it is lower if compared to Cerrado butterflies (0.66) or Atlantic Forest scarabs (0.40) (Silva and Hernández, 2014; Pereira, 2016). Moreover, beta diversity of bats in the Serra da Bodoquena is compatible with that estimated for bats in this region of Cerrado by Silva et al. (2018). Turnover and nestedness equally contribute to total beta diversity when abundance data are used. Species turnover is mediated by the distance to the national park while any of the studied variables justified the species nestedness. The consistent effect of the distance to the national park for bat alpha and beta diversities highlights the high importance of this reserve for structuring bat assemblages and, ultimately, for maintaining the regional biodiversity. On the other hand, for presence-absence data species turnover, rather than nestedness, was the main component of beta diversity thus acting as the main mechanism structuring composition of bat assemblages across the landscape gradient.

Forest loss and fragmentation, as well as distance to the national park, do not appear to affect species richness of local bat assemblages in the Serra da Bodoquena, as the number of species was unrelated with our predictor variables. Patch size decreasing and isolation increasing are expected to negatively affect species richness (Ferraz et al., 2007; Fahrig, 2013). Both measures are strictly related with habitat amount in a landscape, i.e. as patch size increases and distance to the next-nearest patch decreases the habitat amount in a landscape tend to be higher (Fahrig, 2003). However, our results do not corroborate these expectations, likewise found for bat assemblages in fragmented Amazonian forest (Klingbeil and Willig, 2009). Thus, species replacement seems to quantitatively compensate species loss across the studied landscapes.

The sensitivity of bats to forest borders remains poorly understood because the response is ensemble and species-specific, and because bat responses depend on the environmental contrast between forested areas and the matrix. In landscapes with marked contrast between habitat fragments and matrix, as terrestrial patches surrounded by water, species richness and composition are highly associated with border density (Meyer and Kalko, 2008), while in low contrast fragment-matrix this relation is tenuous or inexistent (Faria, 2006). Thus, land

conversion for human uses in the Serra da Bodoquena likely forms a relatively contrasting matrix to forest patches, as length of forest border affected bat assemblage composition across the study landscapes. Some species are known to be tolerant to borders due to a tendency for higher fruit availability in these areas compared with those within the forests or because they benefit from the contact with the matrix that can provide additional resource opportunities (e.g. *D. rotundus* in our study region; Fig. S4.4). However, we found that taxonomic diversity tends to decrease with borders. This could be justified by the sensitivity of other species to these areas. Some gleaning animalivorous are considered sensitive to forest borders possibly because these areas are poorer in their preferred arthropod prey or due to restrictions in their flight maneuverability (Rocha et al., 2017). Additionally, *L. dekeyseri* and *A. geoffroyi*, two nectarivorous species, seem to be more related with landscapes with less forest borders, which could indicate some vulnerability of these species to these areas. Forest borders also lead to a decrease in functional diversity which indicate that functionally unique species are lost in these areas while functionally redundant species persist (Flynn et al., 2009). Borders could act as environmental filters favouring species with intermediate aspect ratio and wing loading and with highly manoeuvrable flights, traits that enable species to fly in cluttered environment in understory and that feed on pioneer species (e.g. *Carollia perspicillata*; Fleming 1988; Marinello and Bernard, 2014). Closely related species tend to share similar sets of traits. So, phylogenetic diversity is a good predictor of ecosystem functioning because this measure incorporates even those species traits that we do not recognized as important (Cadotte et al., 2008). As occur for functional diversity in this work, we found that phylogenetic diversity is negatively correlated with forest borders, which could indicate a loss of evolutionarily distinct lineages associated with forest borders, reinforcing the idea that these areas act to filter species with narrow niches and with more distinct phylogenetic characteristics.

Contrary to expected, our results showed a negative relation between forest area and the three diversities analysed at the largest scale both when include all bat species or only phyllostomids, suggesting a reduction in the dominance of species that benefit from forest interior or that some species benefit from a decrease in forested areas at least at some point. In fact, Estrada and Coates-Estrada (2002) suggested that bat species diversity may be higher in fragmented landscapes composed by mosaics of different habitat types and small forest fragments. High functional diversity in less forested areas could be due to the presence of different landscape structures that enable the coexistence of species with diverse functional traits. As mentioned before, understory frugivores of the subfamily Carolliinae feed on pioneer species which are abundant in early- and mid- successional forests, in forest borders but also in agroforest areas. These species have low aspect ratio and low wing loading, which enables them to feed on cluttered environment (Norberg and Rayner, 1987; Fleming, 1988). Stenodermatinae species feed mainly on *Ficus* spp., usually a patchily distributed resource with asynchronized

fruiting periods (Milton et al., 1982). So, they tend to show wide home-ranges to respond to their feeding demands, being quite resilience to fragmentation and habitat loss. These trees are maintained in degraded habitats, as crops and agroforest systems, with the main aim to provide shadow for cattle (Galindo-González and Sosa, 2003), so they may provide essential foraging resources for bats in fragmented landscapes once provide ripe fruits; additionally, these trees also can act as stepping stones, when bats are commuting between fragments and continuous habitats, and can provide protection against predators (Galindo-González and Sosa, 2003). This subfamily is composed by morphological diverse species with low aspect ratio and wing loading slightly above average for the family (Norberg and Rayner, 1987). Additionally, their wide wings with a large dactylopatagium (Norberg and Rayner, 1987) enables them to reduce flight speed which indicates higher flexibility in the use of space and also higher ability to move in a fragmented landscape. The response of nectarivorous bat species, subfamily Glossophaginae, to habitat loss and fragmentation is controversial. While some studies reported that nectarivores are positively related with native vegetation amount (Gorresen et al., 2005; Gorresen and Willig, 2004), other showed that they benefit from mosaics of agricultural habitats (Avila-Cabadilla et al., 2012) due to their feeding plasticity, as they feed on nectar but also on insects, fruit pulp and pollen (Alvarez et al., 1991; Clare et al., 2014). The Phyllostominae are considered highly sensitive to forest fragmentation, and species of this family are considered good indicators of the level of integrity of an ecosystem (Medellín et al., 2000). Nevertheless, some Phyllostominae are commonly captured in highly disturbed areas (Sousa et al., 2013), as also occurred in our study; for example, in our most fragmented landscape, with solely 4% of forest cover at the largest scale, we captured *Lophostoma brasiliense* and *Lophostoma silvicolum*. The Vespertilionidae and the Molossidae present low abundance in our sampling area but were recorded both in well-preserved areas and in areas with low forest cover. *Myotis nigricans* forages mainly in open space and rainforest gaps. However, its call structure shows some plasticity enabling this species to also forage in edge environments (Siemers et al., 2001). Sousa et al. (2013) refer to *Molossops temminckii* as a species with generalist habits, so this species could be indifferent to landscape modification and forest cover reduction in landscapes. In fact, species of the Molossidae tend to forage in open areas and above canopy, maintaining populations in agricultural and cattle areas (Gonçalves et al., 2017). Shortly, the high diversity of feeding and morphological traits of species assemblages in the study areas and their resilience to inhabit and exploit changed habitats can justify the increase on functional diversity in areas with less forest cover. Contrary to expectations, our results show that assemblages became more phylogenetic clustered in more forested areas. A possible explanation for this result is that a mosaic of forested and non-forested areas could favour different lineages enhancing the phylogenetic diversity. In fact, Cisneros et al. (2015) reported that phylogenetic diversity of bat

assemblages in Costa Rica increases in areas composed by a mosaic of forest and pastures, which could indicate that heterogeneity favour phylogenetic dispersion.

The three studied metrics of diversity - taxonomic, functional and phylogenetic - were negatively affected by the linear distance to the Serra da Bodoquena National Park. All diversities decrease from landscapes near the national park to farther landscapes. The national park is the largest continuous forested area of this region however taxonomic, functional and phylogenetic diversities decrease with forest cover at the large studied scale. Apparently, these results are somewhat contradictory, but this could indicate that bat assemblages in Serra da Bodoquena benefit both from forested and non-forested areas. This can occur because heterogeneous landscapes fulfil the requirements of different bat species, providing more feeding resources for them to explore, as was also reported elsewhere (Estrada and Coates-Estrada, 2002). Additionally, we cannot exclude the hypothesis that the observed patterns are in fact due to other factors strictly related to distance to the national park that we were unable to quantify in this study. For example, we do not quantify land cover types in buffers and this variable has been pointed as important for bats because different cover types provide different resources (Cisneros et al., 2015). Additionally, our results are in accordance with other studies that show that bat responses to landscape variables are scale-dependent (Klingbeil and Willig, 2010; Pinto and Keitt, 2008), i.e. the importance of landscape variables, in our case forest borders and forest area, changes with the scale under study. While forest borders are important at scales higher than 314.16 ha, forest area is important only at large scale (1963.50 ha). Thus, our results show that the three studied dimension of bat biodiversity in Serra da Bodoquena respond at higher scales.

Briefly, Serra da Bodoquena belongs to a set of plateaus that encircles the Pantanal wetland and, comparing to other plateaus, still retains a well-preserved landscape (Oliveira et al., 2009) and consequently a diverse bat fauna. As a karstic region, Serra da Bodoquena is rich on roosts for several species that depends on large caves to roost, for example *Glossophaga soricina*, *C. perspicillata*, *D. rotundus*, *A. caudifer* and *A. geoffroyi* (Trajano, 1985, 2000; Baumgarten and Vieira, 1994; Bredt et al., 1999;). Our results show that even areas with less forest cover are important in terms of taxonomic, functional and phylogenetic diversities, possibly because these remnants could be used as feeding areas, which highlight the need to preserve the remaining vegetation. Bats in these more impacted areas are extremely important because they service forest regeneration (Muscarella and Fleming, 2007). Additionally, individuals in landscapes with less vegetation cover can benefit from well-preserved forests around the studied buffers.

4.6 Acknowledgements

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CHAPTER 5

SPECIES–GENETIC DIVERSITY CORRELATION IN PHYLLOSTOMIDS OF THE BODOQUENA PLATEAU, BRAZIL

Species–genetic diversity correlation in phyllostomids of the Bodoquena plateau, Brazil

Ana Lino[1], Eduardo Ferreira[1], Carlos Fonseca[1], Erich Fischer[2], Maria João Ramos Pereira[1,3]

[1] Department of Biology & Centre for Environmental and Marine Studies (CESAM), University of Aveiro, Campus Universitário de Santiago 3810-193 Aveiro, Portugal.

[2] Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil

[3] Department of Zoology, Institute of Biosciences, Universidade Federal do Rio Grande do Sul, Av. Bento Goncalves 9500, Porto Alegre RS 91540-000, Brazil.

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5.1 Abstract

Recent theories suggest that processes shaping species diversity are the same shaping genetic diversity, which may lead to a correlation between the two levels of diversity. Using neotropical bat assemblages, and the genetic diversity of two co-distributed species with distinct life-history traits, *Artibeus planirostris* and *Carollia perspicillata*, we evaluated the correlation between taxonomic and genetic diversity in both species and examined potential underlying mechanisms for such correlations, namely the distance to the nearest border of the Serra da Bodoquena National Park, forest area, forest borders and number of forest fragments. We found that genetic diversity in *A. planirostris* was not explained by any of the analysed variables and that allelic richness and expected heterozygosity in *C. perspicillata* were negatively related to distance to the national park and forest area, but significance changed according to the scale of analysis. For *A. planirostris*, we found a negative correlation between evenness and expected heterozygosity and between mean presence-absence assemblage divergence and mean genetic divergence based on microsatellites. For *C. perspicillata*, we found a positive correlation between species richness and haplotype richness and between evenness and expected heterozygosity. Genetic differentiation based on microsatellites in *C. perspicillata* was positively related to geographic distance and landscape differentiation. We concluded that species-genetic diversity correlations vary according to bat species under study. Thus, *A. planirostris* seems to be an outlier species, while *C. perspicillata* seems to be ecologically more similar to the other species in assemblages.

Keywords: Chiroptera; Fragmentation; Genetic diversity; Habitat loss; Species diversity.

5.2 Introduction

Biodiversity has historically been studied at inter (taxonomic) and intraspecific (genetic) levels by two independent disciplines, community ecology and population genetics, respectively. However, researchers have increasingly pointed out that processes shaping species diversity are similar to those shaping genetic diversity (Antonovics, 1976; Vellend, 2003). In community ecology, processes shaping species assembly are community (assemblage) drift, migration, coexistence mechanisms and speciation; in population genetics the equivalent processes are genetic drift, gene flow, natural selection and mutation (Vellend, 2010). Community or assemblage drift and genetic drift are responsible for the stochasticity in the sorting of species and individuals within communities or assemblages and of alleles and gene copies within populations, respectively (Kimura, 1983; Hubbell, 2001), and these processes tend to rise in communities or assemblages with few species or populations with few individuals. Migration enables interchanging individuals between communities or assemblages as gene flow enables interchanging alleles between populations (Kimura, 1983; Hubbell, 2001). Processes as competition and predation affect the coexistence of individuals and species in a non-random way, while natural selection can non-randomly change the frequency of alleles in populations (Kimura, 1983; Shurin and Allen, 2001). Finally, speciation and mutation are parallel processes that respectively act in communities and populations, the former representing the surge of new species and the last the surge of new alleles.

Based on these parallelisms, Vellend (2003) hypothesized that species and genetic diversities should vary in the same direction, which he called species-genetic diversity correlation (SGDC), due to similar influences of environmental characteristics on both levels of diversity. To test SGDC, Vellend (2003) compiled data from birds, reptiles, mammals and plants from island systems and found that SGDC is generally positive. Subsequent studies have shown, however, that the direction of that correlation is not always the same. In fact, although several studies have supported a predominance of a positive relationship between species and genetic diversities (Vellend, 2003, 2004; Cleary et al., 2006; Struebig et al., 2011; Blum et al., 2012), other studies detected negative SGDC or failed to find a clear correlation trend (Wehenkel et al., 2006; Puşcaş et al., 2008; Whitlock, 2014). These contrasting results indicate that, in some situations, the species and genetic levels of diversity are differentially regulated by the spatial variation among sites or landscapes under study. Habitat area, connectivity and environmental heterogeneity are the main factors affecting SGDC (Kahilainen et al., 2014). The roles of area and connectivity in driving SGDC generally agree throughout the literature. Community or assemblage drift and genetic drifts are unexpected or less intense in communities or assemblages and populations living in larger habitat areas, which support more species and larger populations thus leading to higher species and genetic diversities (Vellend, 2003, 2004;

Lamy et al., 2013; Kahilainen et al., 2014). Well-connected habitat patches facilitate the movement of individuals and alleles, which maintains high levels of species and genetic diversities, or at least prevents them from being lost (Lamy et al., 2013). However, results concerned with environmental heterogeneity are not so clear. On the one hand, heterogeneous habitats promote diversification and coexistence of species and genotypes creating a positive SGDC, and, on the other, heterogeneity could favour generalist species that widely exploit the available range of habitats thus reducing the number of species and genetic variation (Kassen, 2002; Stein et al., 2014). Despite the growing number of studies on the topic, information on SGDC remains insufficient and biased toward plant species. It is therefore crucial to understand whether generalization of SGDC is possible for more taxa and in what situations it should be expected.

Current evidences show both species and genetic diversity losses on bat assemblages and populations from fragments compared to those in continuous habitats (Brosset et al., 1996; Meyer et al., 2009; Ripperger et al., 2012). Struebig et al. (2011) reported a parallel loss in both diversities – species and genes – in co-distributed insectivorous bats in Southeast Asia, highlighting the need to increase knowledge on the impact of habitat loss and fragmentation on bats. Here we aim to: i) test the species-genetic diversity correlation (SGDCs) in phyllostomid bat assemblages and populations in Bodoquena plateau; ii) test whether composition and structure of landscape shape bat species richness and genetic diversity and affect assemblage and genetic divergences; and iii) evaluate if landscape characteristics and geographic distance affect assemblage and genetic distinctiveness in similar ways. We selected two highly common Neotropical frugivore bats – the Seba's short-tailed bat, *Carollia perspicillata*, and the flat-faced fruit-eating bat, *Artibeus planirostris* – for our tests on genetic diversity. We predict that i) as studied species has different ecological characteristic and different vagilities, they should respond differently to landscape characteristics; ii) geographic distance should be more strongly related with genetic differentiation in the less vagile species, *C. perspicillata* than in *A. planirostris*; and iii) areas with similar landscape characteristics should retain similar species and genetic diversities.

5.3 Material and methods

Study site

This study was conducted in the Serra da Bodoquena, state of Mato Grosso do Sul, Brazil (Fig. 5.1). This region still retains large areas of native vegetation that are mostly composed by deciduous and semideciduous forests, woodland and arboreal savannas (cerradão

and cerrado *sensu stricto*, respectively) and grasslands (Furtado et al., 1982; Baptista-Maria et al., 2009). To preserve these relict vegetation formations, especially the largest Atlantic Forest remnant in Mato Grosso do Sul state, the 76,481 ha Serra da Bodoquena National Park, an IUCN protected area, was created in 2000 (IBAMA, 2000). The region has a tropical climate, Aw of Köppen-Geiger climatic classification, with wet summer and dry winter (Kottek et al., 2006). Mean annual precipitation ranges between 1300 to 1700 mm and mean annual temperature is approximately 26 ºC. Regional water springs and rivers drain to the Pantanal through the Miranda and Apa basins, which are sub-basins of the Paraguay river. During the last decades, human activities have changed the native physiognomy of the region. Around the park, natural habitats have increasingly been transformed for livestock and cash crop (corn and soybean) productions, along with areas explored for ecotourism and adventure like rafting and cave diving (Mato Grosso do Sul, 2014; IBGE, 2017).

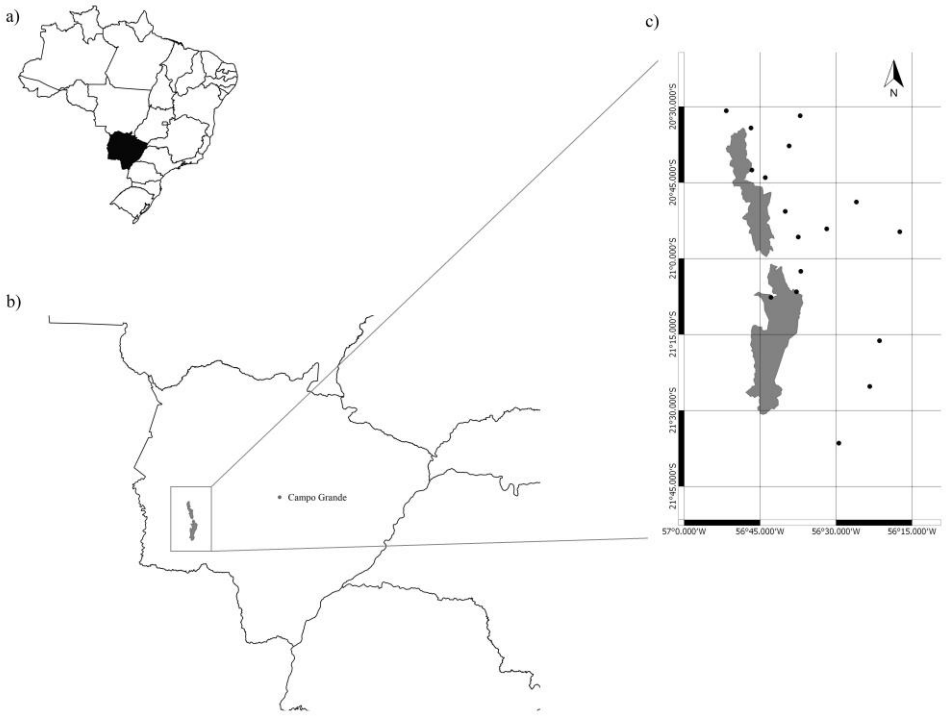

Fig. 5.1 – Location of the study area. a) Mato Grosso do Sul in Brazil, b) Serra da Bodoquena and c) Serra da Bodoquena National Park (in grey); circles represent the 17 study sites.

Bat surveys

We used satellite images to select the sampling sites. Firstly, we divided the full extension of the Serra da Bodoquena (18,000 km^2) in 360 hexagons of 5,000 ha each, from

which we randomly selected 17 representing a gradient of forest cover that vary from 0 to 100%. Additional criteria for site selection were accessibility, presence of watercourses, and avoidance of close hexagons representing similar positions in the forest cover gradient. For bat surveys, we established one place with forest near the centre of each selected hexagon.

We surveyed bats in the 17 sites during dry season (June to September) in 2015 and 2016 and wet season (January to March) of 2016 and 2017. In each location, we set 343.2 m^2 (132 x 2.6 m) mist nets for 6 h after dusk, with net area equally distributed between deciduous and adjacent semideciduous forest understories; where deciduous forest was absent, we placed all nets in semideciduous forest (n = 7). The netting effort per site was 8,236.8 m^2h, and the total effort was 140,025.6 m^2h. We measured forearm length (to ± 1 mm), body mass (to ± 1 g), recorded sex and reproductive state, and pre-identified in the field all the captured individuals. We collected wing tissues using 3-mm diameter biopsy punches, which were stored in absolute ethanol until DNA extraction. We marked bats with collar bands to recognize recaptures and released them at the same site of captures, except for some specimens which were collected for confirmation of identifications and inclusion as voucher in the Zoological Collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS).

Focal species

We selected two frugivorous bats, *Artibeus planirostris* and *Carollia perspicillata*, to perform genetic analyses. These species are widely distributed in South America (Cloutier and Thomas, 1992; Hollis, 2005) and are the most abundant bats in the study region (Fischer et al., 2018), which is important to gather a suitable number of samples. They conspicuously differ in life history traits. Body mass and forearm length are nearly two times larger for *A. planirostris* (40-69 g and 57.40-69.3 mm, respectively) than for *C. perspicillata* (18-38 g; 38.90-47.4 mm, respectively). *Carollia perspicillata* frequently forages in forest understory and feeds mainly on fruits of *Piper* shrubs, while *A. planirostris* forages in the forest canopy or open savannas and uses *Ficus* and *Cecropia* trees as core fruit sources (Ramos Pereira et al., 2010; Marques et al., 2012; Lim and Engstrom, 2015; Fischer et al., 2018; Silveira et al., 2018). Fruiting individuals of *Piper* are predictable in space and time and often clumped at small scales, whereas individuals of *Ficus* fruit massively and asynchronously through trees widely scattered in the landscape (Janzen, 1979; Milton et al., 1982). For these reasons, *C. perspicillata* tends to explore spatially concentrated sources, and *A. planirostris* is expected to commute long distances to meet its food requirements. Indeed, *A. planirostris* presents higher aspect ratio and wing loading compared to *C. perspicillata* (aspect ratio 6.39 and 6.22; wing loading: 40.18, and 38.80, respectively), which confer high dispersal ability for *A. planirostris* but increased

manoeuvrability in clutter habitats for *C. perspicillata* (Marinello and Bernard, 2014). Therefore, negative effect of habitat fragmentation on genetic diversity should be stronger in *C. perspicillata* than in *A. planirostris*.

Genetic analyses

We analysed genetic variation in *A. planirostris* and *C. perspicillata* using two types of DNA markers: mitochondrial DNA and nuclear autosomal microsatellites. DNA extractions from all samples were carried out using a variation of the salt-extraction method (Bruford et al., 1992). Total DNA was stored in TE buffer, quantified in NanoDrop (Thermo Scientific, USA) and refrigerated. We amplified mitochondrial DNA from the COI region using the polymerase chain reaction with one primer pair: LCO1490 (5'-ggt caa caa atc ata aag ata ttg g-3') and HC02198 (5'-taa act tca ggg tga cca aaa aat ca-3') (Folmer et al., 1994). To obtain the sequences, we amplified mtDNA in a total volume of 25 µl contained 1mg/ml BSA, 2.0mM MgCl2, 0.2 mM dNTPs, 0.12 µM of each primer, 1 U Taq polymerase and 2 µl DNA template at a concentration of 30 ng/ul. The PCR was programmed with the following conditions: an initial denaturation step at 94ºC for 3 minutes, followed by 35 cycles at 94ºC/1 minute (denaturation), 48ºC/2 minutes (primer annealing) and 72ºC/90 seconds (extension steps), and a final extension step of 72ºC for 10 minutes. We purified the PCR products using ExoSap-IT® (USB Corporation) and sequenced them on automatic sequencers ABIPRISM® 3730-XL DNA Analyser from Applied Biosystems™.

We also screened all samples with 16 microsatellites for *A. planirostris* (DKU6N, CW4QZ, BS15V, AJ8AZ, DZ8Y0, C03AB, CPS1J, CRS13, DR2F6, AO8V6, EJRJM, CX8S8, DAVVT, CKI31, D3UAB and EMC0R; McCulloch and Stevens, 2011) and 12 microsatellites for *C. perspicillata* (CC7, CC18 and CC19 - Cleary et al., 2016; AAGG117, AAGG91, AAGG112, AAGG143 and AAGG7 - Bardeleben et al., 2007; BS15V, C03AB, AO8V6 and DKU6N - McCulloch and Stevens, 2011), from which only 12 in *A. planirostris* and 10 in *C. perspicillata* were successfully amplified. Polymerase chain reaction conditions consisted in an initial activation step of 15 minutes at 95ºC, followed by 36 cycles at 94ºC/30 seconds (denaturation), 57ºC/45 seconds (primer annealing) and 72ºC/90 seconds (extension steps), and a final extension step of 10 min at 72ºC.

From the 17 sampled sites, we genotyped 268 *A. planirostris* and 148 *C. perspicillata* individuals. We excluded from the analyses those landscapes with less than five individuals sampled, the minimum value considered suitable to avoid bias in genetic analyses. Thus, we included all 17 landscapes in the analyses regarding *A. planirostris* but only 11 for *C.*

perspicillata. Additionally, as we failed to sequence and genotype some samples of *C. perspicillata*, we ended with 128 and 134 samples for mtDNA and microsatellites, respectively.

Measures of diversity and divergence

We focused the analysis only in phyllostomid species. We followed Vellend (2004) for measures of diversity and divergence. We considered species diversity as the number of species in each site (species richness; Sr) and by the probability that two randomly chosen individuals in each site are from different species (evenness; Eve). As a measure of evenness, we used a version of Simpson index diversity that is analogous to expected heterozygosity (H_E). So, if f_i is the frequency of species in an assemblage, evenness is $1-\sum f_i^2$. To reduce positive skewness in the distribution of Eve, we expressed evenness by its odds ratio, E/(1-E).

We measured the mtDNA diversity as the number of haplotypes (H) and haplotype diversity (h) in each landscape. We considered microsatellite diversity as the mean number of alleles across loci, rarefied to the minimum sample size (allelic richness; Ar), and by the probability that two randomly chosen alleles at a given locus in a population were different (expected heterozygosity; H_E).

We measured divergence at assemblage and genetic levels. We evaluated assemblage divergence using presence-absence and frequency data. For presence-absence data we used the dissimilarity index of Raup and Crick (1979) (β_{RC}). This probabilistic index compares the observed number of species that occur in two assemblages with the distribution of co-occurrences after 1000 random draws from the global pool; it ranges from zero (no dissimilarity) to one (high dissimilarity). To compute assemblage divergence using frequency data we used an equivalent form of the population differentiation coefficient (F_{ST}) considering the entire assemblage as a single locus and each species as an allele, thus using species' relative frequency rather than allele frequencies in the equation ($F_{ST\text{-}assemblages}$; see Vellend (2004) for a detailed description).

To measure genetic divergence based on mtDNA ($F_{ST\text{-}mtDNA}$), we built a distance matrix using the Maximum Composite Likelihood model (Tamura et al., 2004). To measure genetic divergence based on microsatellites, we calculated the population differentiation coefficient ($F_{ST\text{-}G}$) among all populations and between each pair of populations as follow, $F_{ST} = (H_T\text{-}H_S)/H_T$, where H_T is the Hardy-Weinberg expected heterozygosity based on mean allele frequencies across all populations (or pair of populations), and H_S is the mean of He across populations (Nei, 1977). As a measure of divergence of an assemblage or population, we calculated the mean of pairwise β_{RC}, $F_{ST\text{-}assemblages}$, $F_{ST\text{-}mtDNA}$ and $F_{ST\text{-}G}$ for the focal assemblage or population versus all the others and denotated them as β_{RC}*, $F_{ST\text{-}assemblages}$ *, $F_{ST\text{-}mtDNA}$* and $F_{ST\text{-}G}$*.

Predictor variables for diversity and divergence

Based on Landsat 2012 images, each survey site was encircled by buffers of 300, 1000 and 2500 m for landscape metrics using Fragstats (McGarigal et al., 2012). We recorded forest cover (squared meters, FORE), forest border length (meters, BORD) and number of forest fragments (FRAG) in each of the three buffer sizes, and also the distances (meters, DIST) from the netting sites to the nearest border of the Serra da Bodoquena National Park. To evaluate scale-dependence of bat responses to landscape attributes, we used the three buffer sizes that likely encompass home-range differences among bat species in our study region (Bonaccorso et al., 2006; Esbérard et al., 2011; Arnone et al., 2016; Martins, 2016). To evaluate whether geographic distance and/or landscape variables shape assemblage and genetic divergence, we created two types of distance matrices: i) a matrix of pairwise geographic distances, built using Google Earth (Google Inc., 2018) and, ii) an Euclidian distance matrix based on landscape variables, computed for each buffer including all the aforementioned variables – FORE, BORD, FRAG and DIST. The mean distance of a site to all the others (GEOdist*) was computed to understand if distance between sampling sites affect β_{RC}*, $F_{ST\text{-}assemblages}$ *, $F_{ST\text{-}mtDNA}$* and $F_{ST\text{-}G}$*.

Data analysis

All analyses were done in the R statistical environment (R Core Team, 2013). We examined whether species richness (Sr), species evenness (Eve), allelic richness (Ar), expected heterozygosity (H_E), haplotype richness (H), haplotype diversity (h), mean frequency-based assemblage divergence ($F_{ST\text{-}assemblage}$*), mean presence-absence assemblage divergence (β_{RC}*), mean genetic divergence based on microsatellites ($F_{ST\text{-}G}$*) and mean genetic divergence based on mtDNA ($F_{ST\text{-}mtDNA}$*) vary with the landscape metrics (FORE, BORD, FRAG and DIST) at the three studied scales (300, 1000 and 2500 meters) using generalized linear models (GLM). Additionally, the mean distance of a site versus all other (GEOdist*) was used as explanatory variable in models of β_{RC}*, $F_{ST\text{-}assemblages}$*, $F_{ST\text{-}G}$* and $F_{ST\text{-}mtDNA}$*. Before the analyses, continuous variables were standardized, i.e. transformed to standard scores, which sets data from different sources onto the same scale. We used Poisson error distribution with log link-function for count data (Sr and H) and normal error distribution with identity link-function for all the other response variables (allelic richness is not a count as it was obtained from rarefaction, so it should be normally distributed, according to the central limit theorem). Previously to the modelling procedure, we tested for multicollinearity of predictor variables using the Variance Inflation Factor (VIF) in 'car' R package (Fox, 2007); and considered VIF < 5 as negligible collinearity. For each buffer size, we produced all combinations of explanatory variables to

build a set of possible models. For each model we calculated the Akaike's information criterion corrected for small samples (AICc) (Burnham and Anderson, 2002) in package 'AICcmodavg' (Mazerolle, 2017). Candidate models were then compared and ranked; models with $\Delta AICc < 2$ were considered as having substantial support and equally best models (Burnham and Anderson, 2002). Thus, GLMs testing Sr, Eve, Ar, H_E, H and h included FORE, BORD, FRAG and DIST as explanatory variables when studying the small and intermediate buffers (300 and 1000 meters) and excluded the variable FRAG in the buffer of 2500 meters. For GLMs testing β_{RC}*, $F_{ST\text{-}assemblages}$*, $F_{ST\text{-}G}$* and $F_{ST\text{-}mtDNA}$* in *A. planirostris* it was included FORE, BORD, FRAG, DIST and GEOdist* as explanatory variables in the buffers of 300 and 1000 meters and FORE, FRAG, DIST and GEOdist* in the buffer of 2500 meters. Finally, for GLMs testing β_{RC}*, $F_{ST\text{-}assemblages}$*, $F_{ST\text{-}G}$* and $F_{ST\text{-}mtDNA}$* in *C. perspicillata* it was included BORD, FRAG, DIST and GEOdist* in the buffer of 300 meters; FORE, BORD, FRAG and GEOdist* in the buffer of 1000 meters and FORE, FRAG and GEOdist* in the buffer of 2500 meters.

After testing for normality with the Shapiro-Wilk test, we tested the association between species diversity and genetic diversity and between mean assemblage divergence and mean genetic divergence in the two species. For this, we used the Pearson correlation test, when both variables had normal distribution, or the Spearman test, when at least one of the variables presented non-normal distribution. For significant correlations, we then analysed partial correlations controlling for each of the predictor variables at three buffer sizes. If the raw correlation was much higher than the partial correlation, then we considered the predictor variable an important driver of the raw correlation. Finally, we used Mantel tests for testing correlations between assemblage ($F_{ST\text{-}assemblages}$ and β_{RC}) and genetic dissimilarities matrices ($F_{ST\text{-}G}$ and $F_{ST\text{-}mtDNA}$) with pairwise geographic distances and pairwise differences in landscape variables.

5.4 Results

We captured 1889 phyllostomid bats from 19 species. Species richness of phyllostomids in the studied landscapes varied from 6 to 12 and evenness varied from 0.32 to 0.79. In *A. planirostris*, the mean number of alleles per locus was 14.58 ranging from 4 (DKU6N) to 32 (CW4QZ) and the total number of haplotypes in all study areas was 30. Allelic richness varied from 5.94 to 6.60, expected heterozygosity from 0.73 to 0.80, haplotype number from 3 to 13, and haplotype diversity from 0.24 to 0.97. For *C. perspicillata*, the mean number of alleles per locus was 16.9 ranging from 4 (BS15V) to 34 (CC18) and the total number of haplotypes in all study areas was 26. In this species, allelic richness varied from 5.51 to 6.54, expected

heterozygosity from 0.65 to 0.76, haplotype number from 4 to 11, and haplotype diversity from 0.75 to 0.95 (Table 5.1).

Table 5.1 – Summary measures of species diversity and genetic diversity for *A. planirostris* and for *C. perspicillata*.

			Artibeus planirostris				*Carollia perspicillata*			
Study Sites	Species Richness	Evenness (odds ratio)	Allelic Richness	Expected Heterozygosity	Number of Haplotypes	Haplotype Diversity	Allelic Richness	Expected Heterozygosity	Number of Haplotypes	Haplotype Diversity
P92	8	2.769	6.287	0.767	6	0.648				
P139	7	1.219	6.389	0.784	6	0.647	5.505	0.652	7	0.944
P182	12	1.158	6.314	0.769	8	0.842				
P205	9	1.737	6.486	0.785	5	0.576	5.999	0.711	8	0.924
P206	8	3.331	6.319	0.748	6	0.833	6.000	0.699	5	0.857
P218	9	2.351	5.935	0.759	8	0.688	6.110	0.728	10	0.900
P243	9	2.311	6.209	0.764	3	0.242				
P244	9	1.102	6.596	0.797	8	0.889				
P249	10	3.378	6.294	0.766	8	0.791	6.541	0.762	9	0.945
P252	6	0.469	6.553	0.789	7	0.692				
P264	8	0.475	6.073	0.760	6	0.675				
P268	7	3.728	6.167	0.727	4	0.643	6.064	0.726	6	0.848
P275	9	3.026	6.088	0.766	6	0.733	6.054	0.745	8	0.808
P295	9	3.675	6.287	0.766	6	0.750	6.119	0.718	7	0.781
P303	9	2.215	6.235	0.770	8	0.758	5.889	0.726	11	0.952
P310	9	2.205	6.522	0.783	8	0.758	5.754	0.694	4	0.750
P312	8	0.735	6.551	0.777	13	0.967	6.100	0.699	4	0.810

None of the predictor variables affected richness of phyllostomid species in any of the subgroups of landscapes included, those with records of *A. planirostris* or those with records of *C. perspicillata*. On the other hand, species evenness was negatively affected by DIST in both cases (Tables 5.2 and 5.3).

Table 5.2 – Significant predictors of species and genetic diversity and divergence for *A. planirostris* identified through generalized linear models (GLM).

	Buffer 300 m					Buffer 1000 m					Buffer 2500 m			
	Estimate	**SD**	**p-value**	**R^2**		**Estimate**	**SD**	**p-value**	**R^2**		**Estimate**	**SD**	**p-value**	**R2**
Evenness														
Model 1				0.371	Model 1				0.510	Model 1				0.371
Intercept	2.111	0.220	< 0.001		Intercept	2.111	0.201	< 0.001		Intercept	2.111	0.220	< 0.001	
DIST	-0.655	0.220	0.009		BORD	-0.404	0.203	0.066		DIST	-0.655	0.220	0.009	
					DIST	-0.702	0.203	0.004						
					Model 2				0.371	Model 2				
					Intercept	2.111	0.220	< 0.001		Intercept	2.111	0.192	< 0.001	0.586
					DIST	-0.655	0.220	0.009		FORE	-0.502	0.249	0.065	
										BORD	-0.374	0.194	0.076	
										DIST	-0.970	0.247	0.002	
										Model 3				0.468
										Intercept	2.111	0.210	< 0.001	
										FORE	-0.429	0.269	0.133	
										DIST	-0.924	0.269	0.004	
										Model 4				0.457
										Intercept	2.111	0.212	< 0.001	
										BORD	-0.315	0.212	0.160	
										DIST	-0.656	0.212	0.008	
Allelic richness														
					Model 1				0.064	Model 1				0.078
					Intercept	6.312	0.046	< 0.001		Intercept	6.312	0.045	< 0.001	
					BORD	-0.046	0.046	0.327		BORD	-0.051	0.045	0.279	
Expected heterozygosity														
Model 1				0.073	Model 1				0.073	Model 1				0.073
Intercept	0.769	0.004	< 0.001		Intercept	0.769	0.004	< 0.001		Intercept	0.769	0.004	< 0.001	
DIST	0.004	0.004	0.294		DIST	0.004	0.004	0.294		DIST	0.004	0.004	0.294	
Haplotype richness														
					Model 1				0.109	Model 1				0.118
					Intercept	1.764	0.148	< 0.001		Intercept	1.911	0.094	< 0.001	
					FRAG	0.049	0.035	0.152		BORD	0.134	0.092	0.144	
					Model3				0.078					
					Intercept	1.914	0.093	< 0.001						
					BORD	0.110	0.093	0.239						
Mean frequency-based assemblage divergence ($F_{ST\text{-}assemblages}$*)														
Model 1				0.072	Model 1				0.079	Model 1				0.104
Intercept	0.065	0.010	< 0.001		Intercept	0.066	0.011	< 0.001		Intercept	0.057	0.007	< 0.001	
FRAG	-0.006	0.005	0.296		FRAG	-0.003	0.003	0.276		FORE	0.009	0.007	0.206	
Model 2				0.060	Model 2				0.063	Model 2				0.098
Intercept	0.057	0.007	< 0.001		Intercept	0.057	0.007	< 0.001		Intercept	0.071	0.013	< 0.001	
BORD	-0.007	0.007	0.345		FORE	0.007	0.007	0.331		FRAG	-0.002	0.001	0.222	
										Model 3				0.255
										Intercept	0.057	0.006	< 0.001	
										FORE	0.017	0.008	0.050	
										DIST	0.014	0.008	0.115	
Mean presence-absence assemblage divergence (β_{RC}*)														
Model 1				0.630	Model 1				0.125	Model 1				0.125
Intercept	0.291	0.024	< 0.001		Intercept	0.337	0.022	< 0.001		Intercept	0.337	0.022	< 0.001	
FORE	0.063	0.020	0.008		GEOdist*	0.033	0.022	0.163		GEOdist*	0.033	0.022	0.163	
BORD	-0.063	0.020	0.008											
FRAG	0.034	0.013	0.022											
GEOdist*	0.060	0.018	0.005											
					Model 2				0.245					
					Intercept	0.296	0.035	< 0.001						
					FRAG	0.014	0.009	0.159						
					GEOdist*	0.045	0.023	0.071						

Mean genetic divergence based on microsatellites ($F_{ST\text{-}G}$*)

Model 1				0.075	Model 1				0.145	Model 1				0.075
Intercept	0.017	0.001	< 0.001		Intercept	0.018	0.001	< 0.001		Intercept	0.017	0.001	< 0.001	
DIST	-0.001	0.001	0.287		FRAG	-0.0003	0.0002	0.132		DIST	-0.001	0.001	0.287	
Model 3				0.057	Model 3				0.273					
Intercept	0.017	0.001	< 0.001		Intercept	0.019	0.001	< 0.001						
BORD	0.001	0.001	0.356		FRAG	-0.0004	0.0002	0.052						
					GEOdist*	-0.001	0.001	0.138						
					Model 4				0.099					
					Intercept	0.017	0.001	< 0.001						
					FORE	0.001	0.001	0.219						
					Model 5				0.075					
					Intercept	0.017	0.001	< 0.001						
					DIST	-0.001	0.001	0.287						
					Model 6				0.244					
					Intercept	0.018	0.001	< 0.001						
					FRAG	-0.0003	0.0002	0.099						
					DIST	-0.001	0.0005	0.197						
					Model 7				0.240					
					Intercept	0.019	0.001	< 0.001						
					BORD	0.001	0.001	0.206						
					FRAG	-0.0004	0.0002	0.060						

Table 5.3 – Significant predictors of species and genetic diversity and divergence for *C. perspicillata* identified through generalized linear models (GLM).

	Buffer 300 m					**Buffer 1000 m**					**Buffer 2500 m**			
	Estimate	**SD**	**p-value**	**R2**		**Estimate**	**SD**	**p-value**	**R2**		**Estimate**	**SD**	**p-value**	**R2**
Evenness														
Model 1				0.281	Model 1				0.281	Model 1				0.281
Intercept	2.509	0.272	< 0.001		Intercept	2.509	0.272	< 0.001		Intercept	2.509	0.272	< 0.001	
DIST	-0.510	0.272	0.093		DIST	-0.510	0.272	0.093		DIST	-0.510	0.272	0.093	
					Model 2				0.196	Model 2				0.512
					Intercept	2.509	0.287	< 0.001		Intercept	2.509	0.237	< 0.001	
					BORD	-0.425	0.287	0.173		FORE	-0.541	0.278	0.088	
										DIST	-0.793	0.278	0.022	
Allelic richness														
Model 1				0.188	Model 1				0.250	Model 1				0.152
Intercept	6.012	0.073	< 0.001		Intercept	5.866	0.110	< 0.001		Intercept	6.012	0.073	< 0.001	
DIST	-0.106	0.073	0.183		FRAG	0.042	0.024	0.117		BORD	-0.106	0.073	0.183	
					Model 3				0.513					
					Intercept	6.012	0.060	< 0.001						
					FORE	-0.144	0.062	0.050						
					DIST	-0.144	0.062	0.050						
					Model 4				0.189					
					Intercept	6.012	0.073	< 0.001						
					FORE	-0.106	0.073	0.181						

					Model 5				0.188					
					Intercept	6.012	0.073	< 0.001						
					DIST	-0.106	0.073	0.183						
Expected heterozygosity														
Model 1				0.672	Model 1				0.827	Model 1				0.846
Intercept	0.715	0.006	< 0.001		Intercept	0.715	0.004	< 0.001		Intercept	0.715	0.004	< 0.001	
FORE	-0.013	0.006	0.052		FORE	-0.017	0.004	0.003		FORE	-0.020	0.004	0.002	
DIST	-0.019	0.006	0.009		DIST	-0.023	0.004	0.001		DIST	-0.029	0.004	< 0.001	
Model 2				0.458										
Intercept	0.715	0.007	< 0.001											
DIST	-0.019	0.007	0.022											
Haplotype richness														
Model 1				0.338	Model 1				0.219					
Intercept	1.781	0.166	< 0.001		Intercept	1.741	0.186	< 0.001						
FRAG	0.108	0.063	0.090		FRAG	0.062	0.037	0.093						
Model 2				0.251										
Intercept	1.960	0.114	< 0.001											
FORE	-0.153	0.110	0.162											
Model 3				0.149										
Intercept	1.958	0.114	< 0.001											
BORD	-0.177	0.146	0.226											
Haplotype diversity														
Model 1				0.276	Model 1				0.273					
Intercept	0.826	0.029	< 0.001		Intercept	0.822	0.031	< 0.001						
FRAG	0.024	0.013	0.097		FRAG	0.012	0.007	0.099						
Model 2				0.263										
Intercept	0.865	0.020	< 0.001											
BORD	-0.035	0.020	0.106											
Mean presence-absence assemblage divergence (β_{RC}*)														
Model 1				0.184	Model 1				0.603	Model 1				0.496
Intercept	0.434	0.025	< 0.001		Intercept	0.366	0.029	< 0.001		Intercept	0.365	0.038	< 0.001	
GEOdist*	0.036	0.025	0.188		GEOdist*	0.050	0.019	0.032		FRAG	0.009	0.004	0.057	
					FRAG	0.020	0.007	0.020		GEOdist*	0.054	0.023	0.043	
Model 2				0.180	Model 2				0.184	Model 2				0.184
Intercept	0.434	0.025	< 0.001		Intercept	0.434	0.025	< 0.001		Intercept	0.434	0.025	< 0.001	
DIST	0.035	0.025	0.193		GEOdist*	0.040	0.025	0.188		GEOdist*	0.036	0.025	0.188	
Mean genetic divergence based on microsatellites (F_{ST-G}*)														
Model 1				0.534	Model 1				0.534	Model 1				0.534
Intercept	0.026	0.001	< 0.001		Intercept	0.026	0.001	< 0.001		Intercept	0.026	0.001	< 0.001	
GEOdist*	0.003	0.001	0.011		GEOdist*	0.003	0.001	0.011		GEOdist*	0.003	0.001	0.011	

For *A. planirostris*, none of the predictor variables explained genetic diversity, measured as Ar, H_E, H and h (Table 5.2). Additionally, β_{RC}* was positively related with FORE, FRAG and GEOdist* and negatively related with BORD at the small scale. Mean genetic divergence ($F_{ST\text{-}G}$* and $F_{ST\text{-}mtDNA}$*) in this species was not related with any of the studied variables. We found significantly negative correlations between Eve x H_E ($r = -0.631$; $p < 0.05$) and β_{RC}* x $F_{ST\text{-}G}$* ($r = -0.557$; $p < 0.05$) (Fig. 5.2). None of the partial correlations presented a strong reduction in the raw correlations indicating that none of the variables was a significant driver of the correlations between species and genetic diversity or between assemblage and genetic divergence (Table 5.4). Mantel tests show that pairwise differences in assemblage composition were not correlated with pairwise differences in genetic diversity computed with microsatellites or mitochondrial DNA for *A. planirostris*. Positive correlations between frequency-based assemblage differentiation and pairwise differences in landscape variables at buffers of 1000 and 2500 meters were found (Table 5.5). Genetic divergence ($F_{ST\text{-}G}$ and $F_{ST\text{-}mtDNA}$) in *A. planirostris* was not affected by geographic distance, nor by landscape differentiation at any of the three studied buffers.

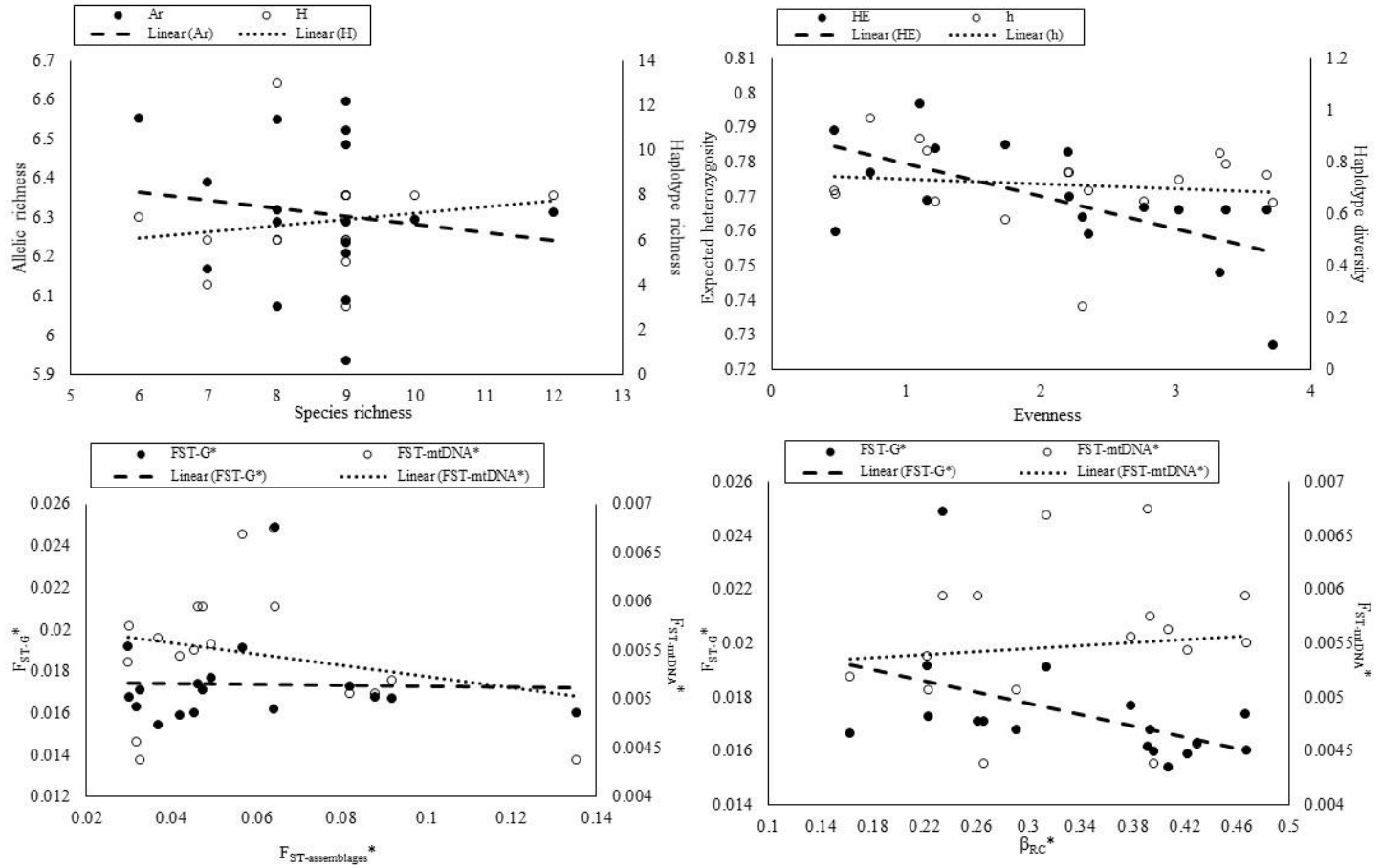

Fig. 5.2 – *Artibeus planirostris*: correlations between a) species richness and allelic richness (r = -0.123; p = 0.639 (S)) and species richness and haplotype richness (r = 0.319; p = 0.212 (S)); b) evenness and expected heterozygosity (r = -0.631; p = 0.007 (P)) and evenness and haplotype diversity (r = -0.166; p = 0.526 (S)); c) mean frequency-based assemblage divergence ($F_{ST\text{-}assemblages}$*) and genetic divergence based on microsatellites ($F_{ST\text{-}G}$; r = 0.016; p = 0.952 (S)) and mean frequency-based assemblage divergence ($F_{ST\text{-}assemblages}$*) and genetic divergence based on mitochondrial DNA ($F_{ST\text{-}mtDNA}$; r = -0.032; p = 0.903 (S)); d) mean presence-absence-based assemblage divergence (β_{RC}*) and mean genetic divergence based on microsatellites ($F_{ST\text{-}G}$*; r = -0.557; p = 0.020 (S)) and presence-absence-based assemblage divergence (β_{RC}*) and genetic divergence based on mitochondrial DNA ($F_{ST\text{-}mtDNA}$*; r = 0.010; p = 0.703 (P)). S and P indicate if it was performed a Spearman rank correlation test or a Pearson product-moment test, respectively.

Table 5.4 – *Artibeus planirostris*: partial correlations between species and genetic diversity and between community and genetic divergence for those with significant or marginally non-significant raw correlation. The correlation values were estimated controlling for the distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG) in each of the three buffer sizes.

Buffer 300	Raw correlation	DIST	FORE	BORD	FRAG
Eve x H_E	r = -0.631;	r = -0.610;	r = -0.613;	r = -0.646;	r = -0.628;
(Pearson correlation)	p = 0.007	p = 0.010	p = 0.012	p = 0.007	p = 0.009
β_{RC}* x $F_{ST\text{-}G}$*	r = -0.557;	r = -0.536;	r = -0.634;	r = -0.574;	r = -0.562;
(Spearman correlation)	p = 0.020	p = 0.032	p = 0.008	p = 0.020	p = 0.023
Buffer 1000					
Eve x H_E	r = -0.631;	r = -0.610;	r = -0.621;	r = -0.739;	r = -0.630;
(Pearson correlation)	p = 0.007	p = 0.012	p = 0.010	p = 0.001	p = 0.009
β_{RC}* x $F_{ST\text{-}G}$*	r = -0.557;	r = -0.536;	r = -0.576;	r = -0.556;	r = -0.584;
(Spearman correlation)	p = 0.020	p = 0.032	p = 0.020	p = 0.025	p = 0.017
Buffer 2500					
Eve x H_E	r = -0.631;	r = -0.610;	r = -0.638;	r = -0.689;	
(Pearson correlation)	p = 0.007	p = 0.012	p = 0.008	p = 0.003	
β_{RC}* x $F_{ST\text{-}G}$*	r = -0.557;	r = -0.536;	r = -0.530;	r = -0.556;	
(Spearman correlation)	p = 0.020	p = 0.003	p = 0.035	p = 0.025	

For *C. perspicillata*, Ar was negatively related to DIST and FORE at the intermediate buffer, and H_E was negatively related with DIST at the three buffers and with FORE at the intermediate and large buffers (Table 5.3). Additionally, β_{RC}* was positively related with GEOdist* and FRAG at intermediate scale and with GEOdist* at large scale, and $F_{ST\text{-}G}$* was positively related with GEOdist*. For *C. perspicillata*, we found positive trend and marginally non-significant values for Sr x H (r = 0.557; p = 0.075) and Eve x H_E (r = 0.593; p = 0.054) (Fig. 5.3). Partial correlation analyses between Sr and H showed larger reduction in the raw correlation when controlling for the number of fragments in small (300 meters) and intermediate (1000 meters) buffers (Table 5.6). Similarly, partial correlation between Eve and H_E showed lower values than the raw correlation when controlling for DIST. Mantel tests show that pairwise differences in assemblage composition based on frequency-based data were positively but marginally correlated with genetic differences based on microsatellites (p = 0.094) and mitochondrial DNA (p = 0.068) in *C. perspicillata*. Positive correlations between frequency-based assemblage differentiation and pairwise differences in landscape variables at buffers of 1000 and 2500 meters were found (Table 5.5). The same occur when testing the relation between presence-absence-based assemblage divergence and pairwise differences in landscape variables at buffers of 1000 and 2500 meters ($r_{buffer1000}$ = 0.364, p = 0.010; $r_{buffer\ 2500m}$ = 0.344, p = 0.012). Genetic differentiation ($F_{ST\text{-}G}$) in *C. perspicillata* was positively related with geographic distance (r = 0.549; p = 0.001) and with landscape differentiation at the intermediate and larger buffers ($r_{buffer1000}$ = 0.291, p = 0.039; $r_{buffer\ 2500m}$ = 0.304, p = 0.022).

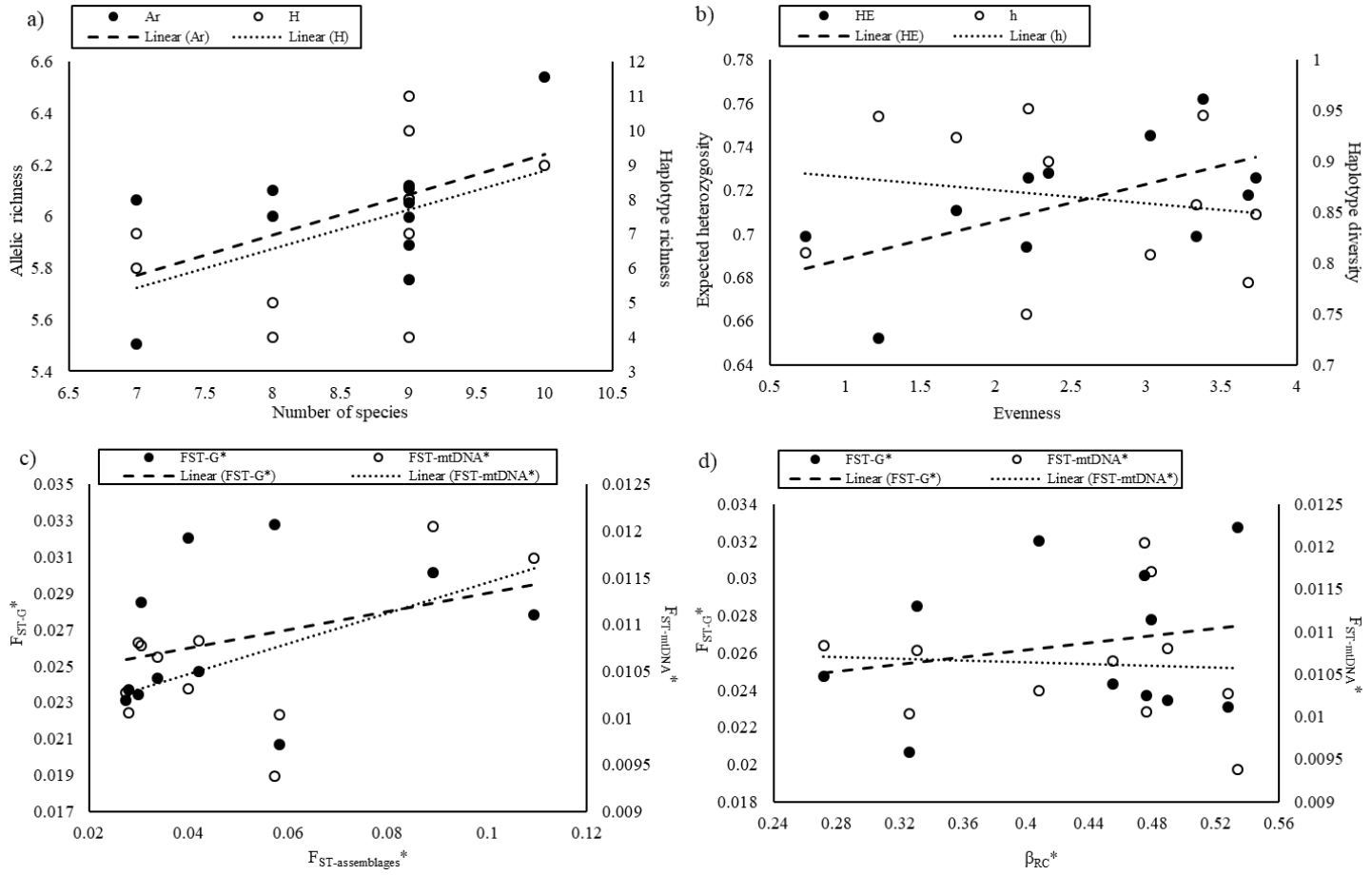

Fig. 5.3 – *Carollia perspicillata*: correlations between a) species richness and allelic richness (r = 0.374; p = 0.258 (S)) and species richness and haplotype richness (r = 0.557; p = 0.075 (S)); b) evenness and expected heterozygosity (r = 0.593; p = 0.054 (P)) and evenness and haplotype diversity (r = -0.181; p = 0.595 (P)); c) mean frequency-based assemblage divergence ($F_{ST\text{-}assemblages}$*) and mean genetic divergence based on microsatellites ($F_{ST\text{-}G}$*; r = 0.418; p = 0.203 (S)) and mean frequency-based assemblage divergence ($F_{ST\text{-}assemblages}$*) and mean genetic divergence based on mitochondrial DNA ($F_{ST\text{-}mtDNA}$*; r = 0.318; p = 0.341 (S)); d) mean presence-absence-based assemblage divergence (β_{RC}*) and mean genetic divergence based on microsatellites ($F_{ST\text{-}G}$*; r = 0.214; p = 0.527 (P)) and mean presence-absence-based assemblage divergence (β_{RC}*) and mean genetic divergence based on mitochondrial DNA ($F_{ST\text{-}mtDNA}$*; r = -0.062; p = 0.856 (P)). S and P indicate if it was performed a Spearman rank correlation test or a Pearson product-moment test, respectively.

Table 5.5 – Correlations between community (F_{ST} and βRC) and genetic distance (F_{ST}-G and F_{ST}-mtDNA) with geographic distance and with pairwise landscape divergence at the three studied buffers: B300 – buffer 300 meters; B1000 – buffer 1000 meters, and B2500 – buffer 2500 meters. Correlations were estimated using Mantel tests.

	A. planirostris (17 landscapes)	*C. perspicillata* (11 landscapes)
$F_{ST\text{-}assemblages}$ vs $F_{ST\text{-}G}$	r = -0.004; p = 0.430	r = 0.295; p = 0.094
$F_{ST\text{-}assemblages}$ vs $F_{ST\text{-}mtDNA}$	r = -0.191; p = 0.838	r = 0.340; p = 0.068
β_{RC} vs $F_{ST\text{-}G}$	r = -0.187; p = 0.904	r = 0.144; p = 0.191
β_{RC} vs $F_{ST\text{-}mtDNA}$	r = 0.048; p = 0.408	r = -0.079; p = 0.651
$F_{ST\text{-}assemblages}$ vs geographic distance	r = 0.012; p = 0.425	r = 0.145; p = 0.202
$F_{ST\text{-}assemblages}$ vs B300	r = -0.124; p = 0.727	r = -0.135; p = 0.622
$F_{ST\text{-}assemblages}$ vs B1000	r = 0.227; p = 0.050	r = 0.337; p = 0.023
$F_{ST\text{-}assemblages}$ vs B2500	r = 0.449; p = 0.001	r = 0.445; p = 0.007
β_{RC} vs geographic distance	r = 0.115; p = 0.158	r = 0.074; p = 0.310
β_{RC} vs B300	r = -0.152; p = 0.809	r = -0.020; p = 0.551
β_{RC} vs B1000	r = 0.093; p = 0.211	r = 0.364; p = 0.010
β_{RC} vs B2500	r = 0.042; p = 0.344	r = 0.344; p = 0.012
$F_{ST\text{-}G}$ vs geographic distance	r = -0.136; p = 0.852	r = 0.549; p = 0.001
$F_{ST\text{-}G}$ vs B300	r = 0.033; p = 0.298	r = 0.175; p = 0.267
$F_{ST\text{-}G}$ vs B1000	r = 0.257; p = 0.984	r = 0.291; p = 0.039
$F_{ST\text{-}G}$ vs B2500	r = -0.191; p = 0.929	r = 0.304; p = 0.022
$F_{ST\text{-}mtDNA}$ vs geographic distance	r = 0.102; p = 0.239	r = -0.168; p = 0.804
$F_{ST\text{-}mtDNA}$ vs B300	r = -0.018; p = 0.507	r = 0.009; p = 0.472
$F_{ST\text{-}mtDNA}$ vs B1000	r = 0.029; p = 0.452	r = 0.030; p = 0.408
$F_{ST\text{-}mtDNA}$ vs B2500	r = -0.153; p = 0.839	r = -0.034; p = 0.561

Table 5.6 – *Carollia perspicillata*: partial correlations between species and genetic diversity and between community and genetic divergence for those with significant or marginally non-significant raw correlation controlling for the distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG) in each of the three buffer sizes.

Buffer 300	Raw correlation	DIST	FORE	BORD	FRAG
Sr x H (Spearman correlation)	r = 0.557; p = 0.075	r = 0.533; p = 0.113	r = 0.557; p = 0.094	r = 0.554; p = 0.096	r = 0.365; p = 0.299
Eve x H_E (Pearson correlation)	r = 0.593; p = 0.054	r = 0.375; p = 0.285	r = 0.587; p = 0.075	r = 0.589; p = 0.073	r = 0.623; p = 0.054
Buffer 1000					
Sr x H (Spearman correlation)	r = 0.557; p = 0.075	r = 0.533; p = 0.113	r = 0.522; p = 0.121	r = 0.589; p = 0.073	r = 0.390; p = 0.265
Eve x H_E (Pearson correlation)	r = 0.593; p = 0.054	r = 0.375; p = 0.285	r = 0.601; p = 0.066	r = 0.690; p = 0.027	r = 0.736; p = 0.015
Buffer 2500					
Sr x H (Spearman correlation)	r = 0.557; p = 0.075	r = 0.533; p = 0.113	r = 0.570; p = 0.09	r = 0.544; p = 0.104	
Eve x H_E (Pearson correlation)	r = 0.593; p = 0.054	r = 0.375; p = 0.285	r = 0.584; p = 0.076	r = 0.677; p = 0.031	

5.5 Discussion

Our results show that evenness is mediated by the distance to the national park, with more diverse assemblages near the national park. Still, contrary to our predictions, we fail to detect more species in areas bordering the national park. Also, we did not find a significant relation between species richness and the predictor variables used in this study.

The allelic richness of *C. perspicillata* is negatively affected by forest area and by the distance to the nearest border of the national park at the intermediate scale and expected heterozygosity is negatively affected by forest area at intermediate and high scales and at all scales by the distance to the nearest border of the national park. On the other hand, it was not found any relationship between the genetic diversity of *A. planirostris* and the studied landscape variables. The different responses of these species to landscape variables may result from the manner as they perceive the environment. *Artibeus planirostris* has generalist feeding habits. This species is considered a canopy frugivore that feeds on *Ficus* spp., usually a patchily distributed resource with asynchronized fruiting periods (Milton et al., 1982). However, *A. planirostris* also occurs in open vegetation with scattered trees (Silveira et al., 2018) and, beyond *Ficus* spp, this species commonly feeds on *Cecropia pachystachya* and less frequently on pollen, nectar and insects (Munin et al., 2012; Teixeira et al., 2009). Probably because of its diet, *A. planirostris* tends to present wide home-ranges, feeding in large areas or performing migrations due to seasonal shifts in the availability of its preferred fruits. For these reasons the species probably only perceives habitat loss and fragmentation at large scales (Silveira et al., 2018) as occur with its close congener *A. lituratus* (McCulloch et al., 2013). Thus, *A. planirostris* is a vagile species with high plasticity in feeding habits and habitat use, characteristics that may confer to its populations high resilience to changing landscapes. Contrary to our predictions we detect a negative relation between forest cover and the genetic diversity of *C. perspicillata*, which may also be explained by its feeding behaviour. *Carollia perspicillata* is a *Piper* specialist; *Piper* plants tend to present higher densities in early- and mid-successional forests, in forest borders and in gaps between forests used as small agricultural areas (Fleming, 1988; Marinho-Filho, 1991; Klingbeil and Willig, 2009), so gene flow between populations of *C. perspicillata* may be facilitated by the presence of these hiatuses in forest continuity, justifying the negative relation between genetic diversity and forest cover.

Most correlations between species diversity and genetic diversity are negative for *A. planirostris* and significant only when comparing evenness with expected heterozygosity and mean presence-absence-based assemblage divergence with mean genetic divergence (based on mtDNA). This negative correlation between species and genetic diversity indicates that these two levels of diversity respond in opposite ways to the same variables or are driven by different factors (Vellend and Geber, 2005; Lamy et al., 2017). In fact, our regression models show that

while evenness is affected by the distance to the national park, none of the predictor variables is related with the genetic diversity in this species. The opposite pattern was observed for *C. perspicillata*. For this species, almost all correlations revealed to be positive and only marginally non-significant when comparing species richness with haplotype richness and evenness with expected heterozygosity. This seems to indicate that parallel processes affect both phyllostomid assemblages and populations of *C. perspicillata* (Vellend and Geber, 2005), reinforcing the thesis that landscape variables affect species and genetic diversities in the same direction. In fact, the extent and direction to which species and genetic diversity are correlated depend on the 'ecological similarity' between the focal species under study and the species present in the assemblage (Lamy et al., 2017). Thus, if the focal species is ecologically dissimilar from the other species in the assemblage, no pattern or a negative pattern of SGDC emerges, as occurred for *A. planirostris* in our study. The higher dispersal ability and the greater plasticity in feeding habits and habitat use may differentiate *A. planirostris* from most species in the studied bat assemblages. On the other hand, when the focal species and the other species in the assemblage are ecologically similar, they show a positive SGDS (Lamy et al., 2017). Thus, we can conclude that bat assemblages in the Serra da Bodoquena region tend to be more similar to *C. perspicillata* rather than to *A. planirostris*. In fact, bat assemblages in this region are composed mainly by small phyllostomids, which should have a dispersal ability similar to *C. perspicillata*.

Studies on SGDC in bats are scarce. Based on species and genetic data of Ricklefs and Lovette (1999) and Carstens et al. (2004), respectively, Kahilainen et al. (2014) computed the SGDC on *Artibeus jamaicensis* and *Brachyphylla cavernarum* from the northern Lesser Antilles and found non-significant values for correlation between species and genetic diversities. Struebig et al. (2011) evaluated the effect of fragmentation of the Malaysian rainforest on co-distributed bat species that have dissimilar life-history traits. These authors showed that the species with more limited dispersion capacity, *Kerivoula papillosa*, had a nearly significant positive SGDC and that the forest area affected that relation. On the other hand, the least dispersal-limited bat, *Rhinolophus lepidus*, showed non-significant SGDC. Authors attributed this difference to the dispersal ability of the two species. *Rhinolophus lepidus* is able to move over longer distances and can easily transpose barriers imposed by fragmentation, while *K. papillosa*, perceives the landscape at smaller scales. Due to different SGDC patterns on these species, authors suggested that *K. papillosa* is ecologically similar to remaining species in its assemblages while *R. lepidus* is considered an outlier and more resilient species.

Our Mantel tests show a positive correlation between assemblage divergence and pairwise differences in landscape characteristics at intermediate and large buffers, meaning that similar assemblages are found in landscapes with similar characteristics at these scales. Mantel tests do not report correlations between the assemblage and the genetic divergence for *A.*

planirostris; its genetic divergence is not affected by pairwise differences in landscape characteristics, again suggesting that *A. planirostris* is less sensitive to landscape characteristics and responds at largest scales than most of the local phyllostomid species. On the other hand, assemblage divergence and genetic divergence in *C. perspicillata*, while marginally, are positively correlated. Additionally, genetic pairwise differences are positively related with landscape differences at the intermediate and large scales, and with geographic distance, indicating an isolation by distance pattern in this species, and that most regional phyllostomids likely shows a similar pattern. Dispersal ability influences patterns of genetic diversity by increasing or decreasing gene flow between populations (Frankham et al., 2002). *Carollia perspicillata* presents limited dispersal, so we may expect gene flow between populations to be restricted to closely located sites, producing the observed pattern of genetic isolation. In fact, a pattern of isolation by distance was already reported for this species in a small-scale fragmented system with high degree of fragment-matrix contrast (Meyer et al., 2009).

From a conservation viewpoint, it is important to increase the number of studies evaluating SGDC to draw general patterns. In some situations, it is difficult to sample species richness so, studying the genetic diversity of more abundant species may give a reasonable enough insight to define measures as to protect both dimensions of diversity (Kahilainen et al., 2014). Thus, if positive SGDC is expected, conservation actions focusing on one species will act to conserve not only the intrapopulation genetic diversity of that focal species but the overall diversity in that assemblage. However, if a negative SGDC is expected, conserving the genetic diversity of such a single species can have the opposite effect (Kahilainen et al., 2014). Thus, our results indicate that monitoring *C. perspicillata* is better than *A. planirostris* as a focal species for conservation plans in the Serra da Bodoquena region, because it represents an umbrella for protecting most of the regional phyllostomid fauna. Many studies on SGDC focus only one species (e.g. Vellend, 2004; Odat et al., 2010; Blum et al., 2012; Wei and Jiang, 2012). However, a multispecies approach is recognized as more informative because it provides a more general view of the processes that act both on populations and assemblages (Papadopoulou et al., 2011; Struebig et al., 2011; Robinson et al., 2010). In our study, we used two bat species with contrasting life-history traits, which provides different results and highlights the need to include more than one species in studies on SGDC.

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CHAPTER 6

GENERAL DISCUSSION

General discussion

Landscape changes leading to habitat loss and fragmentation are key research topics in conservation biology because they are recognized as the primary cause for biodiversity decline (Haila, 2002; Lindenmayer and Fischer, 2006). However, understanding the effect of these changes on the biota is still not totally understood as the potential consequences depend on species traits, as well as on the magnitude of those changes, and on the characteristics of the remaining habitat (Ewers and Didham, 2006). Moreover, outcomes of these processes are not strictly demographic, altering not only species' composition and abundance, but also affecting the genetic structure of populations in longer temporal scales.

The central objective of this thesis was to understand the effects of landscape changes, through habitat loss and fragmentation, on multiple dimensions of biodiversity, using bats as model taxa. Initially, we did a meta-analysis of the effects of habitat loss and fragmentation on genetic diversity in mammals (chapter 3). In the following chapters (chapters 4 e 5), we address the effects of landscape characteristics on taxonomic, functional and phylogenetic diversity, on species turnover and on genetic diversity. Additionally, in chapter 5 we tested species-genetic diversity correlation (SGDC) in two co-distributed species. The studied landscapes are characterized by a forest cover gradient which varies from well-preserved areas to more degraded and fragmented landscapes.

6.1 Species traits matter! Effect of habitat loss and fragmentation on mammals

Habitat loss and fragmentation are responsible in decreasing population sizes and in splitting populations into subpopulations, responses that may be correlated depending on species' and landscape characteristics. Such landscape changes lead to a decrease in forest remnants and to an increase in isolation between patches, altering the magnitude and spatial patterns of microevolutionary forces. Changes in genetic diversity within and among populations have implications for population persistence at the short- and long-term. Several studies on the effect of habitat loss and fragmentation have emerged in the last decades and, while the majority followed the predictions and reported that habitat loss and fragmentation reduce genetic diversity of fragmented populations (e.g. Struebig et al., 2011), others were unable to detect significant changes due to fragmentation (Mossman and Waser, 2001). This can occur because species have demographic and life-history traits which confer them distinct resilience levels in fragmented landscapes. Thus, the effect of habitat loss and fragmentation

depends on how the species perceive the altered habitat; if the altered habitat is considered suitable, species will use altered areas to roost or for food supplementation and, thus, mitigate the negative effects of habitat loss and fragmentation. In such cases, populations are able to maintain reasonably healthy levels of gene flow, and genetic diversity does not drop significantly. But, if species perceive the altered habitat as unsuitable, they will be confined to their remnants and gene flow is reduced, making those populations more susceptible to significant genetic drift than populations occurring in continuous habitats.

In our paper *A meta-analysis of the effects of habitat loss and fragmentation on genetic diversity in mammals* (Lino et al., 2018; chapter 3) we aimed to detect general patterns of loss of genetic diversity on mammals under habitat loss and fragmentation impacts and explored species traits that could be related with each species response. We found a clear pattern of loss of genetic diversity in mammalian species due to habitat loss and fragmentation in the four genetic parameters evaluated – allelic richness, allelic diversity and observed and expected heterozygosity. Although species' responses are an outcome of complex interactions according to species traits, we showed that genetic susceptibility of species to habitat loss and fragmentation increases with body mass. In fact, body mass and body size, two strictly related measures, are commonly used as predictors of species sensitivity to fragmentation (Henle et al., 2004; Meyer et al., 2008; Newmark et al., 2014). Even so, some studies were unable to detect a clear relationship between body size and fragmentation sensitivity (Vetter et al., 2011), possibly because body size is closely related to other ecological attributes such as dispersal ability, habitat requirements and dietary specialization (Swihart et al., 2003; Henle et al., 2004); this may sometimes hamper for a clear pattern to emerge. Large-bodied species are in average more vagile, are able to transpose larger distances (Swihart et al., 2003), and are expected to respond at broader geographical scales (Gehring and Swihart, 2003), as they tend to present larger home-ranges and lower population densities (Thornton and Fletcher, 2014); still, they usually need larger areas with abundant resources to survive (Biedermann, 2003). So, resource limitation due to fragmentation may not support viable populations of large-bodied mammals and densities of such species will, thus, tend to be lower in fragmented habitats, potentially increasing their sensitivity to the negative effects of fragmentation (Purvis et al., 2000; Crooks, 2002). A big challenge for animals in fragmented landscapes is crossing a potentially unfavourable habitat matrix. So, locomotion mode – terrestrial, arboreal or aerial –, also influences the response to fragmentation. Our results indicate that both terrestrial and arboreal mammals show higher losses of genetic diversity, suggesting that they are more dependent on the quality of the matrix to maintain persistent gene flow. Although not as strongly, even flying mammals (bats) are negatively affected by fragmentation, indicating that several species are reluctant to transpose gaps between fragments and, thus, risking the maintenance of gene flow. Habitat loss and fragmentation create unfavourable matrices with lower availability of foraging and roosting

resources than fragments or continuous habitats. So, the resilience of species to such changes depends on their ability to use the remaining resources. Forest-dependent species, as the designation suggests, are unable to survive outside forest environments. So, they suffer the strongest negative effects due to forest loss and fragmentation. As these species are unable to use and, often, even to cross the unfavourable matrix, they will be restricted to small remnant patches, leading to significant decrease in their genetic diversity through time due to low gene flow between subpopulations.

Knowledge and synthesis provided by meta-analyses are important to support researchers, resource managers, and policy-makers because, the identification of general patterns and trends, is a crucial guide for decision-making (Joricheva et al., 2013). Thus, our results may subsidize the understanding of how habitat loss and fragmentation govern patterns of loss of genetic diversity on mammals and on which species traits promote higher vulnerability to those changes, contributing with relevant information towards landscape planning and biodiversity conservation and management.

6.2 Factors affecting species and genetic diversity on neotropical bats

Brazil is the second richest country in bat species but information on species distribution is still focused on a small portion of the territory (Bernard et al., 2011). The state of Mato Grosso do Sul was identified as understudied in respect to bat species occurrence (Bernard et al., 2011), but several studies have been done in recent years to revert this condition (reviewed in Fischer et al., 2015; this thesis).

Some studies have shown that human-induced changes such as the decrease of remaining forest area negatively affect species persistence in landscapes (Gorresen and Willig, 2004; Meyer and Kalko, 2008; Struebig et al., 2008). In chapter 4, *Bat diversity in a gradient of forest loss and fragmentation* (Lino et al. *in prep*.), we did not find a relation between species richness and the study variables – distance to the nearest border of the Serra da Bodoquena National Park, forest cover, forest border and number of forest fragments – indicating that landscape characteristics do not seem to affect the number of species present. Such result may be a reflex of the progressive change of some species by others, i.e. species turnover, across the vegetation gradient present in the study region, the Serra da Bodoquena. The partitioning of total beta diversity computed with incidence data, showed that species turnover – more than species nestedness – shapes bat assemblages in the Serra da Bodoquena. This means that even if species considered less tolerant to human changes are lost in more deforested habitats, they are replaced by others with more generalist habits that are able to persist in degraded environments (Beca et al., 2017). Beyond species richness, studies evaluating the effect of habitat loss and

fragmentation have focused on species diversity (e.g. Klingbeil and Willig 2010). However, both metrics (species richness and species diversity) do not take into account species' ecological and phylogenetic relationships, which are important characteristics affecting the way in which species respond to landscape characteristics. Thus, lately, a more integrative approach is being followed, using not only taxonomic diversity but also functional and phylogenetic diversities, to understand the effect of anthropogenic landscape changes in different dimensions of biodiversity (Flynn et al., 2009; Cisneros et al., 2015; Ramos Pereira et al., 2018). Contrary to other studies (e.g. Cisneros et al., 2015), taxonomic, functional and phylogenetic bat diversity in Serra da Bodoquena region are affected by the same variables at the same scales. With the increase of forest borders in landscapes, the three levels of diversity decrease. In fact, several studies showed that neotropical bats respond to forest borders but its effect is ensemble- and species-specific (Faria, 2006; Meyer and Kalko, 2008) and varies according to functional traits (Cisneros et al., 2015). At the large studied scale, borders and forest area seem to act on the three diversities in opposite ways, i.e. while forest borders decrease diversity, an increase in forest area also negatively affect them. These results seem to be somewhat contradictory; however, this could occur because bat assemblages in Serra da Bodoquena are largely composed by generalist species with foraging plasticity. Additionally, species living in this region seem to be able to use the matrix between fragments and partially benefit from these human-dominated areas. This can occur because humanized matrices have higher compositional diversities providing new or alternative resources for bats to exploit. In fact, this pattern of higher diversity in moderately fragmented landscapes was already reported elsewhere (Gorresen and Willig, 2004; Klingbeil and Willig, 2009). Beyond bat diversities, genetic diversity measured by allelic richness and expected heterozygosity of the understory frugivores *C. perspicillata*, was also negatively affected by forest area, reinforcing the idea that at least some bat species do not perceive the altered habitat as completely unsuitable. A different pattern was observed when populations of *C. perspicillata* are separated by a matrix composed of water, even if evaluated on a smaller scale than those of our study. In Panama, the genetic diversity of *C. perspicillata* was negatively affected by the construction of a large artificial reservoir. Here, populations of *C. perspicillata* that inhabit islands show significantly lower levels of genetic diversity – measured by haplotype diversity – than those inhabiting mainland areas (Meyer et al., 2009). These results can indicate that the type and quality of the matrix mediate the dispersion of individuals and consequently the gene flow and levels of genetic diversity of populations. Additionally, least limited-dispersal species, such as *A. planirostris*, should perceive the landscape at larger scales than those studied here because neither the allelic richness nor the expected heterozygosity was related with the landscape variables at any of the studied scales. In fact, severe forest fragmentation in Atlantic Forest areas did not cause genetic subdivision of *Artibeus lituratus* (McCulloch et al., 2013), a closest congener of *A. planirostris*. So, as both

species share similar life-history traits, i.e. broad distribution, potential high mobility, and plastic foraging strategy, a similar pattern for *A. planirostris* in Serra da Bodoquena was to be expected. These contrasting results reinforce the idea that life-history traits are of prime importance to define the way in which species respond to landscape changes as reported in chapter 3 of this thesis and elsewhere (e.g. Farneda et al., 2015).

6.3 Species-genetic diversity correlations and its conservation implications

Species diversity and neutral genetic diversity are shaped by parallel processes and correlated patterns (Vellend, 2005). So, through one level of diversity we should be able to predict patterns in another. However, this is not straightforward and largely depends on the 'ecological similarity' between the studied species and the remaining species in that specific assemblage (Lamy et al., 2017). In chapter 5, *Species–genetic diversity correlation for phyllostomid bats from Bodoquena plateau* (Lino et al., *in prep.*), we found that species-genetic diversity correlations (SGDC) in *A. planirostris* and *C. perspicillata* populations of Serra da Bodoquena have opposite directions: while SGDC's in *A. planirostris* were mostly negative, SGDC's in *C. perspicillata* were mostly positive. These results suggest that processes shaping these assemblages are not the same shaping genetic diversity in *A. planirostris* or that the same processes shape each diversity in opposite ways. This negative relation could also indicate that *A. planirostris* is not ecologically similar to the rest of the community (Lamy et al., 2017) and, for this reason, responds to landscape processes differently. Contrariwise, the results concerning *C. perspicillata* indicate that this species is more similar to remaining species in the assemblages, suggesting that species diversity and the genetic diversity in this species are shaped by the same processes and in the same direction (Lamy et al., 2017). These contrasting results are possibly attributed to different dispersal abilities of the two species, i.e. *A. planirostris* should present higher dispersal ability than most of the remaining species in the studied assemblages, and so should be less sensitive to landscape changes. On the other hand, *C. perspicillata* should have similar dispersal ability to the majority of the species in the studied assemblages, so the population genetic diversity in *C. perspicillata* and the assemblage diversity should respond similarly to the same landscape variables. In fact, the difference in dispersal abilities between both studied species is reinforced by the pattern of the isolation by distance found in *C. perspicillata*.

Both positive and negative SGDC have been observed in natural systems (Sei et al., 2009; Odat et al., 2010; Papadopoulou et al., 2011; Struebig et al., 2011; Wei and Jiang, 2012; Kahilainen et al., 2014; Vellend et al., 2014). However, positive SGDC are considered the most

common (Vellend, 2003; Vellend and Geber, 2005), especially in studies done in discrete sampling units as islands and forest fragments (Vellend et al., 2014). As we found in this study, species with different life-history traits can vary on SGDC depending on how much they are ecologically similar from the other species in their communities. Such results have several conservation implications (Kahilainen et al., 2014): as *C. perspicillata* is ecologically similar to the rest of community, conservation measures that intend to preserve species diversity of communities will also preserve intrapopulation genetic diversity.

Understanding SGDC patterns is extremely important because often it is not possible to adequately sample a large area to evaluate assemblage diversity or to study genetic diversities across populations of several species. In such cases, one level of diversity can be used as a surrogate of the other level (Kahilainen et al., 2014) to subsidize, with caution, management decisions.

6.4 Study limitations and future research

Our study revealed important aspects of how bat species assemblages change according to landscape characteristics and how species and genetic diversity covary in our study region. However, we are aware of some weaknesses that could be improved in future studies. The field work done during this thesis was done under a broader program – the 'Long-Term Ecological Research Program' (http://www.cnpq.br/sitios-peld) – that aims to evaluate and understand the biological dynamics along a landscape gradient and during an extended time scale. However, as this program is just beginning, we could only include two sampling years. So, we do not have a very robust sampling to evaluate the effect of landscape changes by season and, as demonstrated by some studies (e.g. Klingbeil and Willig, 2010, Ramos Pereira et al., 2010, Cisneros et al., 2015), seasonality is an important factor in responses of bats to landscape attributes. Additionally, different species tend to respond differently to landscape changes (e.g. Klingbeil and Willig, 2010). So, we believe it would have been important to understand bat responses to the studied landscape characteristics at the species level. Although this study gave a broad view on how several diversity dimensions change across a landscape gradient, several other questions remain unanswered. For example, other landscape variables should be evaluated to understand if similar or distinct patterns arise. Compositional and configurational landscape characteristics that we were unable to include in this work, such as diversity of cover types, area of pastures and distance between patches in each buffer, have been pointed out as important variables for patterns of bat diversity (Gorresen et al., 2005, Cisneros et al., 2015) and could aid in a better understanding of how bat assemblages respond to landscape changes. Finally, as bat species vary in their habitat preferences, subsequent samplings to be done in Serra da Bodoquena

should include other physiognomies in order to capture the entire landscape heterogeneity present in this region.

6.5 Conclusions

This thesis provided valuable information on how genetic diversity of mammalian species changes due to human induced alterations. We detected an overall loss of genetic diversity in species that live in fragmented habitats but the susceptibility to these threats varies according to species traits. Body mass, locomotion mode, trophic guild and habitat preferences are those characteristics mostly influencing species responses to landscape changes.

Our results also provided evidence that bat diversity responds to landscape characteristics at different scales. The distance to the largest continuous and preserved area was important at all studied scales; forest borders were important at the intermediate and large scales; forest area was only important at the large scale. Also, species turnover, more than species nestedness, governs the changes in bat assemblages in Serra da Bodoquena, which could explain the absence of a relation between species richness and the studied landscape variables.

Finally, we also detected significant correlations between species and genetic diversities in two focal species, although with opposite trends. Species with distinct life-histories may show different SGDC depending on how much they are ecologically similar to the other species in their assemblages. Our results suggest that *C. perspicillata* is ecologically similar to the majority of species present in the Serra da Bodoquena assemblages, and so, measures towards its conservation should, in thesis, also preserve the whole of bat diversity in this area.

6.6 References

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Chapter 7

Supplementary Material

Supplementary material

7.1 Figures

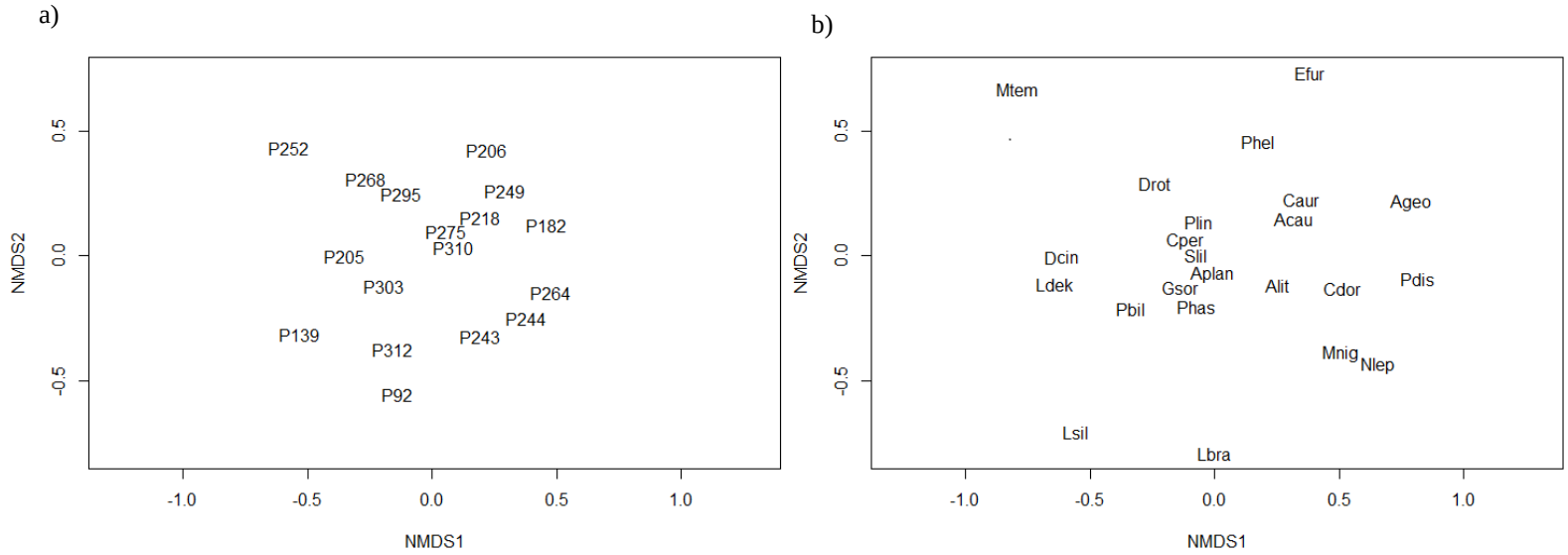

Fig. S4.1 – Ordination of a) the 17 study sites and b) the 23 species along non-metric multidimensional scaling axes for the bats captured in Serra da Bodoquena region (NMDS stress = 0.19). Legend: Aplan - *Artibeus planirostris*; Slil - *Sturnira lilium*; Plin - *Platyrrhinus lineatus*; Alit - *Artibeus lituratus*; Phel - *Platyrrhinus helleri*; Cdor - *Chiroderma doriae*; Dcin - *Dermanura cinerea*; Pbil - *Pygoderma bilabiatum*; Cper - *Carollia perspicillata*; Gsor - *Glossophaga soricina*; Acau - *Anoura caudifer*; Ldek - *Lonchophylla dekeyseri*; Ageo - *Anoura geoffroyi*; Drot - *Desmodus rotundus*; Lsil - *Lophostoma silvicolum*; Caur - *Chrotopterus auritus*; Phas - *Phyllostomus hastatus*; Pdis - *Phyllostomus discolor*; Lbra - *Lophostoma brasiliense*; Mnig - *Myotis nigricans*; Efur - *Eptesicus furinalis*; Mtem - *Molossops temminckii* and Nlep - *Noctilio leporinus*.

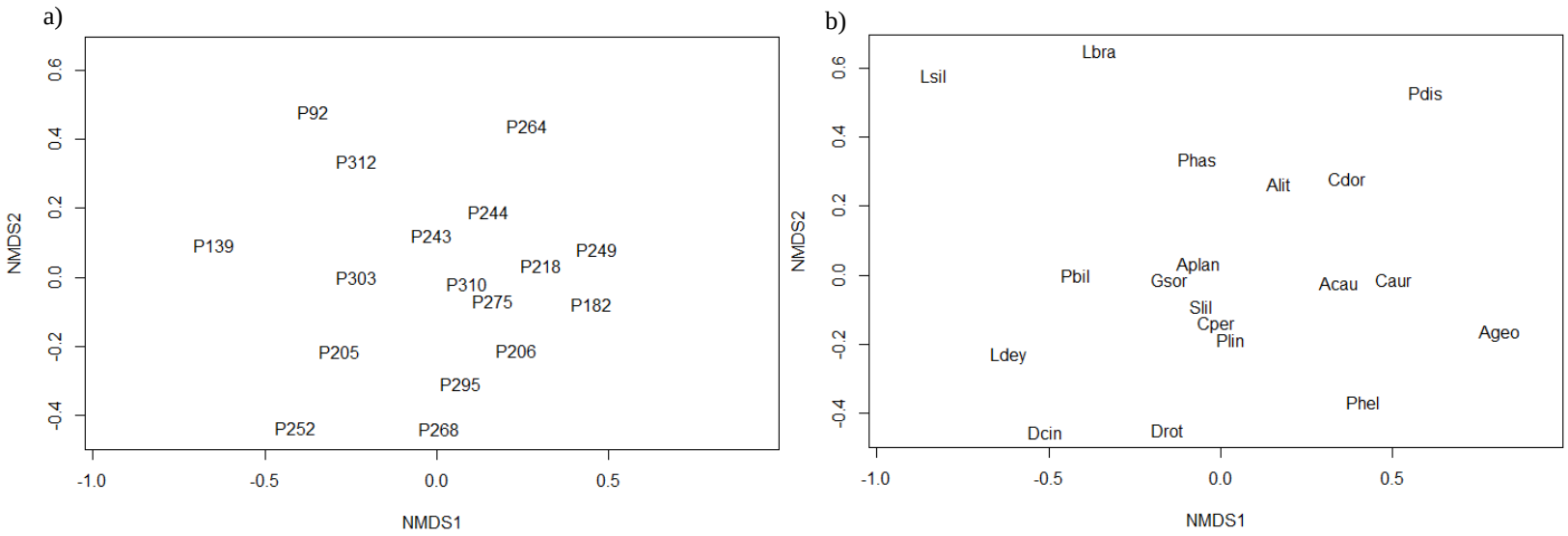

Fig. S4.2 – Ordination of a) the 17 study sites and b) the 19 phyllostomid species along non-metric multidimensional scaling axes for the bats captured in Serra da Bodoquena region (NMDS stress = 0.18). Legend: Aplan - *Artibeus planirostris*; Slil - *Sturnira lilium*; Plin - *Platyrrhinus lineatus*; Alit - *Artibeus lituratus*; Phel - *Platyrrhinus helleri*; Cdor - *Chiroderma doriae*; Dcin - *Dermanura cinerea*; Pbil - *Pygoderma bilabiatum*; Cper - *Carollia perspicillata*; Gsor - *Glossophaga soricina*; Acau - *Anoura caudifer*; Ldek - *Lonchophylla dekeyseri*; Ageo - *Anoura geoffroyi*; Drot - *Desmodus rotundus*; Lsil - *Lophostoma silvicolum*; Caur - *Chrotopterus auritus*; Phas - *Phyllostomus hastatus*; Pdis - *Phyllostomus discolor* and Lbra - *Lophostoma brasiliense*.

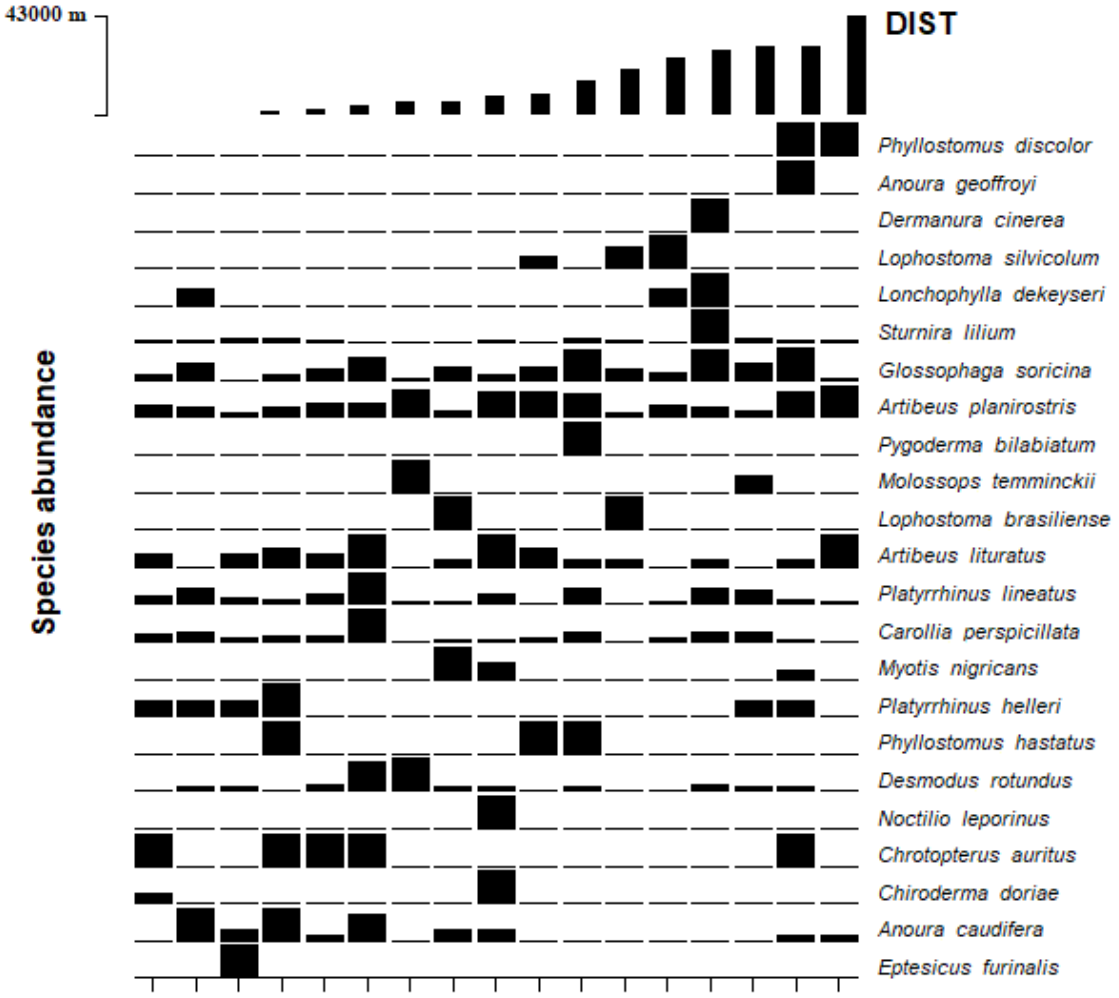

Fig. S4.3 – Species abundance of all bat species present in Serra da Bodoquena according to the distance to nearest border of Serra da Bodoquena National Park (DIST).

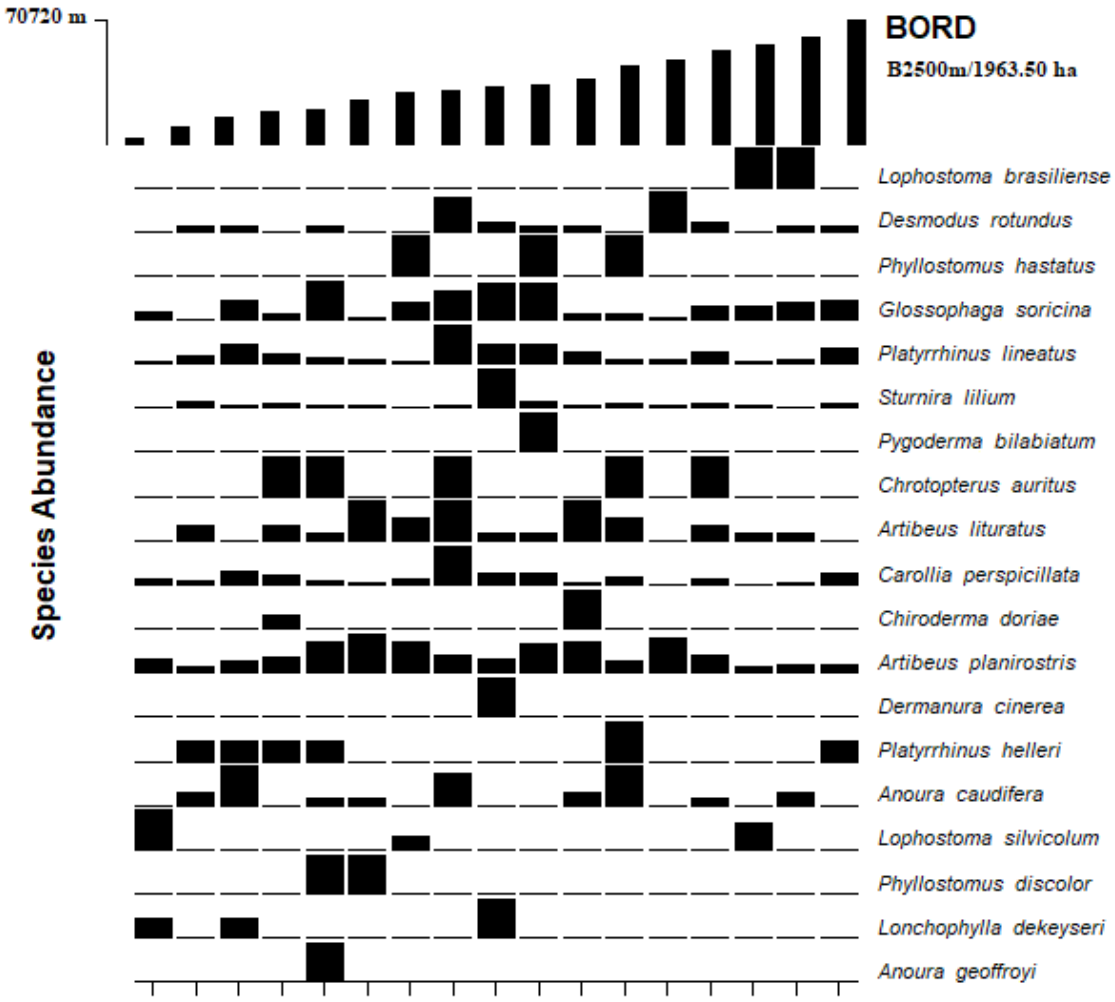

Figure S4.4 – Species abundance of phyllostomid bat species present in Serra da Bodoquena according to the forest border length (BORD).

7.2 Tables

Table S3.1 – Studies included in the meta-analysis and description of habitats used as control and fragments, area of each treatment, number of sampled individuals, and the molecular marker used. Unavailable information is indicated as NA.

Species	Characterization of habitats and sampling design	Area (ha)		Sampled individuals (N)		Molecular marker	Authors
		Controls	Fragments	Controls	Fragments		
Alouatta caraya	Samples were taken in four continuous forests and in six modified habitats corresponding to control and fragmented areas, respectively.	NA	NA	56	82	Microsatellites	Oklander et al., 2017
Alouatta palliata	Sampling was conducted in one continuous habitat in a Biosphere Reserve and in 3 small fragments surrounded mainly by pastures.	640	4-93	25	25	Microsatellites	Jasso-del Toro et al., 2016
Alouatta pigra	Sampling was conducted in one continuous habitat in a Biosphere Reserve and in four small fragments surrounded mainly by pastures.	331 200	1-1700	17	30	Microsatellites	García et al., 2005
Antechinus flavipes	Samples were collected in six regions that differ in remnant forested area. As controls, it was considered three regions with a high proportion of forested area. The other three regions have lower forested areas, so they were considered as fragmented.	43 720-68 720	2610-9020	482	235	Microsatellites	Lada et al., 2008
Carollia perspicillata	Sampling was conducted in 3 sites of Barro Colorado Nature Monument. As fragmented habitats, it was sampled 11 artificial islands formed by the construction of a large artificial reservoir but *C. perspicillata* was caught only in 8 of them and authors only provided genetic data for populations with more than five individuals, i.e. for five islands.	5400	7.2-50	39	38	mtDNA	Meyer et al., 2009
Cricetus cricetus	As controls, it was considered samples from zoological collections that represent the genetic diversity before fragmentation. Samples representing the current populations were from five fragments.	NA	NA	33	52	Microsatellites	La Haye et al., 2012
Eulemur collaris	Two sampling sites were in large continuous forest of a protected area and in three forest fragments separated by degraded littoral forest, grasslands, eucalyptus plantations and small rivers.	60 000	220-290	13	36	Microsatellites	Bertoncini et al., 2017
Glis glis	Authors sampled individuals in two sites of a continuous forest in a Nature Reserve and in 4 fragments surrounded by agriculture field and meadows, tarmac roads and rail trails, that are located near cities and villages.	15 000	11-135	201	179	Microsatellites	Fietz et al., 2014
Kerivoula papillosa	Samples were taken in five sites in a continuous forest of a natural reserve and in 27 forest fragments, however individuals of only 11 fragments were genotyped.	137 000	102-11 339	223	99	Microsatellites	Struebig et al., 2011
Marmosops incanus	Authors studied three landscapes of 10 000 ha. The first was considered the continuous habitat with 86% of native vegetation and individuals were sampled in 12 sites. The other two landscapes only retain 49 and 31% of native vegetation and individuals were sampled in 14 and in 11 fragments, respectively.	8600	3.5-197.6	140	389	Microsatellites	Balkenhol et al., 2013
Melomys cervinipes	Two grids were used to sample individuals in a continuous rainforest. Three forest fragments surrounded by agricultural land and one island created by a dam were used as fragmented habitats.	290 000	2.5-97.5	12	65	Allozyme	Leung et al., 1993
Melomys cervinipes	Sampling was conducted in four sites within two national parks and in seven fragments, respectively representing the control and fragmented areas.	2039-106 975	2.53-17.48	81	143	Microsatellites	Geurts, 2013
Mico argentatus	Samples were taken in a large forest representing the original forest cover, which was considered the control, and in three smaller fragments of different sizes.	NA	30-4500	2	23	Microsatellites	Gonçalves et al., 2003
Microcebus bongolavensis	Sampling was conducted in a large forest representing the continuous habitat and in two isolated forest fragments surrounded by savannas.	9900	20-1110	27	18	Microsatellites	Olivieri et al., 2008

Microcebus ravelobensis	Sampling was performed in a large forested area and in two sites inside a national park, which were considered the control areas. The fragmented areas were six isolated forest fragments surrounded by savannas.	9900 - 104 000	20 – 3680	48	66	mtDNA	Guschanski et al., 2007
Microcebus ravelobensis	Sampling was performed in four sites inside a national park that were considered the control areas, in addition four forest fragments surrounded by savannas were considered fragmented areas.	104 000	400-3640	77	126	Microsatellites	Olivieri et al., 2008
Muscardinus avellanarius	Sampling was conducted in two distinct landscapes. One corresponding to a large and continuous forest, representing the control area. The second landscape used as fragmented area presented woodland fragments surrounded by croplands and urban areas to a lesser extent.	2700	4-250	126	87	Microsatellites	Bani et al., 2017
Myodes californicus	Sampling was conducted in two unfragmented forests representative of control areas and in two small fragments.	>1000	3-3.7	70	69	Microsatellites	Tallmon et al., 2002
Myotis macropus	Controls considered samples collected in three large forest while fragmented habitats were two riparian vegetation remnants.	2250-27 300	NA	98	75	Microsatellites	Campbell et al., 2009
Nyctophilus geoffroyi	Sampling was performed in five sites of an 80 km transect of continuous forest and in two extensive forest sites defined as the control areas. Seven sites with small and isolated forests embedded in an agricultural and pine plantation matrix were used as fragmented areas.	NA	60-2800	222	280	Microsatellites	Fuller, 2013
Nyctophilus gouldi	Sampling was performed in four sites of an 80 km transect of continuous forest and in two sites of unfragmented forests defined as the control areas. Additionally, samples from three small and isolated forest fragments were used as fragmented areas.	NA	396-2800	127	129	Microsatellites	Fuller, 2013
Panthera onca	Samples representing the control were collected at the largest remnant of Upper Paraná Atlantic Forest, and those representing the fragmented habitats were collected in three forest fragments.	1100000	~10 000 - ~73 000	18	41	Microsatellites	Haag et al., 2010
Peromyscus leucopus	Sampling was conducted in 17 sites within eight continuous forests considered controls and in 10 woodlots isolated by roads, pastures and/or corn or soybean fields, smaller forests.	90-25 300	1-14.75	194	147	Microsatellites	Mossman and Waser, 2001
Peromyscus melanophrys	Samples were taken from 10 sites that differ in vegetation quantity and quality. Three sites have a dense, continuous and heterogeneous Tropical Dry Forest and were used as control areas. Low vegetation cover and a high proportion of agricultural fields, grasslands and livestock activity characterize three other sites, so they were treated as fragmented areas. Four sites with no information on the percentage of vegetation were not included.	NA	NA	47	62	SNP	Vega et al., 2017
Petauroides volans	Controls were considered samples from three sites of continuous forests and samples from museum collections that were collected at the time of initial clearing of the native forest. Sampling representing fragmented habitat were taken in 11 patches.	NA	1.6-124	65	80	Microsatellites	Taylor et al., 2007
Petaurus breviceps	Sampling was conducted in two sites of a large continuous forest and 12 remnant patches of native forest surrounded by clearing agricultural land or pine plantation.	5200	43-2216	14	236	Microsatellites	Malekian et al., 2015
Petrogale brachyotis	Samples were collected in four sites of a well-preserved environment, considered the control habitat, and in two artificial islands created due to a river dam.	NA	NA	66	18	Microsatellites	Potter et al., 2012
Pseudocheirus peregrinus	Sampling was conducted in three sites in a continuous forest and in seven patches of native forest surrounded by agriculture fields.	5000	10-312	41	189	Microsatellites	Lancaster et al., 2016
Rattus leucopus	Sampling was conducted in four sites in two national parks (but only one site had enough samples to perform genetic analysis) and in seven fragments, representing the control and fragmented areas respectively.	2039	2.53-17.48	12	96	Microsatellites	Geurts, 2013
Rhinolophus lepidus	Samples were taken from five sites in a continuous forest of a Natural Reserve and in 27 forest fragments; however, only 12 fragments had individuals genotyped.	137 000	31-11 339	125	150	Microsatellites	Struebig et al., 2011
Rhinolophus trifoliatus	Samples were taken from five sites in a continuous forest of a Natural Reserve and in 27 forest fragments; however, only nine fragments had individuals genotyped.	137 000	32-11 339	152	98	Microsatellites	Struebig et al., 2011

Saguinus bicolor	Samples were from a Natural Reserve connected to a large continuous forest and in three isolated fragments embedded in an urban matrix, representing the control and fragmented areas, respectively.	NA	NA	13	44	Microsatellites	Farias et al., 2015
Spermophilus suslicus	Four sampling sites were taken in a region with high habitat connectivity and suitability, which were considered as control, and in ten sites of unsuitable habitat considered as fragmented habitats.	NA	NA	56	195	Microsatellites	Biedrzycka and Konopiński, 2008
Syncerus caffer caffer	It was considered the six larger remnants as control and the four smaller remnants as fragmented habitat.	100 000 - 2 860 000	11 700-39 200	138	71	Microsatellites	Heller et al., 2010
Uroderma bilobatum	Sampling was conducted in three sites of Barro Colorado Nature Monument. As fragmented habitats, it was sampled 11 artificial islands formed by the construction of a large artificial reservoir but *U. bilobatum* was caught only in 10 of them and authors only provided genetic data for populations with more than five individuals, i.e. for nine islands.	5400	2.5-50	34	113	Microsatellites	Meyer et al., 2009
Uromys caudimaculatus	Sampling was taken in one continuous forest inside a national park, used as control area, and in three small forest patches surrounded by cattle pastures and a road.	94 000	5.5-80	28	203	Microsatellites	Streatfeild, 2009
Ursus arctos	Samples representing control areas were from a well-connected region with suitable habitat and without expressive human settlements or transportation corridors. Samples representing fragmented habitats were from areas separated by human settlements and high traffic roads and highways.	150 000-158 000	311 700-958 200	80	470	Microsatellites	Proctor et al., 2005
Ursus thibetanus	Samples representing the control were from one region inhabited by a continuous population, and those representing fragmented populations were taken from four regions with less suitable habitat.	NA	NA	56	218	Microsatellites	Ohnishi et al., 2007

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Table S3.2 – Mammalian species included in the meta-analysis and their quantitative and categorical traits. We provide the lower, mean and higher values for body mass (Ml – lower body mass; Mm – mean body mass; and Mh – higher body mass) and home range size (HRl - lower home range; HRm – mean home range; HRh – higher home range) found in the literature and the lower and higher values of reproductive rate (RRl – lower reproductive rate; and RRH – higher reproductive rate). Forest dependency classes are: 1 – species that exclusively use forests (forest habitats); 2 – species that use forests and intermediate habitats as shrubs, bushes and parks (intermediate habitats); 3 – species that use open habitats as fields and grasslands (open habitats), in addition to forest and intermediate habitats; 4 – species that mostly occur in open areas with short grasses (e.g. steppes and grasslands).

Species	**Order**	**Biogeographic region**	**Mass (g)**			**Home range (ha)**			**Reproductive rate**		**Locomotion**	**Trophic guild**	**Forest dependency**	**References**
			Ml	Mm	Mh	HRl	HRm	Hrh	RRl	Rrh				
Syncerus caffer caffer	Artiodactyla	Afrotropical	600000	637500	700000	52500	64688	76875	0.3	0.8	Terrestrial	Herbivore	3	Alden et al., 1995; de Magalhaes, 2013; Melletti and Burton, 2014; Millar and Zammuto, 1983; Ng, 2015
Panthera onca	Carnivora	Neotropical	75650	87966.7	102000	3400	12974	39000	1		Terrestrial	Carnivore	1	de Magalhaes, 2013; Quigley et al., 2017; Reis et al., 2006; Seymour, 1989
Ursus arctos	Carnivora	Neartic	73500	159333.3	298000	1800	46820	86000	0.8		Terrestrial	Omnivore	3	de Magalhaes, 2013; Pasitschniak-arts, 1993
Ursus thibetanus	Carnivora	Paleartic	103750			1250			1		Terrestrial	Omnivore	1	de Magalhaes, 2013; Sathyakumar et al., 2013
Carollia perspicillata	Chiroptera	Neotropical	18	18.4	18.8	6			2		Aerial	Herbivore	1	Bonaccorso et al., 2006; Cloutier and Thomas, 1992; Meyer et al., 2009
Kerivoula papillosa	Chiroptera	Oriental	8.6			100			1		Aerial	Insectivore	1	Khan et al., 2010; Struebig et al., 2011
Myotis macropus	Chiroptera	Australian	10			22			1		Aerial	Insectivore	1	Kerth et al., 2001; Strahan, 1983
Nyctophilus geoffroyi	Chiroptera	Australian	7			25			1	2	Aerial	Insectivore	2	Strahan, 1983
Nyctophilus gouldi	Chiroptera	Australian	9			25			1	2	Aerial	Insectivore	1	Strahan, 1983; Threlfall et al., 2013
Rhinolophus lepidus	Chiroptera	Oriental	6.5			415			1		Aerial	Insectivore	1	Rossiter et al., 2012; Russo et al., 2002
Rhinolophus trifoliatus	Chiroptera	Oriental	14.8			100			1		Aerial	Insectivore	1	Soisook et al., 2015; Struebig et al., 2011
Uroderma bilobatum	Chiroptera	Neotropical	17			114			2		Aerial	Herbivore	2	Loayza and Loiselle, 2008; Meyer et al., 2009; Reis et al., 2006
Antechinus flavipes	Dasyuromorphia	Australian	38	41.5	45	0.28	1	2	7		Terrestrial	Insectivore	2	de Magalhaes, 2013; Fisher et al., 2013; Marchesan and Carthew, 2008; Marlow, 1961; Strahan, 1983
Marmosops incanus	Didelphimorphia	Neotropical	60.4	68	80	0.25			7		Arboreal	Insectivore	1	Bezerra et al., 2015; Cáceres, 2012; Goin et al., 2016; Loretto and Vieira, 2008; Reis et al., 2006
Petauroides volans	Diprotodontia	Australian	1250			2	5	7	1		Arboreal	Herbivore	1	Burbidge and Woinarski, 2016; de Magalhaes, 2013; Nagel, 2003; Pope et al., 2004; Smith et al., 2007
Petaurus breviceps	Diprotodontia	Australian	120			3	4	5	2.6		Arboreal	Omnivore	2	de Magalhaes, 2013; Goldingay and Scheibe, 2000; Quin et al., 2010, 1992; Smith, 1973

Petrogale brachyotis	Diprotodontia	Australian	3900	4200	4500	18			1		Terrestrial	Herbivore	4	de Magalhaes, 2013; Null, 2001; Richardson, 2012; Telfer and Griffiths, 2006
Pseudocheirus peregrinus	Diprotodontia	Australian	700			0.84			3		Arboreal	Herbivore	2	de Magalhaes, 2013; Hermsen et al., 2015; Lancaster et al., 2016; Welsh, 2002
Alouatta caraya	Primates	Neotropical	5400	5450	5500	10			1		Arboreal	Herbivore	1	de Magalhaes, 2013; Fernandez-Duque et al., 2008; Hutchins et al., 2003; LaValle, 2000; Ludwig, 2006
Alouatta palliata	Primates	Neotropical	5258	6042.8	7003.5	25			0.6		Arboreal	Herbivore	1	Cuarón et al., 2008; de Magalhaes, 2013; Estrada, 1984; Glander, 2006; Lau, 2007
Alouatta pigra	Primates	Neotropical	8895			25			1		Arboreal	Herbivore	1	de Magalhaes, 2013; Lau, 2007; Marsh et al., 2008
Eulemur collaris	Primates	Afrotropical	2150			75			1		Arboreal	Herbivore	1	Campera et al., 2014; Garbutt, 2007
Mico argentatus	Primates	Neotropical	354.0			11	16	25	4		Arboreal	Herbivore	1	Albernaz and Magnusson, 1999; Corrêa, 2006; Reis et al., 2006; Rylands and Silva Jr., 2008
Microcebus bongolavensis	Primates	Afrotropical	56.2			0.90			2		Arboreal	Omnivore	1	de Magalhaes, 2013
Microcebus ravelobensis	Primates	Afrotropical	61	63.5	65.9	0.90			2		Arboreal	Omnivore	1	de Magalhaes, 2013; Guschanski et al., 2007; Louis Jr et al., 2008; Olivieri et al., 2008; Thorén et al., 2011; Zimmermann et al., 1998
Saguinus bicolor	Primates	Neotropical	430			12	56	100	1.63		Arboreal	Herbivore	1	de Magalhaes, 2013; Kutschera, 2004; Mittermeier et al., 2008
Cricetus cricetus	Rodentia	Paleartic	350	418.9	506.7	1			14	16	Terrestrial	Herbivore	4	de Magalhaes, 2013; Hutchins et al., 2003; O'Briena, 2015
Glis glis	Rodentia	Paleartic	100	117.5	135	1	2	3	4.8	6	Arboreal	Herbivore	2	de Magalhaes, 2013; Fietz et al., 2014; Fitzke, 2014; Jurczyszyn and Zgrabczyńska, 2007; Kryštufek, 2008; Ściński and Borowski, 2008
Melomys cervinipes	Rodentia	Australian	78.0			0.42			2	4	Arboreal	Herbivore	1	Rader and Krockenberger, 2006; Strahan, 1983; Wood, 1971
Muscardinus avellanarius	Rodentia	Paleartic	27.5	29.1	30.6	0.51	0.71	0.90	6		Arboreal	Herbivore	2	Bright and Morris, 1991; Buchner et al., 2003; Goodwin et al., 2018; Hutchins et al., 2003; Juškaitis, 2008; Juškaitis et al., 2015
Myodes californicus	Rodentia	Neartic	27.5			0.20	0.32	0.44	7	8.4	Terrestrial	Mycophage	1	Cassola, 2016; de Magalhaes, 2013; Thompson et al., 2009; Watson, 2002
Peromyscus leucopus	Rodentia	Neartic	21	21.5	22	0.10	0.38	0.65	14.8	16.65	Terrestrial	Omnivore	3	de Magalhaes, 2013; Fleming, 1970; Fleming and Rauscher, 1978; Graves et al., 1988; Lackey et al., 1943; Morand and Poulin, 1998
Peromyscus melanophrys	Rodentia	Neotropical	38	40	42	0.31			3		Arboreal	Herbivore	4	Reid, 1997; Tovar-Sánchez et al., 2012; Vega et al., 2017; Wood et al., 2010
Rattus leucopus	Rodentia	Australian	116			5.8			11.6		Terrestrial	Omnivore	2	de Magalhaes, 2013; Pryde et al., 2005; Strahan, 1983

Spermophilus suslicus	Rodentia	Paleartic	200			15			6		Terrestrial	Herbivore	4	Nutter, 2013; Volodin et al., 2008
Uromys caudimaculatus	Rodentia	Australian	546	689.5	833	8			2.5		Terrestrial	Herbivore	1	Strahan, 1983; Streatfeild, 2009

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Table S3.3 – Spearman correlation coefficients between continuous species traits. Significant correlations are given at bold. (Legend: Ml – lower body mass; Mm – medium body mass; Mh – higher body mass; HRl – lower home range: HRm – medium home range; HRh – higher home range; RRl – lower reproductive rate; RRh – high reproductive rate).

Allelic diversity	**Ml**	**Mm**	**Mh**	**HRl**	**HRm**	**HRh**
HRl	-0.29	-0.27	-0.27			
HRm	-0.3	-0.28	-0.28			
HRh	-0.26	-0.25	-0.25			
RRl	-0.09	-0.11	-0.11	**-0.84**	**-0.74**	**-0.64**
RRh	-0.09	-0.11	-0.11	**-0.84**	**-0.74**	**-0.64**
Allelic richness						
HRl	0.19	0.19	0.18			
HRm	0.17	0.18	0.18			
HRh	0.18	0.18	0.18			
RRl	-0.22	-0.23	-0.22	**-0.78**	**-0.77**	**-0.79**
RRh	-0.31	-0.32	-0.31	**-0.77**	**-0.77**	**-0.78**
Observed heterozigosity						
HRl	**0.52**	**0.52**	**0.51**			
HRm	**0.52**	**0.52**	**0.51**			
HRh	**0.52**	**0.52**	**0.51**			
RRl	**-0.39**	**-0.38**	-0.36	**-0.73**	**-0.7**	**-0.64**
RRh	**-0.51**	**-0.51**	**-0.49**	**-0.74**	**-0.72**	**-0.68**
Expected heterozigosity						
HRl	**0.51**	**0.50**	**0.50**			
HRm	**0.52**	**0.52**	**0.51**			
HRh	**0.54**	**0.53**	**0.52**			
RRl	**-0.46**	**-0.45**	**-0.44**	**-0.75**	**-0.74**	**-0.71**
RRh	**-0.54**	**-0.54**	**-0.53**	**-0.74**	**-0.74**	**-0.71**

Table S3.4 – Results of meta-regression analysis for allelic diversity, allelic richness, observed heterozygosity and expected heterozygosity. (Legend: Ml – lower body mass; Mm – medium body mass; Mh – higher body mass; HRl – lower home range: HRm – medium home range; HRh – higher home range; RRl – lower reproductive rate; RRh – high reproductive rate; NS – non-significant).

	Allelic diversity		**Allelic richness**			**Observed heterozygosity**		**Expected heterozygosity**		
	Estimate	p-value	Estimate	p-value	Regression model equation	Estimate	p-value	Estimate	p-value	Regression model equation
Model 1					0.296 + 0.175HRl - 0.812Ml					
HRl	NS	NS	0.175	0.362						
Ml	NS	NS	-0.812	< 0.001						
Model 2					0.291 + 0.216HRm - 0.837Ml					
HRm	NS	NS	0.216	0.262						
Ml	NS	NS	-0.837	< 0.001						
Model 3					0.293 + 0.24HRh - 0.855Ml					
HRh	NS	NS	0.240	0.204						
Ml	NS	NS	-0.855	< 0.001						
Model 4					0.305 + 0.171HRl - 0.809Mm					
HRl	NS	NS	0.171	0.373						
Mm	NS	NS	-0.809	< 0.001						
Model 5					0.301 + 0.212HRm - 0.833Mm					
HRm	NS	NS	0.212	0.269						
Mm	NS	NS	-0.833	< 0.001						
Model 6					0.302 + 0.238HRh - 0.852Mm					
HRh	NS	NS	0.238	0.208						
Mm	NS	NS	-0.852	< 0.001						
Model 7					0.314 + 0.167HRl - 0.804Mh					
HRl	NS	NS	0.167	0.384						
Mh	NS	NS	-0.804	< 0.001						
Model 8					0.31 + 0.209HRm - 0.829Mh					
HRm	NS	NS	0.209	0.276						
Mh	NS	NS	-0.829	< 0.001						
Model 9					0.311 + 0.235HRh - 0.848Mh					
HRh	NS	NS	0.235	0.212						
Mh	NS	NS	-0.848	< 0.001						
Model 10										
Mh						NS	NS			
RRl						NS	NS			
Model 11										-0.043 - 0.372Ml
Ml						NS	NS	-0.372	0.031	
Model 12										-0.066 - 0.359Mm

Mm			NS	NS	-0.359	0.035	
Model 13							-0.084 - 0.348Mh
Mh			NS	NS	-0.348	0.039	

Table S4.1 – Literature used to classify functional attributes of bats species captures in our study region.

Diet
Alvarez, J., Willing, M.R., Jones, J.K., Webster, D., 1991. *Glossophaga soricina*. Mammalian Species
Barros, M.A.S., Rui, A.M., Fabian, M.E., 2013. Seasonal variation in the diet of the bat *Anoura caudifer* (Phyllostomidae: Glossophaginae) at the southern limit of its geographic range. Acta Chiropterologica 15, 77–84
Bernard, E., 2002. Diet, activity and reproduction of bat species (Mammalia, Chiroptera) in Central Amazonia, Brazil. Revista Brasileira de Zoologia. 19, 173–188
Coelho, D.C., Marinho-Filho, J., 2002. Diet and activity of *Lonchophylla dekeyseri* (Chiroptera, Phyllostomidae) in the Federal District, Brazil. Mammalia 66, 319–330
Gardner, A., 2007. Order Chiroptera, in: Gardner, A. (Ed.), Mammals of South America. University of Chicago Press, Chicago, pp. 187–484
Medellín, R., Arita, H., 1989. *Tonatia evotis* and *Tonatia silvicola*. Mammalian Species 334, 1–5
Mello, M.A.R., Kalko, E.K.V., Silva, W.R., 2008. Diet and abundance of the bat *Sturnira lilium* (Chiroptera) in a Brazilian Montane Atlantic Forest. Journal of Mammalogy 89, 485–492
Oprea, M., Wilson, D.E., 2008. *Chiroderma doriae*. Mammalian Species 816, 1–7
Ortega, J., Alarcón-D, I., 2018. *Anoura geoffroyi* (Chiroptera: Phyllostomidae). Mammalian species 818, 1–7.
Reis, N., Peracchi, A., Pedro, W., Lima, I., 2007. Morcegos do Brasil. Londrina
Santos, M., Aguirre, L.F., Vázquez, L.B., Ortega, J., 2003. *Phyllostomus hastatus*. Mammalian Species 722, 1–6
Foraging location
Bernard, E., 2002. Diet, activity and reproduction of bat species (Mammalia, Chiroptera) in Central Amazonia, Brazil. Revista Brasileira de Zoologia 19, 173–188
Carvalho, F., Fabián, M., Menegheti, J., 2013. Vertical structure of an assemblage of bats (Mammalia: Chiroptera) in a fragment of Atlantic Forest in Southern Brazil. Zoologia 30, 491–498
Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D., Meyer, C.F.J., 2015. Trait-related responses to habitat fragmentation in Amazonian bats. Journal of Applied Ecology 52, 1381–1391
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Geipel, I., Jung, K., Kalko, E.K. V, 2013. Perception of silent and motionless prey on vegetation by echolocation in the gleaning bat *Micronycteris microtis*. Proceedings of the Royal Society B 280, 20122830
Meyer, C., 2007. Effects of rainforest fragmentation on Neotropical bats - Land-bridge islands as a model system. Ulm University
Nunes, H.L., 2013. Estratificação vertical da comunidade de morcegos (Mammalia, Chiroptera) em uma área de Mata Atlântica no Nordeste do Brasil. Universidade Federal da Paraíba
Ramos Pereira, M.J., Marques, J.T., Palmeirim, J., 2010. Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. Current Zoology. 56, 469–478
Reis, N.R., Peracchi, A.L., Pedro, W.A., Lima, I.P., 2006. Mamíferos do Brasil. Londrina
Silva, H., 2009. Comunidade de morcegos, interações com flores e estratificação vertical em Mata Atlântica do sul do Brasil. Universidade Estadual de Campinas
Foraging mode
Fleming, T.H., 1988. The Short-tailed Fruit Bat. The University of Chicago Press, Chicago
Sazima, I., Fischer, W.A., Sazima, M., Fischer, E.A., 1994. The fruit bat *Artibeus lituratus* as a forest and city dweller. Ciência e cultura. 46, 164–168
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Silva, H., 2009. Comunidade de morcegos, interações com flores e estratificação vertical em Mata Atlântica do sul do Brasil. Universidade Estadual de Campinas
Foraging strategy
Kalko, E.K. V, Estrada-Villegas, S., Schmidt, M., Wegmann, M., Meyer, C., 2008. Flying high - assessing the use of the aerosphere by bats. Integrative and Comparative Biology. 48, 60–73
Ortega, J., Alarcón-D, I., 2018. *Anoura geoffroyi* (Chiroptera: Phyllostomidae). Mammalian species 818, 1–7
Silva, H., 2009. Comunidade de morcegos, interações com flores e estratificação vertical em Mata Atlântica do sul do Brasil. Universidade Estadual de Campinas
Soriano, P.J., 2000. Functional structure of bat communities in Tropical Rainforests and Andean Cloud Forests. Ecotropicos 13, 1–20
Willig, M.R., Moulton, M.P., 1989. The Role of Stochastic and Deterministic Processes in Structuring Neotropical Bat Communities. Journal of Mammalogy. 70, 323–329
Roost type
Alvarez, J., Willing, M.R., Jones, J.K., Webster, D., 1991. *Glossophaga soricina*. Mammalian Species
Arnone, I.S., 2008. Estudo da comunidade de morcegos na área cárstica do Alto Ribeira - SP: uma comparação com 1980. Universidade de São Paulo
Cloutier, D., Thomas, D., 1992. *Carollia perspicillata*. Am. Soc. Mammologists 417, 1–9
Gardner, A., 2007. Order Chiroptera, in: Gardner, A. (Ed.), Mammals of South America. University of Chicago Press, Chicago, pp. 187–484
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Table S4.2 – Best models explaining values of non-metric multidimensional scaling (NMDS) projected in one dimension for all bat species. Values are present in unstandardized (unstand) and standardized (stand) forms. Independent variables: distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG). Akaike's Information Criterion for small samples (AICc), and variation between the AICc (ΔAICc) and weight for each model are presented. Standard error (SE), t-value and p-value are presented for each variable.

Model	Estimate (unstand|stand)	SE (unstand|stand)	t-value (unstand| stand)	p-value	R^2	K	AICc	ΔAICc	Weight
Buffer 300 meters									
Model					0.26	3	7.15	0	0.41
Intercept	0.14|0.000000000008	0.09|0.06	1.63|0.00	0.12|1.00					
DIST	-0.00001|-0.14	0.000005|0.06	-2.27|-2.27	< 0.05					
Buffer 1000 meters									
Model					0.26	3	7.15	0	0.38
Intercept	0.14|0.000000000008	0.09|0.06	1.63|0.00	0.12|1.00					
DIST	-0.00001|-0.14	0.000005|0.06	-2.27|-2.27	< 0.05					
Buffer 2500 meters									
Model1					0.26	3	7.15	0	0.33
Intercept	0.14|0.000000000008	0.09|0.06	1.63|0.00	0.12|1.00					
DIST	-0.00001|-0.14	0.000005|0.06	-2.27|-2.27	< 0.05					
Model2					0.38	4	7.53	037	0.27
Intercept	-8.45|0.00000000001	0.16|0.06	-0.53|0.00	0.60|1.00					
BORD	0.000006|0.10	0.000004|0.06	1.68|1.68	0.12					
DIST	-0.00001|-0.14	0.000004|0.06	-2.40|-2.40	< 0.05					

Table S4.3 – Best models explaining values of non-metric multidimensional scaling (NMDS) projected in one dimension for phyllostomid species. Values are present in unstandardized (unstand) and standardized (stand) forms. Independent variables: distance to nearest border of Serra da Bodoquena National Park (DIST), forest cover (FORE), forest border length (BORD) and number of forest fragments (FRAG). Akaike's Information Criterion for small samples (AICc), and variation between the AICc (ΔAICc) and weight for each model are presented. Standard error (SE), t-value and p-value are presented for each variable.

Model	Estimate (unstand|stand)	SE (unstand|stand)	t-value (unstand| stand)	p-value	R^2	K	AICc	ΔAICc	Weight
Buffer 300 meters									
Model 1					0.11	3	10.45	0.95	0.20
Intercept	0.1||-0.0000000006	0.1|0.07	0.99|0.00	1.00					
DIST	-0.000007|-0.09	-0.000005|0.07	-1.38|-1.38	0.19					
Buffer 1000 meters									
Model 1					0.16	3	9.43	0	0.23
Intercept	-0.27|-0.0000000006	0.17|0.07	-0.16|0.00	0.13|1.00					
BORD	0.00003|0.11	0.00002|0.06	1.72|1.72	0.11					
Model 2					0.11	3	10.45	1.02	0.14
Intercept	0.10|-0.0000000006	0.10|0.07	0.99|0.00	0.34|1.00					
DIST	-0.000007|-0.09	0.000005|0.07	-1.38|-1.38	0.19					
Model 3					0.25	4	11.10	1.67	0.10
Intercept	-0.17|-0.0000000006	0.19|0.06	-0.88|0.00	0.39|1.00					
BORD	0.00003|0.10	0.00002|0.065	1.60|1.60	0.13					
DIST	0.000006|-0.08	0.000005|0.06	-1.26|-1.26	0.23					
Buffer 2500 meters									
Model1					0.25	3	7.59	0	0.35
Intercept	-0.33|-0.0000000006	0.16|0.06	-2.06|0.00	0.06|1.00					
BORD	0.000008|0.14	0.000004|0.06	2.24|2.24	< 0.05					
Model2					0.36	4	8.31	0.72	0.24
Intercept	-0.23|-0.0000000006	0.16|0.06	-1.41|0.00	0.18|1.00					
BORD	0.000008|0.14	0.000004|0.06	2.34|2.34	< 0.05					
DIST	-0.000007|-0.09	0.000005|0.06	-1.57|-1.57	0.14					