Bats in a fragmented world

Tiago Souto Martins Teixeira

School of Biological and Chemical Sciences

Queen Mary University of London

Mile End Road, E1 4NS

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Abstract

Habitat loss and fragmentation are global threats to biodiversity, however, their impact on ecological function are not well understood. The Atlantic Forest hosts high levels of biodiversity and has experienced a long history of deforestation and fragmentation. To examine the consequences of fragmentation for functional and phylogenetic diversity, and for key ecological interactions, I studied bat metacommunity across this landscape. I conducted repeated surveys of bats in forest fragments and continuous forest sites at the Reserva Ecológica de Guapiaçú. To characterize metacommunity structure and the drivers of species assembly, I combined an "elements of metacommunity structure" analysis with assessments of phylogenetic and functional diversity. I then applied a community occupancy model to evaluate the species-specific responses to habitat fragmentation and test whether landscape configuration or habitat structure predicted species occurrence. Finally, by using DNA barcoding to identify plant species recovered in the guano of bats, I reconstructed mutualistic bat-plant networks and determined how network architecture changed with fragmentation. My results revealed that while the bat metacommunity had a random structure, the meta-ensembles of phyllostomid and animalivorous bats showed nested and quasi-nested metacommunity structures, respectively. Species assembly was driven by stochastic processes in fragments, and by environmental filters in the continuous forest. Species occurrence showed a positive relationship with area, but the community occupancy models were not precise enough to differentiate responses to isolation and habitat structure. The structure of bat-plant networks was maintained in

small fragments due to the persistence of generalists that perform seed dispersal. Although fragmentation of the Atlantic Forest has severe impacts on bat communities, this biome harbours a rich bat fauna at the metacommunity level. Small fragments may not support diverse bat faunas, but those surviving species still act as agents of seed dispersal and can contribute to forest regeneration and restoration.

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Author's Declaration

I, Tiago Souto Martins Teixeira, confirm that the research included with this thesis is my own work or that where it has been carried out in collaboration with, or supported by others, that this is duly acknowledged below, and my contribution indicated. Previously published material is also acknowledged below.

I attest that I have exercised reasonable care to ensure that the work is original and does not to the best of my knowledge break any UK law, infringe any third party's copyright or other intellectual property rights, or contain any confidential material.

I accept that the College has the right to use plagiarism detection software to check the electronic version of the thesis. I confirm that this thesis has not been previously submitted for the award of a degree by this or any other university.

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Signature:

Date:

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CHAPTER ONE

General Introduction

Human activity over the last century has led to dramatic and unprecedented rates of habitat modification (Ripple *et al.* 2017) and extinctions (Pimm *et al.* 1995), with habitat loss and fragmentation representing two of the major global threats to biodiversity (Turner 1996; Haddad *et al.* 2015). Habitat loss refers to the conversion of suitable habitat into unsuitable habitat (Andrén & Andren 1994; Wiegand *et al.* 2005) and its effects may be scale-dependent (Fuhlendorf *et al.* 2002; Blazquez-Cabrera *et al.* 2014). It can cause population declines (Sutherland & Anderson 1993; Sutherland & Dolman 1994) and local extinctions (Brook *et al.* 2003) that can cause the loss of ecological interactions (Spiesman & Inouye 2013) that are the core of critical ecological services (Bascompte 2009). Habitat loss alone can correctly predict the extinction rates of endemic large mammals (Grelle *et al.* 1999) and birds (Gaston *et al.* 2003). The loss of habitat heterogeneity can have severe impacts on biodiversity, as certain types of habitat can have disproportionate contributions to species richness and abundance (Cushman 2006). In a study of migrating birds, such as the oystercatcher *Haematopus ostralegus,* the reduction in wintering and breeding habitat led to significant declines in population numbers (Sutherland 1996).

Habitat fragmentation involves habitat loss and the division of originally continuous habitat, thus simultaneously decreasing the absolute area of habitat available while increasing the number of habitat patches, and their degree of isolation (Fahrig 2003; Ewers & Didham 2007; Hagen *et al.* 2012). Long-term studies of habitat fragmentation have concluded that large areas of primary forest hold more biodiversity than fragmented and altered habitats (Laurance 2008; Haddad *et al.* 2015), but that

species have specific responses to this process (Laurance *et al.* 2002; Zipkin *et al.* 2009; Haddad *et al.* 2015). While some animals thrive in these altered conditions (Pardini *et al.* 2005; Zipkin *et al.* 2009; Rocha *et al.* 2017), many animals are negatively affected by the fragmentation process (Laurance *et al.* 2002; Pardini *et al.* 2009; Haddad *et al.* 2015; Rocha *et al.* 2017) and the decline of population numbers can be so severe that it may lead to the local extinction of entire faunas (Gibson *et al.* 2013). Although it is possible to theoretically separate the effects of habitat loss and fragmentation (Fahrig 1997, 2017), these are landscape-scale processes that usually work in synergy, thereby making the distinction between these two processes complex in field experiments (Fletcher *et al.* 2018). Understanding the consequences of habitat loss and fragmentation is essential to ensure the persistence of natural environments on the planet (Haddad *et al.* 2015; Ripple *et al.* 2017).

As a consequence of fragmentation, habitat patches become isolated and different species occupy different sites (Laurance *et al.* 2002; Haddad *et al.* 2015). As a result, each fragment can have its own discrete community, and these communities may or may not be linked by dispersal to other habitat patches of the same type. When these discrete communities are considered together they are referred as a metacommunity (Leibold *et al.* 2004). Analyses of metacommunities explicitly consider local processes, such as biotic interactions, and regional processes, such as species dispersal, as factors that determine composition and variability among communities (Hanski 1998; Leibold *et al.* 2004; de la Sancha *et al.* 2014). Although there is no unified theory of metacommunities, Leibold & Chase (2018) did an extensive review of the approaches to the metacommunity concept and recognised four metacommunity archetypes that provide an analysis of the importance of four general

processes that influence metacommunity diversity, distribution and composition: niche selection, dispersal, stochastic drift and speciation (Leibold & Chase 2018a).

The four archetypes are:

- *Neutral Theory* (NT): In this archetype, species are treated as having no differences in their traits (niche selection) or dispersal ability, with stochastic events of birth and death rates and dispersal determining metacommunity structure.
- *Species Sorting* (SS): This archetype uses habitat heterogeneity, the ability of different species to explore different habitats and species interactions to explain metacommunity structure, with little importance given to stochastic events and dispersal.
- *Patch Dynamics* (PD): Species are able to explore resources differently (niche selection), have colonization rates and competition trade-offs and are subject to stochastic local extinction and colonization events.
- *Mass Effects* (ME): In this archetype habitat heterogeneity allows species to explore resources differently in space and time, while dispersal allow species to persist in sub-optimal environments because of immigration from adjacent patches. This generates a source-sink dynamic between populations in different patches.

These four archetypes were sometimes used as alternative hypothesis in studies of metacommunities (Leibold & Loeuille 2015), but more recent studies have attempted to reconcile different archetypes in order to explain metacommunitiy structure and processes (Brown *et al.* 2017; Leibold & Chase 2018b). While some studies focus on the mechanisms that structure a metacommunity (Chisholm *et al.*

2011), others try to find patterns in that structure (Presley *et al.* 2009; Tonkin *et al.* 2016). Even if it is not possible to understand the processes that creates certain metacommunity structures by merely studying metacommunity patterns, these patterns can supply evidence for metacommunity theories (Leibold & Chase 2018c).

Leibold and Mikkelson (2002) proposed a method to identify structural patterns of metacommunities. This method relies on reciprocal averaging to order an incidence matrix of species occurrence, and, in a three-step analysis that examines three "elements of metacommunity structure" (EMS), to distinguish between idealised patterns of metacommunity organisation (Leibold & Mikkelson 2002; Presley *et al.* 2010). These key elements of metacommunity structure are coherence, turnover and boundary clumping. The model starts with an assumption that a species has continuous distributions between both ends of its tolerance spectrum to an environmental gradient (Gaussian distribution) (Scheiner & Willig 2008). Coherence is a measure of the extent to which a species' distribution matches this underlying assumption. The absence of coherence in a metacommunity can be interpreted as an evidence for stochastic processes driving species occurrence and therefore metacommunity will present a random structure. Species turnover describes the rate at which one species' distribution substitutes that of another in the community, while boundary clumping measures the co-distribution of species within the metacommunity. If multiple species have the same response to an environmental gradient, it is expected that they will occupy the same habitat patches and have similar distributions (Leibold & Mikkelson 2002). The combination of scores for these three elements has been used to discriminate between six metacommunities structures (Leibold & Mikkelson 2002) and was later expanded to identify six other quasi-structures (Presley

et al. 2010). Each metacommunity structure is based on strong ecological theories and can be defined as:

- **Random structure:** The absence of gradients or patterns of species distribution among sites (Leibold & Mikkelson 2002). It is characterized by non-significant values of coherence.
- **Checkerboard distribution:** Based on the observations of Diamond (1975), in this structure species pairs have mutually exclusive distributions among sites, with different pairs of species being independently distributed (Leibold & Mikkelson 2002). This structure has significant negative values of coherence.
- **Nested subsets:** Species-poor communities are a subset of species-rich communities (Patterson & Atmar 1986; Leibold & Mikkelson 2002). It is characterised by significant positive coherence and significant negative turnover. Presley *et al.* (2010) showed that boundary clumping can differentiate between three patterns of species loss in nested subsets – clumped species loss (significant positive boundary clumping), stochastic species loss (non-significant boundary clumping) and hyperdispersed species loss (significant negative boundary clumping).
- **Clementsian structure:** In this pattern, distinct communities substitute each other along an environmental gradient, proposed by Clements (1916). This structure presents significant positive values of coherence, turnover and boundary clumping.
- **Gleasonian structure:** Species show specific responses to an environmental gradient, resulting in a random structure with high turnover, based on the ideas proposed by Gleason (1926). This structure has significant positive values of coherence and turnover, but non-significant boundary clumping.

- **Evenly spaced distributions:** No discrete community can be identified, but species distributions along an environmental gradient are more evenly distributed than expected by chance. Evenly spaced metacommunities have significant positive coherence and turnover, but significant negative boundary clumping.
- **Quasi-structures:** An expanded EMS framework proposed by Presley *et al.* (2010), where each of the above structures has an equivalent quasi structure in which turnover is not significantly different from random, but with a structure consistent with the conceptual background of Clementsian, evenly spaced distribution, Gleasonian and nested subsets structures.

Metacommunity structure is a result of a complex interplay among abiotic factors, biotic factors, and local and regional processes. Although the study of patterns does not allow direct assumptions on the mechanisms that will shape metacommunity, it can provide evidence for studies of metacommunity processes. In this study I will use the elements of metacommunity structure to assess the impacts of habitat fragmentation on the bat metacommunity structure and on the drivers of species assembly.

A serious problem inherent to any sampling method is that not every species is detected, even when it is present or abundant (MacKenzie *et al.* 2002), introducing serious biases on estimations of species occurrence, abundance and richness (MacKenzie *et al.* 2006; Kéry & Royle 2008; Hein *et al.* 2009). This can lead to poor biodiversity management and conservation strategies (MacKenzie *et al.* 2006; Kéry & Royle 2008). To deal with this uncertainty MacKenzie *et al.* (2002) developed the occupancy model. Occupancy is the proportion of sites occupied by a species in a landscape (MacKenzie *et al.* 2002, 2006; Kéry & Royle 2016), or the probability that a

species occupies a site of interest (Kéry & Royle 2016). Repeated surveys are used to record the presence and absence of a species and estimate its occupancy while accounting for imperfect detection (MacKenzie *et al.* 2006). This model was initially developed to be used with a single species (MacKenzie *et al.* 2006), but alternatives were developed to deal with communities and metacommunities (Dorazio & Royle 2005; Kéry & Royle 2008; Royle & Dorazio 2009) and can incorporate site and observational covariates affecting detection, making it a flexible tool for ecological assessment and management (MacKenzie *et al.* 2006; Royle & Dorazio 2009; Zipkin *et al.* 2009, 2010; Hines *et al.* 2010; Kalies *et al.* 2012; Kéry & Royle 2016; Mendes *et al.* 2017). Although these models have almost endless possibilities, one of its drawbacks is the reliability of its estimates when detection probabilities are low for many species, a condition that is common in many tropical environments. In this study I attempt to use the community occupancy model to evaluate whether landscape configuration or habitat structure is the better predictor of species occurrence, and to assess whether species show taxon-specific responses to habitat fragmentation and contrast this to single species models.

Although there have been few studies that have assessed the impacts of habitat fragmentation on ecological services and functioning, it has been shown that the changes caused by fragmentation are mostly mediated by the loss of specialists in smaller fragments (Layman *et al.* 2007; Hagen *et al.* 2012; Valladares *et al.* 2012). Network theory is a robust mathematical framework that represents interactions between two or more entities as “links” between “nodes” which can represent virtually anything, from genes (Guet *et al.* 2002) and biological species (Hagen *et al.* 2012) up to fragments in a landscape (Teixeira *et al.* 2014). Ecologists have used networks to represent ecological systems for more than 75 years (Lindeman 1942; Odum 1956)

and the versatility of network theory allows us to explain how ecological communities are structured and predict how they will respond to environmental change (Bascompte 2007; Ings *et al.* 2009; Albouy *et al.* 2014). Ecological networks can be divided into three broad categories: antagonistic networks (food webs) (de Ruiter *et al.* 2005), mutualistic networks (Mello *et al.* 2011a) and host-parasitoid networks (Pilosof *et al.* 2014). In this study I will focus on mutualistic networks composed of plants and seed dispersers. These networks provide a vital ecosystem service of seed dispersal and pollination.

Ecological network studies have been criticised for biases caused by uneven taxonomic resolution of their nodes (Ings *et al.* 2009; Hemprich-Bennett *et al.* 2018). One of the solutions to these issues is the application of new technologies such as DNA barcoding (Hebert et al. 2003) to identify species in the ecological network (Ma *et al.* 2018). This technique uses short predefined DNA sequences that are sufficiently similar to each other within a species, but are different between species, such that they can be used to give an unambiguous taxonomic identification. This method can be extremely useful in cases where interactions cannot be directly observed, but where evidence of these interactions can be obtained in the form of trace materials, such as seeds, fruit pulp and pollen contained in faeces. While networks are only starting to incorporate DNA-based node resolution, they have shown promise (García-Robledo *et al.* 2013; Wirta *et al.* 2014) and in this analysis I use DNA barcoding approaches to identify plant genera being dispersed by bats in the fragmented Atlantic Forest of Brazil.

The Atlantic Forest was once one of the largest rainforests in the world, but it has highly heterogeneous environmental conditions and a long history of disturbance. Despite this, it hosts an extraordinary biodiversity with high levels of endemism (Myers

et al. 2000; Ribeiro *et al.* 2009). Brazilian development has been heavily based on agriculture and livestock production, both of which have strongly impacted the Atlantic Forest landscape. Brazil has gone through several economic cycles since the start of its colonization by the Portuguese in 1500. Land conversion into monoculture fields (mostly sugar-cane and coffee) and exploitation (logging and mining) was so severe that, in the late 18th century it was almost impossible to find high quality wood in the southeast of the country (Dean 1996). In Rio de Janeiro, the conversion of the city's surroundings into coffee plantations was so drastic that it caused a hydrological crisis in the city in the early 19th century and triggered one of the most amazing efforts of rainforest restoration to this day (Dean 1996). With the rapid industrial expansion after the second world-war, the process of fragmentation of the Atlantic Forest was intensified (Dean 1996). Today there is only 11-16% of the original forest cover left, distributed over more than 200,000 fragments, the vast majority of them smaller than 50 ha (Ribeiro *et al.* 2009). Because of the great biodiversity it hosts and the high levels of threat from human activity, it is considered one of the world's hotspots for biological conservation (Myers *et al.* 2000). It is important to understand the consequences of habitat fragmentation on this unique biome to guide conservation efforts, in the Atlantic Forest and in other parts of the world that are currently experiencing the same fragmentation process.

Bats are nocturnal mammals that are globally distributed and the only mammals capable of self-powered flight (Reis *et al.* 2007). Bats are also the only mammals to have evolved laryngeal echolocation, which has allowed them to use sound to perceive their surroundings, and to occupy a nocturnal niche (Jones 2005; Jones & Teeling 2006). Bats are ecologically-diverse mammals; while some species are highly mobile (Esbérard *et al.* 2017), others do not disperse more than a few hundred metres

(Heithaus *et al.* 1975). Many bats provide critical ecological services (Kunz *et al.* 2011), acting as pollinators and primary seed dispersers in forest restoration (Duncan & Chapman 1999) and they may also provide biological control of several invertebrate populations (Reis *et al*., 2007).

In the Neotropics, bats of the family Phyllostomidae have undergone a rapid adaptive radiation (Shi & Rabosky 2015). There are more than 200 species described for this family, and in Brazil there are at least 86 species through the country. Rio de Janeiro State has a long tradition of research on bats and there are 44 species recorded in the state (Peracchi & Nogueira 2010). One of the most distinctive characteristics of these bas is the presence of a membrane nasal appendix called noseleaf, which might play a role in their echolocation (Reis *et al.* 2007). This family is the most abundant and diverse lineage of Neotropical bats, and its members have undergone unparalleled dietary diversification among all mammals, with species that feed on fruits, nectar, arthropods, amphibians, small mammals and blood (Reis *et al.* 2007). In Neotropical forests, phyllostomid bats are among the primary agents of pollination and seed dispersal (Fleming & Muchhala 2008). In the analyses performed in my study, I classify phyllostomid bats into two broad dietary groups. First, species that feed primarily on plant matter (fruits, nectar, pollen) are termed ‘plantivorous’, and second, bats that feed primarily on animals (insects, vertebrates, blood) as termed ‘animalivorous’.

Earlier studies have shown that some bats species may benefit from the fragmentation process (Bianconi 2005; Rocha *et al.* 2017), while other species may suffer negative impacts (Meyer 2007; Rocha *et al.* 2017). Despite their apparent importance in habitat restoration in the Neotropics, there are significant gaps in our

knowledge of how these animals are affected by habitat loss and fragmentation (Meyer 2007; Willig *et al.* 2007).

Thesis organisation

In this study I investigate the impacts of fragmentation on bat communities in a highly fragmented landscape in the Atlantic Forest of southeast Brazil. In Chapter 2, I use the 'elements of metacommunity structure' approach to characterise the structure of the bat metacommunity in my study region and investigate the functional and phylogenetic diversity to determine the drivers of species assembly and how they are affected by the fragmentation process. In Chapter 3, I examine the metacommunity and species-specific responses to landscape configuration and habitat structure to determine the best set of predictors of species occurrence. In Chapter 4, I assess the effects of fragmentation on the bat-plant mutualistic network with the use of DNA barcoding to identify the plants consumed and network theory. Finally, in Chapter 5 I summarize my findings and conclusions.

CHAPTER TWO

Bat metacommunities in a fragmented landscape in South-eastern Brazil

ABSTRACT

Habitat fragmentation is one of the most significant global threats to biodiversity, leading to impoverished communities with unpredictable dispersal rates between them. One way to measure the impact of fragmentation in ecological systems, specifically to understand how it affects biodiversity, is to assess metacommunity structure and the drivers of the process of community assembly. The Atlantic Forest is one of the most species-rich rainforests in the world, but severely threatened by a long history of fragmentation, with less than 11% of its original cover left, distributed in more than 200,000 fragments. This makes the Atlantic Forest an excellent location for assessing the process of fragmentation and its consequences for community assembly. To characterise metacommunity structure and the determinants of community assembly in the fragmented Atlantic Forest, I studied bats across 10 fragments and three continuous forest sites. By combining analyses of metacommunity structure with measures of phylogenetic and functional diversity, I show that bat metacommunities are randomly structured, but that the meta-ensembles of New World leaf-nosed bats show a nested structure, while that of the animalivorous bat species show a quasi-nested structure. The observed assembly process is likely driven by competition leading to ecological displacement between closely related

species in the continuous forest, while the process is random in the fragments. My study suggests that maintaining existing fragments, increasing the forested area, and bridging the gaps between fragments should be a conservation priority, in addition to expanding the large protected areas where possible.

Introduction

Habitat fragmentation is one of the most significant threats to the maintenance of biodiversity (Fahrig 2003; Haddad *et al.* 2015) but it can have contrasting impacts. It increases the number of habitat patches, their isolation and the proportion of edge habitats available and may also simultaneously cause a net reduction in the area of natural habitat (habitat loss) (Fahrig 2003; Hagen *et al.* 2012). As a consequence, fragmented biological populations and communities may become impoverished, isolated, and with variable dispersal rates between them (Gonzalez 1998; Laurance *et al.* 2002). A recent discussion is whether fragmentation is detrimental or beneficial to biodiversity. Fahrig *et al.* (2018) did a meta-analysis of fragmentation studies to conclude that when decoupled from habitat loss, fragmentation can have positive effects on biodiversity. In contrast, Fletcher *et al.* (2018) argued that most evidence point to the contrary and that habitat fragmentation is rarely decoupled from habitat loss in the real world. Fragmentation studies have shown that species richness is usually positively associated with fragment size and connectivity (Haddad *et al.* 2015). It is also well-documented that intact forests host more biodiversity per unit area than do fragmented and altered habitats (Preston 1962; Laurance *et al.* 2002; Laurance 2008), and that local extinctions may happen immediately after the fragmentation event, but may also increase with time (Helm *et al.* 2006; Haddad *et al.* 2015). This time lag between the disturbance event and subsequent extinctions is often called the "extinction debt" (Tilman *et al.* 1994; Hanski 1998) and in some cases the full impact may not be seen for >50 years (Metzger *et al.* 2009; Canale *et al.* 2012; Wearn *et al.* 2012). For example, in a study with small mammals in Thailand, Gibson *et al.* (2013)

found that it takes an average of 13-14 years for 50% of mammal diversity to be lost after a severe fragmentation event, and 25-26 years for all the native species to go extinct.

One way to measure the impact of fragmentation in ecological systems is to use a metacommunity approach (Hanski 1998). In a fragmented landscape, each habitat fragment or patch will have its own discrete community that may or may not be linked by dispersal to other habitat patches of the same type. When we consider many of these discrete communities together this is referred to as a metacommunity (Hanski, 1998; Leibold et al., 2004). Models of metacommunities offer a theoretical framework that provides a new way to integrate information across multiple scales in ecology (Hanski 1998) and it is possible to identify four main families of theories, or archethypes, that explain the metacommunity phenomena (Box 1 for more detailed explanations): Neutral Theory (*NT*), Patch Dynamics, Species Sorting (*SS*) and Mass Effects (*ME*) (Leibold & Chase 2018b). Initially these archetypes were called "paradigms" and sometimes they were used as alternative hypothesis (Leibold & Loeuille 2015) but recent studies and reviews treat them as complementary explanations to the real world (Chase 2005; Leibold & Chase 2018a). These archetypes use different assumptions about four main processes that underline metacommunity dynamics: stochastic drift, dispersal, heterogeneity and speciation. While some studies focus on metacommunity patterns (Presley *et al.* 2009; Presley & Willig 2010) others examine metacommunity processes (Leibold & Chase 2018c), but both are needed to explain how metacommunities work (Brown *et al.* 2017). Although the study of patterns doesn't allow us to make assumptions about the underlying processes that shape metacommunity it can provide evidence for metacommunity theories (Leibold & Chase 2018a). Chisholm & Pacala (2010) compared two

simulations of metacommunity structures to show that a SS-based and a NT-based model both provide similar explanations for a plant metacommunity in Panamá (Chisholm & Pacala 2010; Leibold & Chase 2018b). In another comparison, Sanderson *et al.* (2009) analysed the co-occurrence of closely related birds from Bismarck and Solomon Archipelago to refute the idea that the checkerboard distribution of these bird species could be consequence of a neutral process.

Leibold & Mikkelson (2002) proposed a method to identify structural patterns of the metacommunity but without explaining the underlying mechanisms that determine this pattern. For distinguishing between idealized patterns of metacommunity arrangement, this stepwise analysis looks at three key "elements of metacommunity structure" (EMS), termed coherence, turnover, and boundary clumping (Leibold & Mikkelson 2002; Presley *et al.* 2010) that can be used to describe metacommunity structure (Figure 2.1). Briefly, coherence measures the extent to which a species' distribution is continuous along an environmental gradient (Gaussian distribution), turnover measures the extent to which species in a metacommunity replace each other along this same environmental gradient, and boundary clumping measures the extent to which species distributions in a metacommunity are aggregated. Initially the framework proposed by Leibold and Mikkelson (2002) recognized six metacommunity structures: checkerboards distributions, nested subsets, Gleasonian, evenly-spaced distributions, Clementsian and random structures (for explanations of these see Box 2).

Later developments in the field of research led to the recognition of three different patterns of nested subsets according to the nature of species loss (hyperdispersed, random, and clumped) and of quasi-structures related to each of the already-recognised patterns (quasi-nested with the three patterns of species loss):

quasi-Gleasonian, quasi- evenly spaced, and quasi-Clementsian (Presley *et al.* 2010) (Box 2). Subsets of species within a metacommunity, termed 'meta-ensembles', can show different structures if they respond to different environmental gradients. Although it is possible to apply the EMS approach to different geographic scales, few studies have attempted to do so (Willig *et al.* 2007; Presley & Willig 2010; Meynard *et al.* 2013; de la Sancha *et al.* 2014; Tonkin *et al.* 2016) and the question of at what scale can the species assembly process be measured remains unresolved.

An example of the application of EMS at multiple scales concerns the bats of the Caribbean islands (Presley & Willig 2010). Here the metacommunity appears to show Clementsian structure at the regional-scale, but when the compartments within this structure are assessed separately, only the bats of the Bahamas and Lesser Antilles show a Clementsian structure, while the bats of the Greater Antilles show a nested structure (Presley et al 2010), suggesting that the process of bat species assembly may vary across different scales. In the same study the herbivores meta-ensemble showed a random distribution, while the animalivorous meta-ensemble had a Clementsian distribution (Presley & Willig 2010) providing evidence that meta-ensembles respond to different assembly processes.

Although the EMS method doesn't allow inferences of the underlying local processes, metacommunity structure is a consequence of the species assembly process across patches of habitat (Leibold & Mikkelson 2002), and this structure is determined by an interplay between abiotic, ecological and evolutionary factors (Mouquet et al. 2012; Cadotte and Davies 2016). One way that fragmentation can alter metacommunity structure is by disrupting the species assembly mechanisms. Identifying and understanding the underlying specific processes and mechanisms that drive species assembly are key challenges that have been the focus of many studies

(e.g. Webb 2000; Muchhala & Potts 2007). Several important concepts and trends have emerged. First, closely related species may be more similar to each other, and therefore might have similar ecological niches (Mouquet *et al.* 2012). Thus phylogenetic approaches may provide insights into ecological processes that structure communities (Webb *et al.* 2002).

These ecological processes can be studied using a mix of functional traits and phylogenetic diversity measurements. In cases where resources are limited, species will avoid competition by filling more available niches, leaving the community with an imprint of high functional diversity (Schluter 2000; Mouquet *et al.* 2012). High functional diversity may thus result from competitive exclusion in communities, and is then expected to be characterised by communities composed of phylogenetically-distant species (overdispersion), or by character displacement of closely related species, which allows coexistence in communities composed of closely related species (phylogenetically clustered) (Schluter 2000). An example of character displacement among closely related plants of the genus *Burmeistera* was observed by Mucchala and Potts (2007). In this group, congeneric species exhibit changes in the size of their flowers to avoid competition for pollination when growing in close proximity to each other. On the other hand, where resources are not limited but niches are limited by an environmental filter (Mouquet *et al.* 2012), communities tend to show low functional diversity, because selection is for traits that enable survival under this environmental filter (Webb 2000). In such cases, phylogenetic overdispersion indicates that traits converge between distantly related species, and phylogenetic clustering indicates that closely related species share similar traits that enable them to survive under an environmental filter (Webb *et al.* 2002) (Figure 2.2).

The Atlantic Forest has a long history of large-scale clearance and, with only 11-16% of original forest cover left (Ribeiro *et al.* 2009), is one of the most threatened biomes in the world (Myers *et al.* 2000). The remaining forest is distributed across more than 200,000 fragments with 97% of the forest fragments smaller than 250 ha, and 83.4% smaller than 50 ha (Ribeiro *et al.* 2009). Most of the landscape has been modified for more than 50 years, following a rapid increase in deforestation after the 1970s (Canale *et al.* 2012), and most of the extinction debts in these areas are thought to have been paid (Lira *et al.* 2012). As a consequence, species persistence is likely to be related to landscape structure and the amount of forest cover left (Tabarelli *et al.* 2010). Such scenarios make the Atlantic Forest an ideal place for fragmentation research and a particularly interesting location to measure the process of community assembly.

Bats in the Neotropics are characterised by both high functional and phylogenetic diversity, occupy many niches, and perform several key ecosystem services including pollination, seed-dispersal and insect population control (Kunz *et al.* 2011). Bats are the only mammals capable of self-powered flight and some species may be able to disperse through the surrounding matrix between fragments, and thus track preferred habitats across the landscape (Esbérard *et al.* 2017). Due to the high species diversity of Neotropical bat assemblages, metacommunity analysis offers an ideal approach to measure the impact of fragmentation on community assembly (Cisneros *et al.* 2015).

In this study I use elements of metacommunity structure to test whether the bat metacommunity in a fragmented landscape of Atlantic Forest in southeast Brazil is structured according to the theoretical patterns predicted by an EMS approach. If fragments act as islands of habitat in a matrix of non-habitat, then bat communities

should present a nested structure, analogous to predictions of island biogeography and species-area curve relationships. I then test whether landscape and habitat structure can explain patterns of metacommunity structure. To test whether competition or environmental filtering drives species assembly, I use functional diversity (FD), phylogenetic diversity (PD) and the mean phylogenetic pairwise distance (MPD) between species. I test between two competing specific hypotheses. First, bat communities contain higher functional diversity than expected by random models, and limited resources drive species assembly such that species will show different forms and functions to exploit all of the niches available. In this case phylogenetic overdispersion indicates competitive exclusion, while phylogenetic clustering indicates character displacement between closely related species. The alternative scenario is that functional diversity is lower than expected under random models, and environmental filtering drives species assembly. Phylogenetic overdispersion in this case indicates trait conversion between distantly related species, while phylogenetic clustering indicates that closely related species share traits that enable them to exploit specific habitats.

Methods

Study area

This study took place in a fragmented landscape at the Guapiaçú River Basin, located in the municipalities of Guapimirim and Cachoeiras de Macacú, Rio de Janeiro state, southeast Brazil. The region is covered by lowland Atlantic Forest with the biggest continuously forested areas inside natural reserves. My study is based in and around one of these reserves, Reserva Ecológica de Guapiaçú (REGUA). REGUA is a mosaic of pristine forest and secondary forest in different stages of restoration, with a total protected area of 7000ha. At its northern limit, this reserve connects with the Serra dos Órgãos National Park and the Três Picos State Park to form one of the biggest remnants of Atlantic Forest in Brazil (Ribeiro *et al.* 2009). This is a very strategic region for biodiversity conservation (Jenkins *et al.* 2010), as it exhibits high levels of species richness for many taxonomic groups, such as pholcid spiders (it is the locality with most species recorded worldwide) (Huber & Rheims 2011), amphibians, reptiles (Almeida-Gomes *et. al.* 2014), birds (Jenkins *et al.* 2013), and mammals (de Carvalho *et al.* 2014; de França Souza *et al.* 2015).

I selected 10 fragments near the reserve for sampling, with areas ranging from 20ha to 243ha. The distance between fragments (measured as a straight line) ranged from 60m to 600m (Table 2.1, Figure 2.3). These focal fragments represent a mixture of primary and secondary forest patches. As with most fragments in the Atlantic Forest, these forest remnants are primarily confined to tops of hills and steep cliffs. As a control, I also sampled in three different sites of primary forest inside REGUA, hereafter referred to as primary sites REGUA 1, 2 and 3 (Figure 2.3). I treat all

fragments and primary sites as independent samples. While it is possible for some bats to commute between locations it is unlikely to influence analyses in this case. First, in the few cases where nocturnal movements of bats have been measured, results range from 50m (Tschapka 2004) to 380m (Heithaus *et al.* 1975) for medium sized-bats such as *C. perspicillata*,. which is smaller than the distance between fragments sampled, suggesting regular daily movement would not lead to community mixing. Second, within REGUA were the sampling sites were connected making passage between viable over time, the sampling was selected to target very different habitats (e.g. large area in old growth-forest, trails near river and streams, area in initial stages of natural restoration) so while they are geographically connected, they represent very independent habitats. Crucially, recapture rates were low with no bat recaptured in a different fragment suggesting minimal community mixing and supporting the independence of the fragments as distinct sites.

I sampled inside each fragment and primary site for six nights, from May 2016 to January 2017. At each site, mist-nets of different lengths (6, 9 and 12 metres) were set along trails, near to streams, and near to flowering or fruiting plants. Nets were monitored continuously from sunset to midnight. I used between seven and 10 nets and aimed for approximately equal sampling intensity at each site, with a combined net effort of 275.940 m^2h (Table 2.1). Each net was moved to a new position every night to reduce the chance of bats learning their positions and avoiding the area.

Bat captures

I checked mist nets every 30 to 45 minutes, depending on bat activity, and I placed each captured bat into an individual cotton bag for two to six hours to give them

time to defecate (see Chapter 4). Pregnant females were processed as quickly as possible to avoid any unnecessary stress. I used field guides for Neotropical (Emmons and Feer 1998) and Brazilian bats (Reis *et. al.* 2007, 2013) to identify each bat in the field. I collected standard measurements (forearm, body length, body mass), gender, age (adult or juvenile based on level of ossification of the knuckle joints) and, for females, reproductive condition (pregnant, lactating, non-reproductive based on the condition of the abdomen and nipples). From each bat, I also collected a tissue sample using a biopsy punch for a subsequent study, and duplicate samples were deposited at the Museu Nacional/UFRJ – RJ, where specialists were consulted whenever there was any doubt about the identification of any individual bat. I stored tissues in silica gel and guano (faecal) pellets from each bat were placed in a separate tube of ethanol and stored at -20°C. Finally, I searched each bat for ectoparasites for at least 90 seconds and, when present, the parasites were preserved in tubes filled with ethanol for a subsequent study.

Landscape metrics

To calculate the landscape characteristics for each fragment and the primary sites of the REGUA forest I used the software packages ArcGIS 10.1 and Fragstats 3.1. I used the ESRI base maps available in ArcGIS and combined these with maps of forest cover obtained from Instituto Brasileiro de Geografia (IBGE). I then extracted all the areas of Atlantic Forest and combined these data with a map of forest remnants obtained from SOS Mata Atlântica (www.sosmataatlantica.com.br). The resulting map containing the remnants of Atlantic Forest in the study area was then exported as a *geotiff* file and imported into Fragstats 3.1.

With Fragstats 3.1 I calculated the following metrics for the selected fragments and REGUA (Table 2.1):

- Fragment area: measured in hectares.
- Perimeter/area ratio (PARA): this is a simple measure of shape complexity that gives the relative amount of forest edge. One of the problems with this index is that holding shape constant, an increase in area leads to smaller values.
- Isolation: this measurement is the shortest (straight line) distance between two forest fragments.
- Proximity index: this index considers the size and distance of all fragments of the same category that have edges inside a pre-determined buffer (Gustafson and Parker, 1992). It has a value of zero when no fragment of the same category is inside of the buffer zone and it increases with fragment area, proximity and contiguity in the neighbouring area of the focal point. I used a radius of 500m and 1000m to calculate this index. These values were selected based on empirical data on flight distance in the captured species. For example, the longest distance that the same individual of *Carollia perspicillata* was captured within the same night was 380m (Heithaus *et al.* 1975), and Teixeira et al. (2014) used 400m as a proxy for the maximum distance that an individual could fly without needing to stop. I decided to increase this value to 500m to account for differences among all the small species of bats. Since larger bats may move further (e.g. *Artibeus spp*.) I also used a second buffer of 1000m.
- Forest cover: This is a measure of the proportion of the landscape that corresponds to Atlantic Forest inside a pre-determined buffer area. I used

the same two radius sizes from the proximity index (500m and 1000m) to determine the forest cover of a given point.

- Distance to source area: this is measured as a straight line from a focal point of a fragment to the nearest point of contiguous forest at REGUA. Data were obtained from Delciellos *et al.* (2016).

To choose among these metrics, and reduce variable collinearity, I first performed a correlation analysis and identified the least correlated variables (Table 2.2). On this basis I chose variables for this dataset: fragment area and isolation.

To select measurements of habitat structure I followed Delciellos *et al.* (2016). Nine habitat variables (overstory vertical vegetation density, understory horizontal vegetation density, predominant tree size, presence of water courses, *Cecropia* trees, lianas, grasses or bamboos, palms of *Astrocaryum aculeatissimum* and number of fallen logs) were combined and reduced to two components using a PCA with the function *prcomp* in R v. 3.4.1 (R Development Core Team 2018). For more details on how these measurements were obtained, see Delciellos *et al*. (2016). The first principal component (PCAhab1) showed positive associations with the abundance of grasses, *Astrocaryum* and *Cecropia* trees, and a negative association with the abundance of lianas. The second component (PCAhab2) was associated positively with watercourses and increased overstory, understory and fallen logs (Table 2.1, Figure 2.4).

Phylogenetic diversity

For each fragment and primary site in REGUA I calculated the phylogenetic diversity (PD) of the sampled bat community following Faith (1992). Phylogenetic

diversity represents the total amount of evolutionary history in the assemblage and is calculated as the sum of all branch length from the species phylogenetic tree (Faith 1992). To do this I used the function *pd* of the package *picante* (Kembel *et al.* 2010) in R v.1.4.1 (R Development Core Team 2018). To extract branch length information I used the topology of the Chiroptera supertree published by Shi and Rabosky (2015). To eliminate the taxa not present in our study I used the function *treedata* from the package *ape* (Paradis *et al.* 2004; Popescu *et al.* 2012) for R v.1.4.1 (R Development Core Team 2018); this yielded a tree with 24 species. As the two species *Dermanura cinerea* and *Histiotus velatus* were not present in the published phylogeny, these were excluded from this analysis.

Mean pairwise distance

I also calculated the phylogenetic mean pairwise distance (MPD) among all the species in each fragment or primary site, also using the function *pd* in the *picante* package (Kembel *et al.* 2010) in R v.3.4.1 (R Development Core Team 2018). MPD is an average of the phylogenetic distance between all the pairs of species and can be used as a proxy for how phylogenetically different one assemblage is from another (Webb *et al.* 2002). MPD was measured from a distance matrix obtained from the Shi and Rabosky (2015) chiropteran supertree. For this analysis, I included the same species as used for calculating PD.

Functional diversity

Functional diversity (FD) is a measure of how different assemblages are in terms of functional traits and may include intrinsic measures (e.g. body mass) and

extrinsic measures of ecological function (e.g. roosting preferences). To calculate functional diversity, I used mean body mass and mean forearm length from my capture data. From the literature I obtained information about the number of roost categories used (trees, rocks/caves, leaf tents, and human-made structures), the total mandibular length, and the main diet (insectivore, frugivorous, vampire, nectar-feeding, omnivore). I built a distance matrix from the data obtained, with the function *cophenetic* from the package *vegan* (Oksanen *et al.* 2013) for R v.1.4.1 (R Core team 2018). I transformed this distance matrix in a functional tree using the function *as.phylo* from package *ape* (Paradis *et al.* 2004; Popescu *et al.* 2012) for R v.3.4.1 (R Development Core Team 2018). Functional diversity can be measured in an analogous way to phylogenetic diversity, but with the branch length corresponding to the functional distance between two sister taxa. I used the function *pd* from the *picante* (Kembel *et al.* 2010) package to calculate the functional diversity for each bat assemblage in this study *(Kembel et al*. 2010; Cadotte and Davies 2016).

Statistical analysis

To characterise community structure, I performed an elements of metacommunity structure (EMS) analysis following Leibold *et al*. (2004). This approach makes no assumptions about the underlying mechanisms that contribute to a given community structure. I used the function *Metacommunity* from the package *metacom* (Dallas 2014) for R v. 1.4.1 (R Development Core Team 2018). This is a hierarchical analysis (Figure 2.1) and the result in each step defines one type of theoretical metacommunity structure. It uses a presence/absence matrix of species in all the areas sampled. This matrix is ordered through reciprocal averaging to maximise

sites with similar species composition and species with similar distributions are adjacent in the occurrence matrix. The primary axis presents the best ordering possible, while the second axis shows the second best ordination, uncorrelated with the primary axis (Presley *et al.* 2009). The steps of EMS are as follows: In the first step I investigated the coherence of the metacommunity. Coherence – which describes the extent to which a species' distribution is continuous - is calculated by examining the number of embedded absences in species ranges in our matrix, with negative values of coherence indicating a checkerboard structure, and non-significant coherence indicating a random structure. If significant positive coherence is detected, then the turnover of species can be investigated. Turnover is the tendency of one species to be substituted by another over the landscape, in this case among patches of forest. Significant negative values of turnover indicate a nested structure, non-significant negative values indicate a quasi-nested structure, and significant positive values of turnover leads to the third step of the analysis. Boundary clumping describes the extent to which species are co-distributed within the metacommunity. For example, if multiple species respond to the same environmental gradient, then it is expected that they will occupy the same habitat patches and thus overlap in their distributions. The Morisita's index is used to determine if the distributions are clumped. Negative values indicate evenly-spaced distributions, while positive values indicate a Clementsian structure, where distinct communities substitute for each other along a gradient. Non-significant values are related to Gleasonian structure in which the metacommunity is composed of distinct communities that change at random along a gradient (Leibold *et al.* 2004; Presley *et al.* 2009). Boundary clumping can also be used to identify the pattern of species loss in nested subsets, with negative values corresponding to hyperdispersed species loss (i.e. species' distribution ranges within the

metacommunity are different), non-significant values corresponds to random species loss and positive values to clumped species loss (species' distribution range within the metacommunity are aggregated) (Presley *et al.* 2010) (Figure 2.1).

I calculated the elements of metacommunity structure for several different meta-ensembles using the package *metacom* (Dallas 2014) for R vers 3.4.1. (R Development Core Team 2018), These meta-ensembles are as follows:

- All bats;
- Phyllostomidae – As mist nets are biased towards captures of phyllostomids (Bergallo *et al.* 2003), I excluded all non-phyllostomids from the database. If bats from other families are not well sampled, these absences may affect the calculations of the elements of metacommunity structure;
- Plantivores and animalivorous (see General Introduction, Chapter 1 for a description of these guilds) – different guilds may respond differently to environmental gradients and these differences may confound the results of EMS. To address this, I separated the bats of these two guilds, and tested the responses of each one.
- I also calculated the EMS for the whole metacommunity but excluding species that occurred in only one fragment or primary forest site.

For the metacommunity or meta-ensemble that presented a non-random structure I tested the correlation between species metacommunity and meta-ensembles with landscape and habitat metrics using constrained correspondence analysis (CCA). In this analysis the incidence matrix is ordered in the same way as in the EMS analysis, and I used the landscape variables and principal components to determine the association of these factors with the metacommunity/meta-ensemble

structure. I used the function *cca* on package *vegan* for R *v3.4.1* (Oksanen *et al.* 2013), and selected the combination of variables that performed better using the function *step* to add variables starting from the simplest model (no covariates) to the most complex model, and comparing them using the Akaike information criterion (AIC) (Presley *et al.* 2009; Oksanen *et al.* 2013; Cisneros *et al.* 2015).

To test for drivers of community structure I considered extrinsic landscape and fragment characteristics, and intrinsic factors (phylogenetic diversity, PD, mean pairwise distance, MPD, functional diversity, FD). To test the significance of observed PD, MPD and FD, values I used the function *ses.pd* and *ses.mpd* in the package *picante* (Kembel *et al.* 2010) in R v.3.4.1 (R Development Core team 2018). This method compares the observed value with the expected value under a null model with 10, 000 repetitions that keeps row totals constant and it is believed to minimize the chance of type 1 error (Kembel *et al.* 2010). Positive z values and high quantiles ($p>0.95$) indicate phylogenetic evenness or a greater phylogenetic distance between species than expected by chance. Negative z values and low quantiles ($p<0.05$) indicate phylogenetic clustering or smaller phylogenetic distance between species than expected by chance (Kembel *et al.* 2010).

To test whether there is a correlation between PD, MPD, FD and landscape or habitat complexity, I performed a linear regression between the independent variables (PD, MPD and FD) and area, isolation and the first and second principal components of habitat structure. I built models in an additive manner, starting with the simplest model (no covariate) to the most complex model (all covariates) using the function *step* in R v.3.4.1 (R Development Core Team 2018). I used the Akaike Information Criterion (AIC) to select the best fit model. I considered the models statistically

significant if the p-value ≤ 0.05. Due to the large difference in area between the primary forest sites (REGUA1, REGUA2 and REGUA3) and the fragments, I also performed the same linear regression analysis without the three primary sites.

Results

Bat captures

In 78 trap nights I captured 988 bats from 26 species. Phyllostomidae was the most speciose and abundant family in my study area. *Carollia perspicillata* was the most abundant species, with a total of 382 captures, or 38.6% of the total captures (Table 2.3). *Chiroderma doriae, Micronycteris minuta, Tonatia bidens* and *Trachops cirrhosus* were captured only once across all sites. Fragment F5 had the lowest capture rate, with only 19 captures from 7 species. In contrast, F8 had the highest capture rate with 133 captures from 11 different species. The control site REGUA1 had the highest species richness with 15 species recorded, and fragment F1 had the lowest species richness with only 6 species (Table 2.3).

Four species were sampled across all fragments and primary sites: *Artibeus lituratus*, *Artibeus obscurus*, *C. perspicillata* and *Sturnira lilium*. Seven species were captured in only one fragment or primary site: *C. doriae* (REGUA2), *H. velatus* (F6), *M. minuta* (F8), *Peropteryx macrotis* (F8), *T. cirrhosis* (F10), *Pygoderma bilabiatum* (REGUA1) and *T. bidens* (REGUA1).

Elements of metacommunity structure (EMS) and predictors of metacommunity structure

All bats

The metacommunity based on all bats returned a non-significant coherence score (z = 1.84, p=0.06), indicating a random structure for the first axis of ordination.

At the second axis of ordination, coherence was also non-significant (z = -0.11, p= 0.9) and the metacommunity structure was thus random (Table 2.4).

Removing species with single occurrence

If I exclude the seven species that were recorded in only one site from the full dataset, coherence was positive and non-significant for the first axis (z = 0.47, p = 0.63) and negative and non-significant for the second axis (z = -0.89, p = 0.4). On both axes this meta-ensemble follows a random structure (Table 2.4).

Phyllostomidae: The dominant bat family

When only members of the Phyllostomidae were included in the analysis, coherence was positive and significant (z = 2.12, p = 0.03), turnover was negative and significant (z = -2.6, p = 0.009), and boundary clumping was positive and significant (z = 1.93, p = 0.01). The metacommunity thus follows a nested structured with clumped species loss on the first axis of ordination and a random structure on the second axis (Table 2.4). For this meta-ensemble, the constrained correlation analysis recovered a gradient of fragment area, with smaller fragments being subsets of the larger areas (Figure 2.5a).

Plantivores: Species consuming nectar, fruit and pollen

Plantivores presented non-significant scores of coherence (z = 1.19, p = 0.23), indicating a random structure for the herbivore meta-ensemble (Table 2.4). The second axis of ordination also returned non-significant scores of coherence (z = 0.74, p = 0.45), with the metacommunity structure on the second axis also random.

Animalivorous: Species that consume arthropods and small vertebrates

When only the animalivorous bats were considered, on the first axis of ordination coherence was positive and significant (z = 1.9, p = 0.5), turnover was negative but non-significant (z = -0.99, p = 0.72) and boundary clumping was significant and positive (z = 1.86, p = 0.008). These values correspond to a quasi-nested structure with clumped species loss. On the second axis of ordination, the animalivorous meta-ensemble follows a random structure (Table 2.4). For this meta-ensemble the constrained correlation analysis recovered a gradient along the fragment area, with smaller fragments being subsets of the larger areas (Figure 2.5b).

Species assembly

To test the drivers of community assembly I considered extrinsic landscape and forest characteristics, and intrinsic factors relating to phylogenetic diversity and functional diversity. Functional diversity was not different from values expected in a random assemblage, for all sampled areas (Table 2.5), and was not correlated with any of the explanatory variables (Table 2.8). Phylogenetic diversity also showed no deviation from random expectations for most of the sites, with the exception of REGUA1 and REGUA2, both of which had significantly lower PD than expected from random null models (Table 2.6). Phylogenetic diversity was not correlated with any of the explanatory variables used (Table 2.8). Mean pairwise distance was significantly lower than random values in REGUA1 and REGUA2, while all other areas show no significant difference from random models (Table 2.7). The best-fit linear model shows that MPD values were significantly negatively correlated with fragment area ($R^2 = 0.42$, p = 0.01) (Table 2.8, Figure 2.6). This relationship is lost when I remove the sites inside the reserve (Table 2.8).

The species assembly process appears to be random for most of the areas, including all the fragments. The only areas that presented scores different from random were REGUA1 and REGUA2, with a combination of significantly lower values of PD and MPD than expected by chance (REGUA1: PD = 332.14, z = -3.4, p = 0.007; MPD = 54.55, z = -3.11, p = 0.004. REGUA2: PD = 223.11, z = -3.23, p = 0.002; MPD = 50.32, z = -2.7, p = 0.004) (Tables 2.5 and 2.6), indicating an environmental filter in action, leading to phylogenetically clustered communities.

Discussion

The objective of my study was to apply metacommunity analyses to determine whether bats in fragmented habitats of the Brazilian Atlantic Forest are arranged in communities that follow a predictable structure. I then tested the role of functional diversity, phylogenetic diversity and landscape features to assess the potential drivers of community assembly. The combination of these two methods allow inferences on local processes that drive species assembly and the metacommunity structure that arise from these local processes. If we want to prevent biodiversity loss and maintain critical ecological services, it is paramount to understand how metacommunity structure is shaped by ecological and evolutionary processes and how these are affected by landscape change.

My data suggest that the bat metacommunity of the Guapiaçú Basin has a random structure, as does the meta-ensemble containing only herbivores. In contrast, the Phyllostomidae and animalivorous meta-ensembles have nested and quasi-nested structures respectively, in which the communities found in smaller fragments are composed of a subset of the taxa that occur in larger fragments or primary sites in REGUA. Occupancy estimates can be used to calculate the probability of a certain metacommunity structure being actually detected given certain occurrence data (Mihaljevic *et al.* 2009), but occupancy estimates in communities with high rates of rare species are often not reliable (Banks-Leite *et al.* 2014) and can add unwanted uncertainty, which is the case in this study (Chapter 3) thus I do not employ occupancy estimates here. These communities have a core of four abundant and widespread species that occur in all sites sampled: *Carollia perspicillata*, *Artibeus lituratus*,

Artibeus obscurus and *Sturnira lilium.* All four are common Neotropical phyllostomid species and in many inventories are the most abundant species found in the Atlantic Forest (Muylaert *et al.* 2017). The diet of all four species is mostly frugivorous and they are considered important seed dispersers. Another well-known characteristic of these species is that they are very tolerant to disturbance, occurring in a range of habitats, from well-preserved primary forest to disturbed areas (Emmons and Feer, 1997, Reis *et al*. 2013).

The data also suggest that when habitat area decreases the assembly process is driven by stochastic events but when the habitat area is large it is driven by environmental filtering with ancestral traits of bat species enabling survival and leading to phylogenetically clustered communities (Figure 2.2). All the fragments returned values that were not different than expected from random, while REGUA1 and REGUA2 had values of PD and MPD lower than expected from random. In the larger primary sites in REGUA it is likely that the high availability of resources leads to communities that are composed of many more species, which are closely related but, in accordance with niche theory, which show at least small differences in their functional use of niches to avoid competitive exclusion (Pianka 1974; McInerny & Etienne 2012). The phylogenetic clustering found in REGUA could be related to the high richness of phyllostomids, generating low MPD and PD values, but if it was the case, random values should have been low as well and REGUA and REGUA2 would not differ from them. In small areas with fewer resources only a subset of these closely related species exists, and thus small fragments contain only a subset of the communities found in larger fragments. This can be illustrated by the species from the subfamily Stenodermatinae. In the fragments below 100 ha, I recorded four to five species of Stenodermatinae bats, while in the fragments larger than 100 ha, I found at

least five species of Stenodermatinae, with eight Stenodermatinae bats registered at REGUA 2, which is nearest to intact Atlantic Forest to the west of the study region. This pattern is repeated for every genus or family that I examined. One could argue that the coexistence of fewer species in smaller areas is evidence of competition, but the random FD, PD and MPD values in these fragments indicate that with the reduction in area the pattern of species assembly begins to break down and is driven by stochastic events of birth/death and colonization/extinction, as described in the NT archetype. Even though the results did not capture any effect on FD, this may reflect the data available for this analysis which may not encompass all the aspects of bat morphology and ecology needed to differentiate these species functional space. Including information on wing morphology such as wing loading and wing tip index, which are related to how bats manoeuvre and use their niche space, may change this scenario.

One of the most difficult aspects of measuring community assembly is to establish an appropriate scale for analysis (Meynard *et al.* 2013). For example, among the Chiroptera some species may migrate very long distances or commute over landscapes in a single night, while other species travel only very short distances from their natal roost throughout their lives. My study was conducted on a smaller scale than many other cases where elements of metacommunity structure (EMS) have been used to assess metacommunity structure. At this regional scale (this study), the abiotic conditions (i.e. climate, precipitation, seasonality) are much more similar than at larger scales (e.g. the Caribbean). This may result in random distributions, particularly among species that can forage over longer distances, when in larger scales would show distinct patterns (Presley & Willig 2010). In a study of the effects of fragmentation on small mammals in the Atlantic Forest, the metacommunity presented a

Clementsian structure (de la Sancha *et al.* 2014), with the different compartments in this metacommunity corresponding to the centres of endemism of the Atlantic Forest (Costa *et al.* 2000; Silva *et al.* 2004), although the structure within the Clementsian compartments of the metacommunity was not assessed (de la Sancha *et al.* 2014). This study suggests that even in face of severe habitat loss and fragmentation, the rodents still occupy habitats that follow their historical biogeographic distribution. Given that most studies have focused on broad geographic scales, it is interesting that our study shows that fragmentation even at small spatial scales can lead to disruption in the species assembly process.

Here I show that the Phyllostomidae and animalivorous meta-ensembles are characterised by nested and quasi-nested structures, and this might be explained by their tolerance to disturbance and dispersal ability between forest patches (Kadmon 1995; Esbérard *et al.* 2017). This pattern is consistent with the prediction of fragmentation studies and species-area relationships, where large areas are expected to harbour more species than smaller fragments (McGuinness 1984; Laurance *et al.* 2002) and with an experiment involving bat communities in a complex of islands inside an artificial lake in Panama, where it was observed that the small island bat communities are a subset of the communities in bigger islands and mainland forested areas (Meyer 2007). In my case, forest fragments may act very much like islands.

In this study, I observed that the functional diversity of the communities was not different than random expectations. In REGUA however, phylogenetic diversity and mean pairwise phylogenetic distances are significantly lower than expected by chance. FD and PD were not correlated to any of the explanatory variables, however, mean pairwise phylogenetic distance (MPD) was found to be significantly and negatively correlated with fragment area. This trend suggests that more closely related

species are found in larger areas, a finding that is consistent with the hypothesis that larger patches of forest have less resource limitation, making it possible for more similar species to co-exist without leading to competitive exclusion. This is also consistent with the hypothesis of niche theory (Levin 1970; McInerny & Etienne 2012), as small fragments may not have enough resources to sustain many similar species (Laurance *et al.* 2002; Haddad *et al.* 2015). However, this pattern is clearly driven by the REGUA primary sites and when they are removed the pattern is no longer significant. It may be that sampling of fragments of more intermediate size would support the trend, or that there exists a tipping point where this relationship ceases to exist. In my analysis I treat REGUA 1, 2 and 3 as independent sampling units based on distinct differences in the surrounding habitat that likely attract different species and because I visited them at discrete times of the year. However, while it is very unlikely the same individuals were caught in the three sites, it is possible that the communities share members (as might closely located fragments) and are thus not truly independent. For this reason, while I have treated these communities as independent data points, the conclusion around MPD should be treated cautiously. Although I did not observe the expected pattern of functional diversity, MPD, in accordance with the niche conservatism theory (Wiens *et al.* 2010), could be used as a proxy for how different species' niches are across sites if niches are inherited from an ancestor and thus closely related species are expected to share similar functional traits. A study examining the effect of fragmentation on phylogenetic diversity of trees from the Atlantic Forest found that forest fragment size was the most important variable to predict phylogenetic diversity (Matos *et al.* 2017). This is consistent with my finding that MPD was correlated to fragment area.

The NT archetype explains many metacommunity patterns and processes, and my results of random bat metacommunity structure and the breakdown of species assembly in fragments can be understood under this framework. In turn, the nested and quasi-nested metacommunity structure of Phyllostomid and animalivorous bats can be understood with the Patch Dynamics archetype. As at this scale habitat patches are more or less homogeneous in character and as species differ in their colonization and extinction rates, we would hypothesise that larger areas would have more species due to species area relationships. To understand metacommunity dynamics in their totality, we should examine local processes, regional patterns and use the four metacommunity archetypes to describe the metacommunity phenomena. One example is a meta-analysis of the importance of environmental and spatial processes concluded that although the SS archetype was the most common one in real metacommunities, a combination of SS + ME and NT+PD theory can explain metacommunities that don't fall into the SS archetype (Leibold & Chase 2018).

The lack of a clear pattern of species assembly in the fragments among non-phyllostomid bats provides evidence that small and isolated fragments in general do not support biodiverse communities. Despite this, I did detect the presence of several more sensitive species, including *T. cirrhosus*, *P. macrotis* and *H. velatus* in fragments of different sizes. These findings imply that even small fragments may provide the specific habitat requirements to support some bats of conservation concern, and thus may hold conservation value for the Atlantic Forest, even though they are not as species-rich as are the large protected areas. In the case of some resource specialists, patch size *per se* may not be as important as the presence of specific landscape characteristics (e.g. rivers, caves). In general, maintaining existing fragments, increasing the forested area and bridging the gaps between these fragments should

be a conservation priority, in addition to expanding the large protected areas where possible.

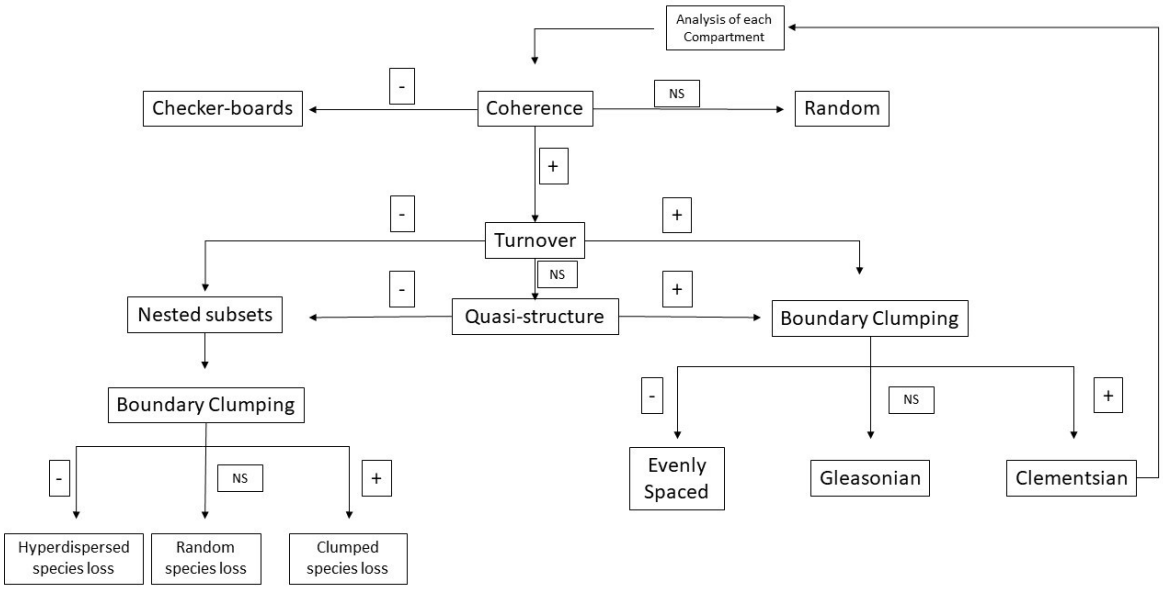


Figure 2.1: A diagram showing the steps of elements of metacommunity structure analysis (modified from Presley, Higgins, & Willig (2010)). At each step (coherence turnover and boundary clumping) the presence of a negative, non-significant or positive value determines the next analysis step in the hierarchical analysis. For example, a positive coherance outcome is followed by a test of turnover, which in turn leads to an analysis of nestedness or boundary clumping.

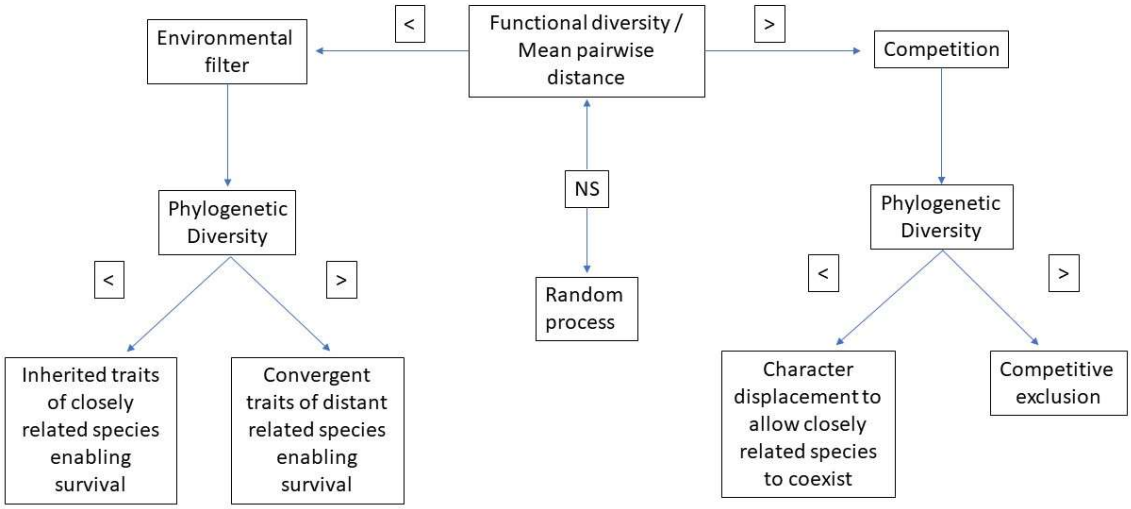


Figure 2.2: A decision tree of factors that may explain the observed metacommunity structure. In this case > indicates a value that is greater than expected by chance while < indicates a value that is lower than expected by chance. You start looking at the functional diversity (or mean pairwise distance, used here as a proxy for how functionally diverse communities are) to differentiate between competition and environmental filters. A second step is to examine the phylogenetic diverse to understand if communities are closely related or not.

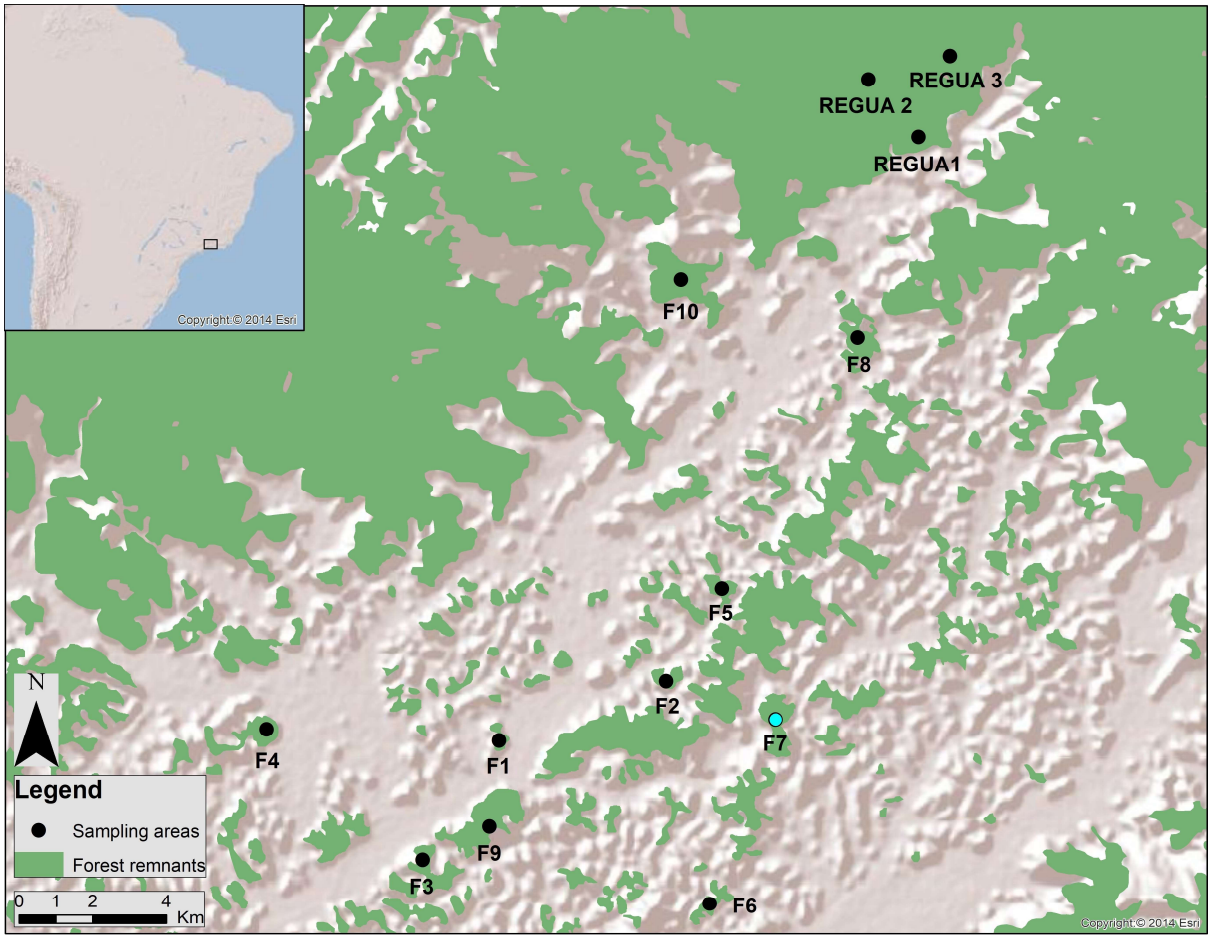


Figure 2.3: Map of study area in Cachoeiras de Macacú Municipality, Rio de Janeiro state, Brazil. F1 to F10 correspond to forest fragments sampled and REGUA 1,2 and 3 are the sites sampled inside the Reserva Ecológica de Guapiaçú. The inset shows the study area in South America map.

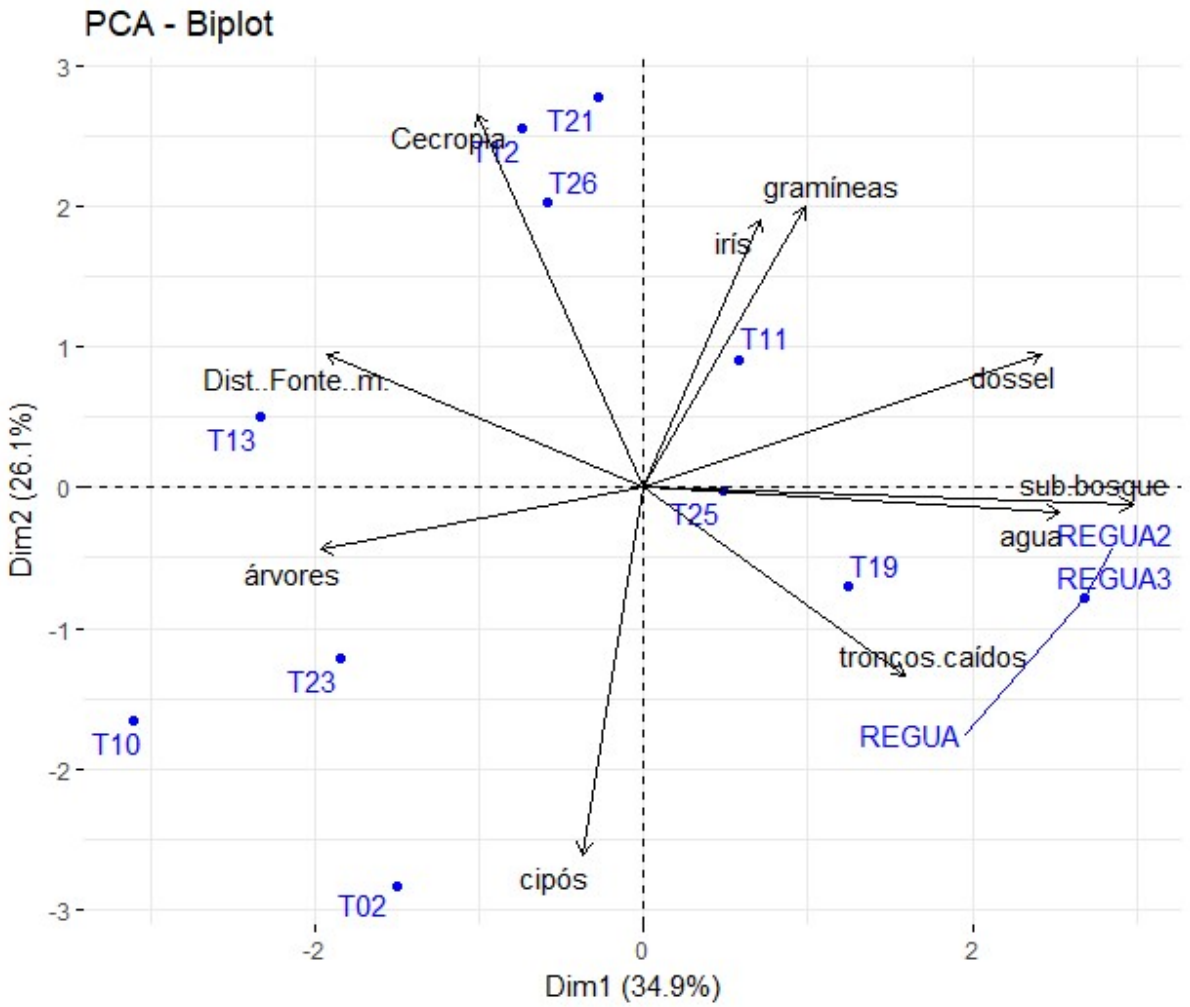


Figure 2.4: Principal Component Analysis of habitat structure in the study area. PCAhab1 has a positive association with grasses, *Cecropia* and *Astrocaryum* trees and negative association with lianas and fallen logs. PCAhab2 has positive association with watercourses and increased overstory and understory and negative association with large trees.

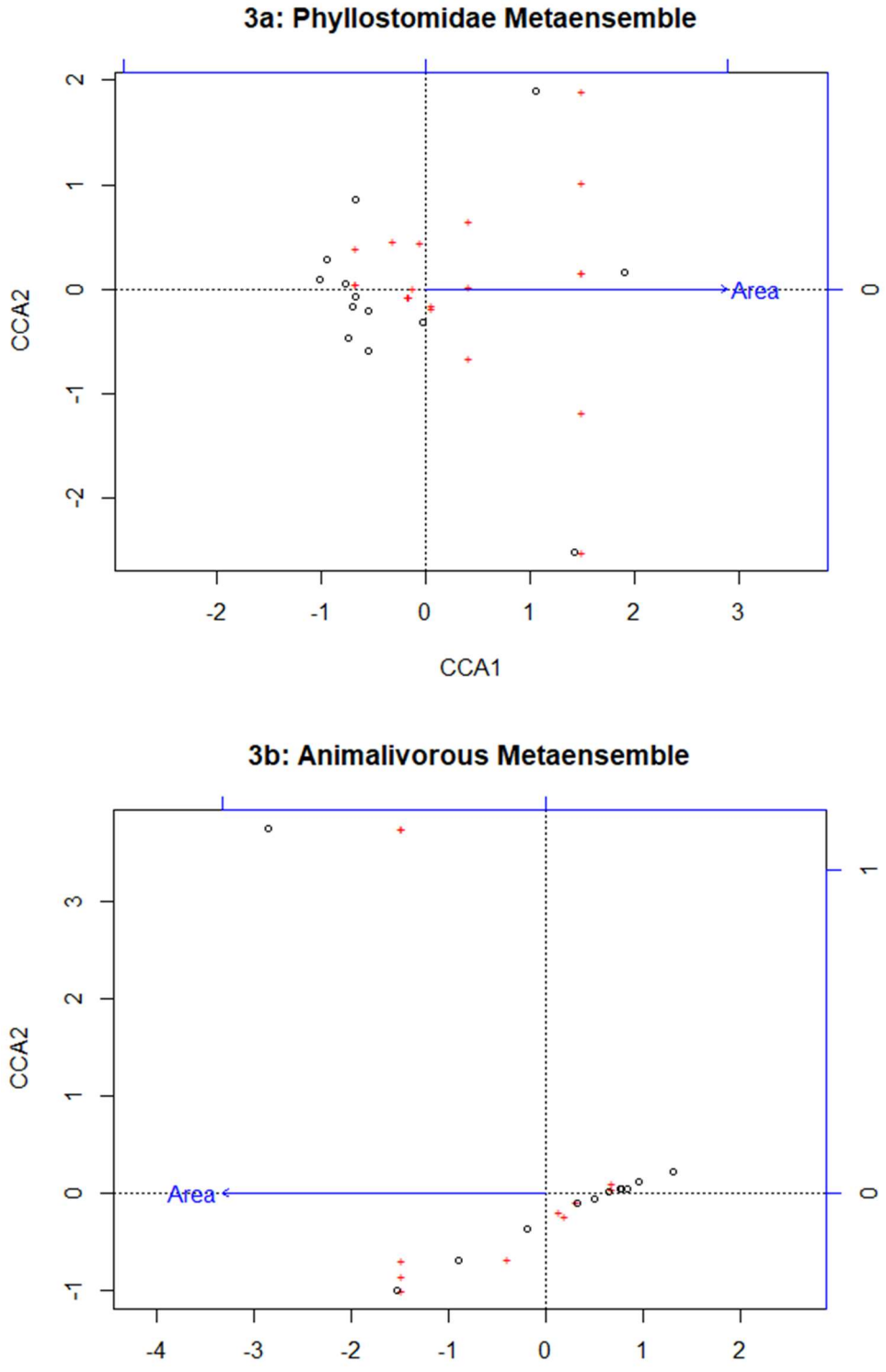


Figure 2.5: Biplot showing the constrained correlation analysis (CCA) results. 2.5a: CCA for the Phyllostomidae meta-ensemble; 2.5b: CCA for the Animalivorous meta-ensemble. Black circles correspond to site scores and red crosses to species scores. Both ensembles are correlated with fragment area.

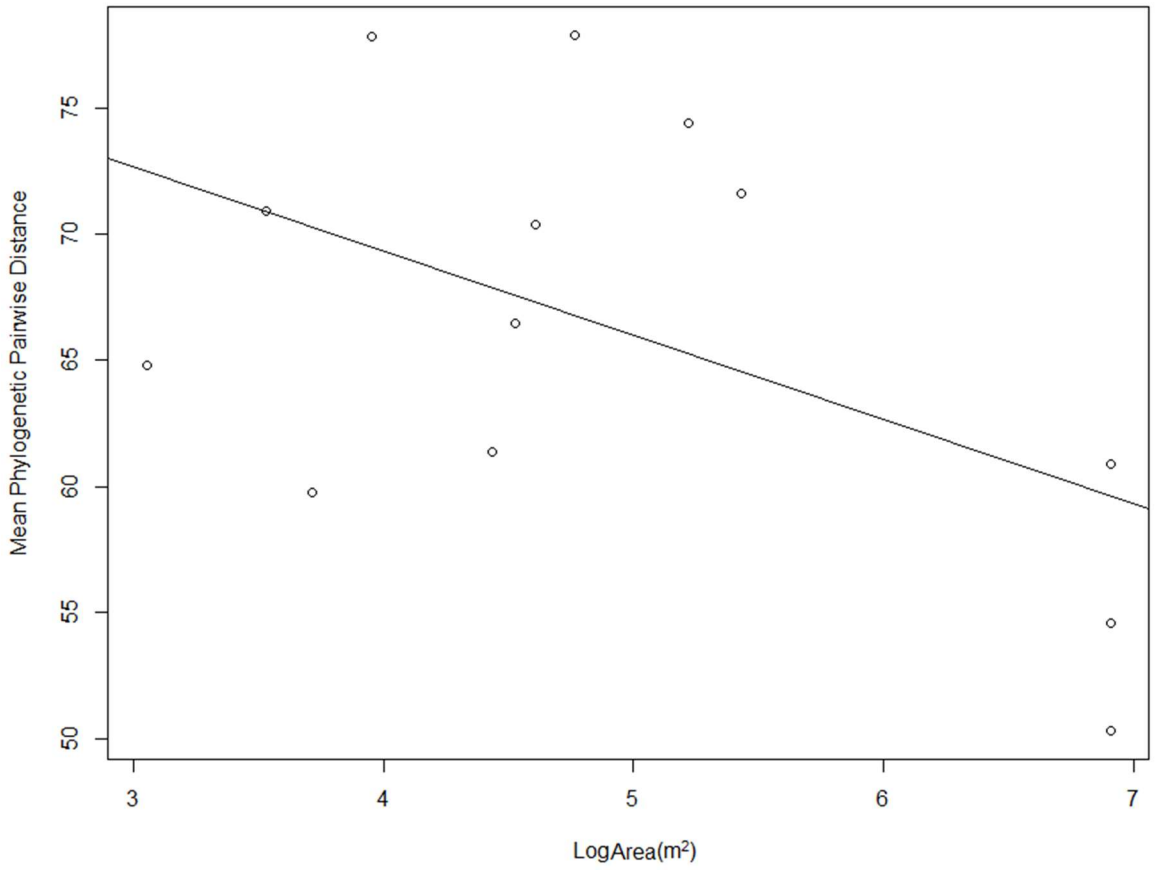


Figure 2.6: Mean pairwise phylogenetic distance x log Area (R^2 = 0.42, p = 0.01). MPD is negative related with fragment area. In larger areas communities are composed by species that are in average more closely related than in small fragments. This relationship diseappears when REGUA 1,2 and 3 are removed.

Box 1: Metacommunity Archetypes

Neutral Theory (*NT*): Based on the ideas of Hubbell (Hubbell 2001), the Neutral Theory archetype assumes that stochastic events of birth/death rates and stochastic events of colonization/extinction largely overcome any effect of speciation and niche or habitat heterogeneity. Species from a regional pool and habitats are practically indifferent and metacommunity composition and structure are product of stochastic events of local colonization and extinction.

+ Stochastic drift

- Niche selection, dispersal

Species Sorting (*SS*): This archetype emphasise in niche selection and species interactions, with little importance given to stochastic drift and dispersal. This is a niche-based approach and it considers that species coexistence is mediated by trade-offs in species abilities to exploit and colonise different habitats. You can understand this archetype as “species can reach everywhere, and the habitat selects those that can survive in it” (Leibold & Chase 2018).

+ Niche selection

- Stochastic drift, dispersal

Patch Dynamics: In this archetype habitat patches have homogeneous conditions. Species have different traits and colonization abilities, but these are not affected by the habitat and population persistence in the patches are driven by stochastic events (i.e. birth and mortality rates, disturbances). Events of local

extinction of superior competitors allow inferior competitors to survive in patches of homogeneous habitats

+ Niche selection (trait heterogeneity), stochastic drift, dispersal

- Niche selection (habitat heterogeneity)

Mass Effects (*ME*): In this archetype species have different life-traits and dispersal abilities. Habitat is heterogeneous and species have different fitness in different habitat types. Species coexistence occurs in a source-sink dynamics, where dispersal from more suitable habitats allows the persistence of an inferior competitor in a suboptimal habitat.

+ Niche selection, dispersal

- Stochastic drift

Box 2: Metacommunity structures as defined by Leibold & Mikkelson (2002) and Presley *et al.* (2010).

Checkerboards distributions: This structured is characterized by pairs of species that do not co-occur (i.e. mutually exclusive distributions), with different pairs of species being independently distributed (Leibold & Mikkelson 2002) . This pattern is based on the observations of Diamond (1975) and it is determined by significant negative coherence scores (Leibold & Mikkelson 2002).

Nested subsets: Species poor communities are a subset of species rich communities. This structure was first described by Patterson & Atmar (1986) and it is determined by significant positive values of coherence and significant negative turnover (Leibold & Mikkelson 2002). Presley *et al.* (2010) expanded the understanding of nested subsets using boundary clumping to distinguish between 3 patterns of species loss – clumped species loss (significant positive boundary clumping), stochastic species loss (non-significant boundary clumping) and hyperdispersed species loss (significant negative boundary clumping).

Clementsian structure: Distinct communities that substitute each other along an environmental gradient. This structure is based on the ideas proposed by Clements (1916) and it can be determined by significant positive values of coherence, turnover and boundary clumping (Leibold & Mikkelson 2002).

Gleasonian structure: Species show specific responses to an environmental gradient, resulting in a random structure with high turnover. This structure is based on the ideas proposed by Gleason (1926) and can be identified by significant positive coherence and turnover and non-significant positive boundary clumping (Leibold & Mikkelson 2002).

Evenly spaced distributions: No discrete community can be identified, but species distribution along an environmental gradient are more evenly distributed than expected by chance. This structure is characterized by significant positive coherence and turnover while presenting significant negative values of boundary clumping (Leibold & Mikkelson 2002).

Quasi-structures: According to the expanded EMS framework proposed by Presley *et. al* (2010) each of the 4 main structures have an equivalent quasi structured where turnover is not significantly different from random, but with a structure still consistent with the conceptual background of Clementsian, evenly spaced distribution, Gleasonian and nested subsets structures.

Table 2.1: Landscape metrics calculated for each fragment and the REGUA control sites.

Fragment code	Lat	Long	Area	Isolation	PARA	Forest cover (500m)	Proximity index (500m)	forest cover (1000m)	Proximity index (1000m)	PCAhab1	PCAhab2	Distance to source (m)	Sampling effort (m^2.h)
REGUA	-22.43	-42.70	62378.64	60	19.02	92.09	112485	68.11	112494	-3.12	0.75	0	26460
REGUA2	-22.41	-42.76	62378.64	60	19.02	100	112485	100	112494	-3.27	0.75	0	22680
REGUA3	-22.40	-42.73	62378.64	60	19.02	100	112485	98.7	112494	-3.27	0.75	0	22680
F1	-22.56	-42.85	21.15	600	139.0071	29.48	0	6.89	0.16	2.79	-1.94	378	20520
F2	-22.54	-42.81	34.11	234	103.7819	44.918	101.71	18.86	115.13	1.32	1.59	241	19440
F3	-22.58	-42.86	84.33	150	89.6478	53.7	83.577	33.58	83.75	0.82	-0.49	129	19440
F4	-22.55	-42.90	92.34	210	96.8161	68.63	2.32	20.97	3.35	0.75	2.72	126	22680
F5	-22.52	-42.79	41.04	85	99.41	52.82	114.52	33.38	114.68	0.82	-0.87	192	19440
F6	-22.59	-42.79	52.11	362	120.8981	45.29	0.45	17.43	1.0424	1.79	1.17	91	20520
F7	-22.55	-42.78	99.99	350	72.6	71.01	40.72	32.26	41.35	0.69	-2.67	302	19440
F8	-22.47	-42.76	117.27	134	93.63	76.78	4266.11	37.89	4266	0.37	0.67	468	24300
F9	-22.58	-42.85	184.77	175	63.322	76.28	27.55	51.54	38.52	0.12	-2.44	126	18900
F10	-22.45	-42.80	228.78	480	54.5502	98.74	2707	59.02	2707	0.19	0.02	544	19440

Table 2.2: Correlation between landscape metrics.

	Area (ha)	Isolation (m)	Perimeter (m)	PARA	Forest cover	Proximity index	Forest cover	Proximity index
Area	1.00	-0.59	0.98	-0.96	0.97	0.73	0.92	0.72
Isolation	-0.59	1.00	-0.64	0.62	-0.59	-0.77	-0.73	-0.74
Perimeter	0.98	-0.64	1.00	-0.94	0.95	0.74	0.94	0.73
PARA	-0.96	0.62	-0.94	1.00	-0.94	-0.76	-0.94	-0.75
Forest cover 500	0.97	-0.59	0.95	-0.94	1.00	0.77	0.94	0.76
PROX500	0.73	-0.77	0.74	-0.76	0.77	1.00	0.85	0.99
Forest cover 1000	0.92	-0.73	0.94	-0.94	0.94	0.85	1.00	0.83
PROX1000	0.72	-0.74	0.73	-0.75	0.76	0.99	0.83	1.00

Table 2.3: Species abundance per fragment.

	REGUA1	REGUA2	REGUA3	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Anoura caudifer	0	0	0	0	0	0	0	0	0	2	7	1	0
Anoura geoffroyi	1	0	1	0	0	0	0	0	0	0	10	0	1
Artibeus fimbriatus	7	4	2	0	0	0	0	0	0	0	1	1	1
Artibeus lituratus	21	29	36	17	1	8	7	3	15	27	4	14	8
Artibeus obscurus	6	18	5	1	1	1	1	2	2	12	5	3	6
Carollia perspicillata	24	30	23	50	25	12	10	7	14	60	60	32	35
Chiroderma doriae	0	1	0	0	0	0	0	0	0	0	0	0	0
Dermanura cinerea	0	1	0	0	1	0	0	3	0	1	1	2	0
Desmodus rotundus	10	8	6	0	2	0	1	1	29	4	0	0	11
Diphylla ecaudata	1	1	0	0	0	0	0	0	0	0	0	0	0
Eptesicus brasiliensis	0	0	0	0	1	0	2	0	2	0	0	0	1
Glossophaga soricina	1	1	0	0	0	1	1	0	0	6	18	1	0
Histiotus velatus	0	0	0	0	0	0	0	0	6	0	0	0	0
Micronycteris microtis	1	0	0	0	0	0	0	0	0	0	0	0	1
Micronycteris minuta	0	0	0	0	0	0	0	0	0	0	1	0	0
Myotis nigricans	0	0	2	1	0	2	12	0	4	1	0	1	0
Myotis riparius	0	0	0	0	0	2	6	1	2	1	0	0	1
Peropteryx macrotis	0	0	0	0	0	0	0	0	0	0	6	0	0
Phyllostomus hastatus	1	0	0	0	0	0	0	0	1	5	4	0	0
Platyrrhinus lineatus	0	0	1	0	0	3	2	0	6	2	4	9	0
Pygoderma bilabiatum	3	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	16	2	4	4	6	1	2	2	8	11	11	2	2
Sturnira tildae	1	1	0	1	1	0	1	0	3	1	2	0	1
Tonatia bidens	1	0	0	0	0	0	0	0	0	0	0	0	0
Trachops cirrhosus	0	0	0	0	0	0	0	0	0	0	0	0	1
Vampyressa pusilla	1	14	2	0	0	0	0	0	0	0	0	1	0

Table 2.4: Coherence, turnover, boundary clumping and resulting metacommunity structure. Meta-ensembles with non-random structures are highlighted in blue.

Meta ensembles	Coherence		Turnover		Boundary			
	z	p	z	p	i	p	df	Metacommunity structure
all taxa - 1st axis	1.84	0.06	-2.67	0.007	1.57	0.01	10	Random
all taxa - 2nd axis	-0.11	0.9	-2.78	0.005	1.69	0.004	10	Random
Phyllostomidae - 1st axis	2.12	0.03	-2.6	0.009	1.93	0.014	10	Nested with clumped species loss
Phyllostomidae - 2nd axis	70	0.73	-0.35	0.72	2.22	0.0006	10	Random
Herbivores - 1st axis	1.19	0.23	-0.49	0.62	1.55	0.08	10	Random
Herbivores - 2nd axis	0.74	0.45	-1.02	0.3	2.83	0.0008	10	Random
Animalivorous - 1st axis	1.9	0.05	-0.89	0.37	1.86	0.008	10	Quasi nested with clumped species loss
Animalivorous- 2nd axis	-0.7	0.48	-1.04	0.29	2.01	0.004	10	Random
no single presence - 1st axis	0.47	0.63	-1.75	0.07	1.05	0.37	10	Random
no single presence - 2nd axis	-0.89	0.4	-2.71	0.006	1.35	0.11	10	Random

Table 2.5: Functional diversity calculated for each fragment and the REGUA control sites.

	R	FD	FD random mean	FD z-value	*p*
REGUA	15	1.60	1.40	0.96	*0.78*
REGUA2	12	1.10	1.23	-0.63	*0.37*
REGUA3	10	1.15	1.09	0.28	*0.64*
F1	6	0.72	0.79	-0.37	*0.41*
F2	8	1.01	0.95	0.28	*0.70*
F3	8	0.85	0.95	-0.52	*0.37*
F4	11	1.05	1.17	-0.58	*0.36*
F5	7	1.00	0.87	0.67	*0.76*
F6	12	1.40	1.23	0.81	*0.70*
F7	13	1.48	1.28	0.95	*0.76*
F8	14	1.39	1.34	0.24	*0.51*
F9	11	1.04	1.16	-0.61	*0.37*
F10	12	1.07	1.23	-0.75	*0.31*

Table 2.6: Phylogenetic diversity calculated for each fragment and the REGUA control sites.

	R	PD	PD random mean	PD z-value	*p*
REGUA	15	332.14	428.31	-3.40	*0.007*
REGUA2	12	223.11	332.09	-3.23	*0.002*
REGUA3	10	267.95	307.91	-1.24	*0.112*
F1	6	174.03	199.58	-0.73	*0.278*
F2	8	205.34	228.08	-0.67	*0.252*
F3	8	229.45	255.44	-0.76	*0.196*
F4	11	311.04	332.67	-0.67	*0.219*
F5	7	196.81	199.91	-0.09	*0.365*
F6	12	310.63	332.62	-0.69	*0.212*
F7	13	322.76	356.12	-1.05	*0.122*
F8	14	330.68	381.00	-1.66	*0.052*
F9	11	261.84	308.22	-1.43	*0.099*
F10	12	344.54	358.20	-0.45	*0.302*

Table 2.7: Mean phylogenetic pairwise distance calculated for each fragment and the REGUA control sites.

	Species richness	MPD	MPD random mean	MPD z-value	*p*
REGUA1	15	54.55	71.93	-3.11	*0.004*
REGUA2	11	50.32	71.94	-2.7	*0.004*
REGUA3	10	60.88	72.02	-1.28	*0.103*
F1	6	64.8	71.78	-0.54	*0.298*
F2	7	66.49	71.93	-0.47	*0.261*
F3	8	74.43	71.98	0.23	*0.596*
F4	11	77.92	72.02	0.73	*0.774*
F5	6	70.93	71.93	-0.08	*0.373*
F6	11	77.83	72	0.73	*0.774*
F7	12	70.41	71.94	-0.21	*0.354*
F8	13	61.38	71.93	-1.58	*0.057*
F9	10	59.79	72	-1.41	*0.095*
F10	12	71.62	71.95	-0.05	*0.421*

Table 2.8: Linear regression models for PD, MPD and FD

PD	DF	AIC
no covariate		105.87
PCAhab2	1	107.75
Isolation	1	107.8
log Area	1	107.82
MPD		
log Area	1	51.653
Isolation	1	55.88
no covariate		56.97
PCAhab2	1	58.86
MPD Without REGUA		
no covariate		37.93
log Area	1	38.262
PCAhab2	1	39.66
Isolation	1	39.8
FD		
no covariate		-34.3
Isolation	1	-33.11
log Area	1	-33.1
PCAhab2	1	-32.4

CHAPTER THREE

Habitat structure or landscape configuration as predictors of bat occurrence in a fragmented landscape of Atlantic Forest

ABSTRACT

Habitat fragmentation is the process by which continuous habitat is broken into more isolated units and it is often accompanied by habitat loss. These processes are considered major threats to biodiversity. This process leads to changes in the overall landscape configuration as well as to the habitat structure within the fragments themselves, with increasing “edge effects” thought to have negative impacts on species occurrence. A long-standing challenge in many biodiversity studies is the difficulty of detecting species that are present. In recent years, the development and application of occupancy models in ecology has offered a mathematical framework that accounts for imperfect detection and allows the use of site and observational covariates to estimate the occupancy and detection probabilities at metacommunity and species level. In this study I surveyed and detected the occurrence of bats at 13 sites across a highly fragmented landscape of the Atlantic Forest by conducting six repeated sampling campaigns. Here I use a community occupancy model to estimate species occupancy and detection probabilities across my study site, and specifically, to determine whether species occurrence is better predicted by either landscape configuration (fragment area and isolation) or by habitat structure. My results show

that detection probability of bats is low overall, but with a number of abundant species that are easily detected. Accounting for imperfect detection can reduce the bias in estimates of species occurrence and richness, but in communities with many rare species, the low capture rates do not allow precise estimation of occupancy or covariates parameters. Fragment area had a positive relationship with bats occupancy, but neither single species models or the community occupancy model did not allow precise estimations of the effect of isolation and habitat on bat species in the metacommunity.

Introduction

Habitat loss and fragmentation are some of the many threats to biodiversity caused by human activity (Turner 1996; Haddad *et al.* 2015) and together they can be defined as processes of landscape change where the total habitat area is reduced (habitat loss) (Wiegand *et al.* 2005) and continuous habitats are broken into smaller and more isolated units (fragmentation) (Fahrig 2003). Although some studies try to assess the relative importance of these two processes (Fahrig 1997; Fahrig *et al.* 2019), in the real world habitat loss and fragmentation are often associated (Fletcher *et al.* 2018). Habitat loss can have severe impacts on biodiversity, causing population decline in many species (Bender *et al.* 1998) and loss of unique and important habitat features that may lead to local and regional extinction of species (Cushman 2006). Long-term studies of fragmentation have suggested that not all species respond to disturbance in the same way (Laurance *et al.* 2002; Pfeifer *et al.* 2017), with some species quickly disappearing from small fragments (Wells *et al.* 2007). In some cases, as reported by Gibson *et al.* (2013), habitat fragmentation had an impact on biodiversity so severe that the mammal fauna was nearly extinct 25 years after a severe fragmentation event. Yet despite these extinctions, some species can persist even in the most disturbed habitats (Gorresen & Willig 2004).

Habitat loss and fragmentation are known to change habitat structure inside fragmented areas, and can have contrasting impacts on biological species (Villard *et al.* 1999; Ewers & Didham 2007; Pfeifer *et al.* 2017). This reconfiguration of habitat can lead to the loss of specific habitats required by sensitive species (Sutherland 1996), but increase the amount of degraded habitat, which in turn increases the

abundance of disturbance-loving species in these habitats or the decline of forest specialists (Laurance *et al.* 2002) causing the loss or change of animal functional groups (Ulrich *et al.* 2018), particularly seed dispersers (Galetti *et al.* 2006). Animals are responsible for 60-80% of all seed dispersal events in tropical forests (Traveset *et al.* 2014) heavily influencing the dynamics of natural forest regeneration and restoration (Holl *et al.* 2000). Habitat quality and structure have been shown to be good determinants of non-volant small mammal diversity in the fragmented landscape of the Atlantic Forest (Delciellos *et al.* 2016). In another study, fragment size was shown to be a good predictor of species richness and abundance in small mammal communities, while habitat structure was a better predictor for some individual species in the Atlantic Forest (Pardini *et al.* 2005). Similarly, in south-east Asia, changes in forest structure because of fragmentation and selective logging caused profound changes in bat species assemblages, with a forest specialist species declining both in number and genetic diversity (Struebig *et al.* 2013). Habitat loss and fragmentation are global threats to biodiversity (Haddad *et al.* 2015), and identifying which species are at risk and what factors causes differential species survival is an enormously challenging yet vital aspect of developing effective conservation strategies for the management of biodiversity in modified landscapes (MacKenzie *et al.* 2006; Zipkin *et al.* 2010; Banks-Leite *et al.* 2013).

Many studies use species occurrence (Presley & Willig 2010; Souza *et al.* 2011; Teixeira *et al.* 2014) and species richness (Grelle 2002; Pardini *et al.* 2005; Konopik *et al.* 2015) to direct conservation efforts to protect biodiversity. Yet one serious problem is that a species are not always detected even when present or abundant in a site of interest (MacKenzie *et al.* 2002; Banks-Leite *et al.* 2014). This uncertainty can introduce considerable bias in inferences about species occurrence or species

richness and can lead to ineffective decisions regarding biodiversity management and conservation (MacKenzie *et al.* 2006; Kéry & Royle 2008). To deal with this issue, several methods were developed which address detection uncertainty and one of the most powerful is the occupancy model, developed by MacKenzie *et al.* (2002).

Occupancy can be defined as the proportion of sites occupied by species *k* (MacKenzie *et al.* 2002, 2006), and can be also interpreted as the probability that species *k* occupies site *i* (Kéry & Royle 2016). Occupancy models use the presence and absence of a species over repeated surveys (i.e. sampling occasions) to estimate species occurrence, while accounting for imperfect detection (MacKenzie *et al.* 2002; MacKenzie & Nichols 2004; Zipkin *et al.* 2010; Banks-Leite *et al.* 2014). Although initially developed to be used with single species (MacKenzie *et al.* 2006), later developments expanded the mathematical framework to model entire communities and metacommunities (Dorazio & Royle 2005; Kéry & Royle 2008; Royle & Dorazio 2009).

The possibility of incorporating covariates to refine estimates of occupancy and detection probability makes the occupancy model a powerful tool to answer many questions about biodiversity and species distributions. For example, Zipkin *et al.* (2009) used the community occupancy model to assess the effect of fragmentation on a bird community, concluding that forest interior specialists had increased occupancy rates in large fragments in a landscape. Another study, in northern Arizona (USA), used the occupancy model to assess the responses of a small mammal community to forest management and found that while four species had high rates of occupancy, eight species were highly affected by forest fire management (Kalies *et al.* 2012). Another interesting study shows that management actions to control populations of white-tail deer (*Odocoileus virginianus*) in the eastern USA have an impact on the bird

community, through changes caused by deer grazing on the understory (Zipkin *et al.* 2010). These examples reinforce the advantages of obtaining species-specific estimates of occupancy to evaluate impacts on biodiversity and the species-specific responses to habitat modification and management. One of the main issues with occupancy models arises when the number of rare and undetected species is high in a community, which is a common situation in tropical regions (Survey *et al.* 2002; Banks-Leite *et al.* 2014). Although correcting for imperfect detection may yield good results when we model a single common/abundant species in the tropics (Mendes *et al.* 2017), the community model often returns results that are too uncertain and not substantially different from analysis based on presence/absence data without any correction for imperfect detection (Banks-Leite *et al.* 2014).The Atlantic Forest of Brazil has a long history of fragmentation that was intensified after the 1950s, when there was a rapid urban and industrial expansion (Dean 1996). This led to an intense impact on the Atlantic Forest landscape, with only around 11% of original forest cover left and distributed over more than 200,000 fragments (Ribeiro *et al.* 2009). Despite the negative impacts of human activity in this biome, it is still one of the most biodiverse regions of the world, with high rates of endemism and a “hotspot” for biology conservation (Myers *et al.* 2000). In a global study on vertebrate diversity and conservation, the Atlantic Forest was ranked as one of the most diverse biomes for birds mammals and amphibians (Jenkins *et al.* 2013) with the forest remnants of Rio de Janeiro state being one of the most threatened areas in the world with regards to bird diversity (Harris *et al.* 2005). Given the combined factors of diversity and extreme habitat threat, predicting species specific responses to changes in landscape configuration and habitat structure in the Atlantic Forest is paramount for conserving this biome and can provide insights into the consequences of the severe ongoing

fragmentation processes in other parts of the world such as Africa, Southeast Asia and in the Amazon.

Bats are highly diverse in the Neotropics (Emmons and Feer 1998) and in the Atlantic Forest (Bolzan *et al.* 2010; Peracchi & Nogueira 2010), playing several ecological roles as pollinators, controlling insect population and, most importantly for forest regeneration, as primary seed dispersers particularly after disturbance (Kunz *et al.* 2011). Different species of bats can respond differently to habitat fragmentation, with some species suffering from the changes it causes to habitats, while others thrive in these altered conditions (Faria *et al.* 2006; Struebig *et al.* 2011). In Neotropical forests, bats are responsible for most seed dispersal and are even more important in fragmented landscape as they can be considered keystone species for forest regeneration (Duncan & Chapman 1999). Because bats have different sensitivities to disturbance, perform several ecosystem services (Kunz *et al.* 2011) and are highly mobile (Esbérard *et al.* 2017), potentially providing very long range ecological impacts, understanding which factors impact the bat metacommunity and which species specific responses can be anticipated from habitat modification, will improve conservation strategies for fragmented landscapes.

In this study I use a Bayesian hierarchical modelling approach, termed the community occupancy model, and single species occupancy models to assess the impact of fragmentation on estimates of occupancy and detection probability for a bat metacommunity in a fragmented landscape of southeast Brazil. I used landscape metrics such as fragment area and isolation and habitat structure measures to determine which set of variables is a better predictor of species occurrence in different sites and which species are more at risk from human disturbance of natural landscapes. I predicted that both landscape and habitat structure metrics have an

impact on occupancy estimates, but species have more heterogeneous responses to habitat structure. In particular, I expected that species that are mostly associated with the forest interior to have lower rates of occupancy in fragments.

Methods

Study area and sampling methods

Sampling locations and methods are described in Chapter 2. Following occupancy modelling procedures (MacKenzie *et al.* 2006; Kéry & Royle 2016), each fragment and three control sites were treated as independent sites, resulting in 13 sites. Each of the sites had six independent sampling occasions, corresponding to each of the sampling nights in these areas. All sampling was considered to be done in a single season, and I assume bat species were independently detected and no new bat species colonized a site or went locally extinct during the short timeframe of sampling.

Species abundance was converted to presence/absence for each sampling occasion to generate a detection history per species, with 1 corresponding to at least one detection in six sampling occasions, and 0 to no detection during that survey at that site. For example, let's assume a species *k* was detected on the first, second and fifth sampling occasion, we would have a detection history that could be noted as:

$$detection\ history\ (k) = 110010$$

Occupancy modelling procedure

The community occupancy model (Dorazio & Royle 2005; Kéry & Royle 2008; Zipkin *et al.* 2010) is a powerful class of hierarchical models that uses repeated sampling occasions to distinguish true absence from non-detection. The procedures assumes that presence of species $k = 1,2\ldots K$ in site $i = 1,2\ldots i$, can be assigned as

z(k,i) = 1 if species *k* is present in site *i*, and *z(k,i)* = 0 if absent. Occurrence is modelled as a latent variable for each species identity (*k*) with a Bernoulli distribution. This allows species-specific responses on parameter estimation. Thus the site- occupancy of a species can be described as:

$$z(k,i) \sim Bernoulli\ (\Psi_{ki}).\ \Psi_{ki}$$

Or the probability of species *k* occurring on site *i.*

In reality, the occurrence latent variable *z(k,i)* is rarely observedperfectly , we are in fact recording the detection of species *k* in site *i* over *j* sampling occasions. This is denoted as *y(k,i)* with a Binomial distribution. Therefore, the probability a species is detected, given that it is present at a site, takes a value of 1, and a value of 0 when the species is absent from a site. The detection process can be described as:

$$y(k,i) \sim Binomial\ (z_{ki} * p_{k,j})$$

This model fulfils the assumption of no detection when the species is absent, as z_{ki} must be equal to 0.

One of the advantages using community occupancy models is the addition of site-specific and survey-specific covariates that be incorporated into the model in a linear fashion through the logit link equation. The addition of site-specific covariates allow differential responses to habitat variables to be included, e.g. canopy height, whereas, survey-specific covariates allow the effects of sampling to be included, e. g. time of day. Site-specific covariates can be added to the estimation of occupancy probability as:

$$logit\ (\Psi_{ki}) = \beta o_k + \beta 1_k * Cov1_i + \beta 2_k * Cov2_i,$$

and survey-specific covariates can be included with the estimation of detection probability as:

$$logit(p_{ki}) = \alpha 0_k + \alpha 1_k * Cov1_i + \alpha 2_k * Cov2_i.$$

More details about modelling community occupancy and detection probability can be found on Dorazio & Royle (2005), Kéry *et al.* (2005), Zipkin *et al.* (2009, 2010).

Modelling bat metacommunity at the Macacú River Basin and around REGUA

To compare which set of covariates better capture the variation of bat species occupancy in my study area, I built two sets of community occupancy models using a Bayesian framework:

Model 1, Landscape level: In this model, I included covariates which differed across sites. I assumed that species occupancy would be affected by site area and isolation, as measured in Chapter 2. Detection probability was assumed to be constant across sites, only affected by species identity.

Model 2, Habitat level: In this model, again keeping detection probability constant, I assumed that species occupany would co-vary habitat complexity. Habitat complexity is measured following Delciellos *et al.* (2016) and described in Chapter 2 as “The first principal component (PCAhab1) shows positive associations with the abundance of watercourses and *Cecropia* trees, and a negative association with the abundance of lianas. The second component (PCAhab2) is associated positively with increased overstory, understory and fallen logs”.

I chose to use two sets of models because models with the four variables did not converge.For each model, I used the same presence/absence matrix (Table S3.1) and the following definitions:

- Sites: 13 sites, corresponding to each of the 10 forest fragments sampled and the three control sites inside the continuous reserve REGUA.
- All the sampling was done in a single season, with no colonization or extinction from fragments happening during the course of this study.
- Each site was sampled for six nights of mist netting, referred as six sampling occasions (j=6).
- All species-specific parameters (Ψ_{ki}, p_k, βo_k, $\beta 1_k$, $\beta 2_k$, $\alpha 0_k$, $\alpha 1_k$ and $\alpha 2_k$) were assumed to be drawn from a wide normal distribution, with mean 0 and variance of 1000.
- All variance parameters were assumed to be drawn from a uniform distribution.
- All covariates (area, isolation, PCA1 and PCA2) were standardised and have mean = 0.

I can then state the models as:

Model 1 (Landscape configuration):

$$z(k,i) \sim Bernoulli\ (\Psi_{ki})$$

$$y(k,i) \sim Binomial\ (z_{ki} * p_{k,j})$$

$$logit\ (\Psi_{ki}) = \beta o_k + \beta 1_k * (fragment\ area)_i + \beta 2_k * (isolation)_i$$

and Model 2 (Habitat configuration):

$$z(k,i) \sim Bernoulli\ (\Psi_{ki})$$

$$y(k,i) \sim Binomial\ (z_{ki} * p_{k,j})$$

$$logit\ (\Psi_{ki}) = \alpha o_k + \alpha 1_k * (PCAhab1)_i + \alpha 2_k * (PCAhab2)_i$$

All models were fitted using the software JAGS (Depaoli *et al.* 2016) through the interface of the package *jagsUI* (Kellner 2017) for the software R v.3.4.1 (R Development Core Team 2018).

Modelling bat species using single species occupancy models

Single species models are built using the same equations as the community model, but in these cases, *k* is always equal to one. I built single species occupancy models using a maximum likelihood approach to estimate the parameters *Ψ, p, α and β*. I used the *unmarked* package for R v.3.4.1 (R Development Core Team 2018) to build a set of individual models using one landscape metric each time as an occupancy covariate. On top of the four covariates included in the community models (*area*, *isolation*, *PCA1* and *PCA2*) I also included 2 other landscape metrics: Proximity index with a 500m radius and Forest cover with 500m radius. I compared the models for each species using the AIC to identify the best models. When the Δ-Akaike weight was < 2, all the models under this threshold were considered as good models. I examined the parameter estimates and the *p*-value to assess their significance to species occupancy (Table S3.2).

Community occupancy model comparisons

I considered the best set of covariates for the estimation of species occupancy and detection the set with narrower posterior confidence intervals and the ones to which species had more heterogeneous responses.

Results

All modelled parameters converged after 100,000 iterations for both community models 1 and 2. Even though both models converged, my data did not allow precise estimations, as most of the posterior confidence intervals (CI) are too wide (Tables 3.1 to 3.8). An overview of each of the parameters estimated for both community models is as follows:

Detection probability

Model 1

Detection probability estimates from Model 1 showed that while most bat species have low detection probabilities, some species showed higher probabilities of detection rates, ranging from p = 0.04 (sd = 0.04, CI: 0.01 – 0.15) for *Trachops cirrhosus* and p = 0.79 (sd = 0.04, CI: 0.69 – 0.87) for *Carollia perspicillata*. At metacommunity level, detection probability of bats was estimated at p = 0.13 (sd = 0.58, CI: 0.07 – 0.22) (Table 3.1, Figure 3.1). This high standard deviation and the posterior confidence interval reflects the variability found in this bat community. I found that 15 species returned very low detection probabilities: *Anoura caudifer* (p = 0.14), *Anoura geoffroyi* (p = 0.14), *Chiroderma doriae* (p = 0.05), *Dermanura cinerea* (p = 0.11), *Diphylla ecaudata* (p = 0.09), *Eptesicus brasiliensis* (p = 0.08), *Histiotus velatus* (0.07), *Micronycteris microtis* (p = 0.07), *Micronycteris minuta* (p = 0.2), *Peropteryx macrotis* (p = 0.05), *Phyllostomus hastatus* (p = 0.12), *Pygoderma bilabiatum* (p =

0.05), *Sturnira tildae* (*p* = 0.14), *Tonatia bidens* (*p* = 0.05) and *Trachops cirrhosus (p* =0.04) (Table 3.1 for standard deviations and posterior confidence intervals).

Model 2

This model returned estimates very similar to the ones from Model 1. *Trachops cirrhosus* was the species with lowest detection probability in my study area, with *p* = 0.04 (sd = 0.04, CI: 0.01 – 0.15). In this model, *Carollia perspicillata* was the species with highest detection probability, with *p* = 0.79 (sd = 0.05, CI: 0.69 – 0.87). Metacommunity had a slightly higher mean detection probability in the model, *p* = 0.15 (sd = 0.58, CI: 0.08 – 0.25) (Table 3.2, Figures 3.2). The high standard deviation and wide posterior confidence intervals are related to the heterogeneity of detection probabilities found in this bat metacommunity. For this model I found 13 species with very low detection rates (MacKenzie *et al.* 2002): *Anoura geoffroyi* (*p* = 0.14), *Chiroderma doriae* (*p* = 0.06), *Dermanura cinerea* (*p* = 0.11), *Diphylla ecaudata* (*p* = 0.1), *Eptesicus brasiliensis* (*p* = 0.1), *Micronycteris microtis* (*p* = 0.07), *Micronycteris minuta* (*p* =0.07), *Peropteryx macrotis* (*p* = 0.08), *Phyllostomus hastatus* (*p* = 0.13), *Pygoderma bilabiatum* (*p* = 0.06), *Sturnira tildae* (*p* = 0.14), *Tonatia bidens* (*p* = 0.06) and *Trachops cirrhosus* (*p* = 0.04) (Table 3.2 for standard deviations and posterior confidence intervals).

Occupancy estimates

Model 1

Occupancy estimations showed great heterogeneity between species occurring at the Macacú river Basin (Figures 3.1). The metacommunity had an estimated mean occupancy of 1 with wide confidence intervals that shows how

imprecise this result is (sd = 0.99, CI: 0.01-1). *Vampyressa pusilla* had the lower occupancy estimation in my metacommunity (Ψ = 0.35, sd = 0.1, CI: 0.24 – 0.52), while *Artibeus lituratus, Artibeus fimbriatus, Artibeus obscurus, Carollia perspicillata* and *Sturnira lilium* were the species with highest occupancy estimation (Ψ = 1) (Table 3.3 for standard deviations and posterior confidence intervals). It is important to note that all confidence intervals are quite wide and usually reach Ψ = 1 for most species, which is a source of uncertainty in my models.

Model 2

Occupancy estimates also showed great heterogeneity between species occurring at the Macacú River Basin in model 2 (Figures 3.2). The metacommunity had an estimated occupancy of 0.99. *Histiotus velatus* had the lowest occupancy estimation in the metacommunity (Ψ = 0.2), while *Artibeus lituratus, Artibeus obscurus, Carollia perspicillata, Sturnira lilium* and *Sturnira tildae* were the species with highest occupancy estimation (Ψ = 1) (Table 3.4 for standard deviations and posterior confidence intervals). As with Model 1, it is important to note that all confidence intervals are quite wide and usually reach Ψ = 1 for most species, which is a source of uncertainty in my community models.

Covariates effects

Model 1

Fragment area and isolation were included as covariates affecting species-specific occupancy estimates. All the estimates of species-specific responses have

large 95% confidence intervals, with most of them overlapping zero. This adds many uncertainties to the models, as I cannot distinguish whether the effect is positive or negative (Figures 3.1). However, there was an overall positive effect of fragment area on metacommunity occupancy probability (β1 = 37.37, 95% CI = 0.07 – 0.22) (Table 3.5). The mean estimates for species-specific responses are all positive but many confidence intervals overlap zero, thus I cannot infer the direction of the relationship (Figure 3.1). There were 10 species for which the effect of the covariates was positive, but the large CRI highlight the uncertainty in the estimates: *Anoura geoffroyi* (β1 = 51.27, CRI: 12.11 – 98.9), *Artibeus fimbriatus* (β1 = 55.02, CRI: 18.09 – 102.76), *Chiroderma doriae* (β1 = 45.88, CRI: 2.51 – 97.44), *Diphylla ecaudata* (β1 = 49.35, CRI: 8.23 – 100.92), *Glossophaga soricina* (β1 = 49.03, CRI: 13.89 - 94), *Micronycteris microtis* (β1 = 48.81, CRI: 3.48 – 100.89), *Platyrrhinus lineatus* (β1 =42, CRI: 0.08 – 87.78), *Pygoderma bilabiatum* (β1 =46.56, CRI: 3.38 – 98.54), *Tonatia bidens* (β1 = 46.63, CRI: 3.47 – 99.69), and *Vampyressa pusilla* (β1 = 54.31, CRI: 14.99 – 105.18) (Table 3.6).

The effect of isolation on occupancy probability cannot be reliably differentiated, for both the metacommunity and single species responses as they all overlap zero, making it impossible to distinguish positive and negative effects (Table 3.6, Figure 3.10).

Model 2

Model 2 used the two principal components of habitat complexity measures (Delciellos *et al.* 2016) as covariates affecting species occupancy. All estimates of covariate effects in these models are unreliable, as they overlap zero, making it

impossible to distinguish positive effects from negative ones (Tables 3.7 and 3.8, Figures 3.2).

Species-specific responses to PCA1 (positive association with watercourses and *Cecropia* trees, negative association with abundance of lianas) shows a decline in occupancy rates with the increased presence of water and *Cecropia* trees and absence of lianas (metacommunity mean $\alpha 1$ = -8.32, sd = 6.76, CI = -24.08 – 0.71).

PCA2 (increased overstory, understory and fallen logs) has a positive effect on occupancy (metacommunity mean $\alpha 2$ = 3.05, sd = 3.21, CI: -1.62 – 10.74), but these estimates are unreliable as all the 95% confidence intervals overlap zero, making it impossible to separate positive from negative effects (Figure 3.2).

Single species models

Estimates of detection probabilities ranged from very low (p = 0.01, *M. minuta*, *T. bidens, T.cirrhosus*) to high (p = 0.8, *C. perspicillata*). *Anoura geoffroyi, D. cinerea, D. ecaudata, E. brasiliensis, M. minuta, P. bilabiatum, P. macrotis, Sturnira tildae, T. bidens and T. cirrhosus* had detection probabilities lower than 0.2 and will not be discussed further as, according to MacKenzie *et al.* (2002), models with detection probabilities < 2 have too much uncertainty to be considered valid. From the remaining species, *A. fimbriatus* (p = 0.25, z = 0.004), *A. lituratus* (p = 0.79, z = 0.0002), *A. obscurus* (p = 0.39, z = 0.04), *C. perspicillata* (p = 0.8, z = 0.001), *G. soricina* (p = 0.26, z = 0.001), *M. nigricans* (p = 0.34, z = 0.05) and *P. lineatus* (p = 0.29, z = 0.02) had significant detection probabilities > 0.2.

All occupancy estimates were not significant and only *M. nigricans* had a significant effect of the covariate (Proximity index) on the non-significant occupancy estimate.

Discussion

I used the community occupancy model to identify predictors of species occupancy in a fragmented landscape of the Atlantic Forest while accounting for imperfect detection. Community models 1 and 2 had high variability in parameter estimators, as we can see from the posterior confidence intervals that overlap zero for many species. The single species models were also not reliable, as most species showed low detection rates and non-significant occupancy estimates. The uncertainty in the estimates of occupancy and detection probability may be caused by the dataset size, with a low number of detections per species. This reflects the natural state of these tropical bat communities, which consist of many rare and elusive species. The use of hierarchical models in certain situations can be advantageous as this method draws power from the whole dataset to enhance the estimation for rare species (Zipkin *et al.* 2009), although their estimates will be pulled towards the community means (Link 1999). However, in order to obtain reliable probability estimates, rare species need to be detected with greater frequency than in this study. Thus, improving the estimates for rare and rarely detected species can only be achieved by the accumulation of more data (MacKenzie *et al.* 2002). Another advantage of the community occupancy model is the ability to obtain estimations for every species in a community, which is of great value for informing decision makers on the impacts of landscape and habitat structure changes caused by natural events, human activity or management actions that may affect biodiversity (Kéry *et al.* 2005; Zipkin *et al.* 2009, 2010), but similarly, if the uncertainty surrounding estimates are too large, there is no way to differentiate among these responses.

Detection Probability of Species in the Fragmented Atlantic Forest

Mean community detection probability estimates were low in both models, averaging $p = 0.13$ in model 1 (landscape) and $p = 0.15$ in model 2 (habitat structure). According to MacKenzie *et al.* (2002) occupancy estimates should be taken with caution when species have low rates of detection (< 0.2) and few detections (< 7). In my study, many species fall into this category: *Anoura caudifer* (model 1), *Anoura geoffroyi* (model 1 and 2), *Chiroderma doriae* (model 1 and 2), *Dermanura cinerea* (model 1 and 2), *Diphylla ecaudata* (model 1 and 2), *Eptesicus brasiliensis* (model 1 and 2), *Histiotus velatus* (model 1), *Micronycteris microtis* (model 1 and 2), *Micronycteris minuta* (model 1 and 2), *Peropteryx macrotis* (model 1 and 2), *Phyllostomus hastatus* (model 1 and 2), *Pygoderma bilabiatum* (model 1 and 2), *Sturnira tildae* (model 1 and 2), *Tonatia bidens* (model 1 and 2) and *Trachops cirrhosus* (model 1 and 2). The single species models were not reliable, as either species had few detections or estimates were non-significant (Table S3.2). The only way of improving these estimates is collecting more data, and even a few additional detections could improve the estimates (MacKenzie *et al.* 2002; Zipkin *et al.* 2009). The low estimates of detection probabilities highlights the necessity for large sampling efforts to obtain enough data to use these models, especially in hyperdiverse biomes like rainforests, where many species combine small distributional ranges, low detectability rates and low abundance (Gaston 1991; Banks-Leite *et al.* 2014).

Occupancy estimates

Occupancy estimates were very similar between Models 1 and 2, although the accuracy of the models is limited as observed in the wide posterior confidence intervals, that for some species ranges from 0.01 to 1 (*Trachops cirrhosus*, Model 2, Table 3.4). Mean occupancy rate was high for the whole metacommunity in both models, but this needs to be interpreted with caution, as the mean metacommunity detection probability is very low (p = 0.13 in model 1, p = 0.15 in model 2) and this may cause some inflation of the occupancy parameter, as the model cannot distinguish between a species' absence and lack of detection (MacKenzie *et al.* 2002).

Species specific estimates of occupancy were more reliable for species with higher rates of detection and which yielded higher rates of occupancy. The correlation of high detection probabilities and high occupancy was described by other studies (Zipkin *et al.* 2010; Banks-Leite *et al.* 2014; Kéry & Royle 2016) and holds true for this study as well. The species that had smaller posterior confidence intervals were: *Artibeus fimbriatus, Artibeus lituratus, Artibeus obscurus, Carollia perspicillata* and *Vampyressa pusilla.* The first four species are abundant generalists and are expected to be found in most Neotropical bat assemblages (Esbérard 2003; Dias & Peracchi 2008; Muylaert *et al.* 2017), and this is no different in my study. This is reflected in the high occupancy and detection probability estimates (Tables 3.1 to 3.4). *Vampyressa pusilla* is a small fig-eating phyllostomid bat of the subfamily Stenodermatinae (Lewis & Wilson 1987) and it was detected a total of 10 times in four sites, returning a detection probability of p = 0.36 in both models and occupancy Ψ = 0.35 and Ψ = 0.37 for models 1 and 2, showing that it is still possible to generate reliable inferences about species occupancy from a few detections.

Predictors of species occurrence in the fragmented Atlantic Forest

Landscape

Fragment size had a positive effect on all species of the bat metacommunity of the Macacú River Basin. This relationship is based on theories of island biogeography and the species-area relationships (McArthur & Wilson 1967; Connor & McCoy 1979), and also supports several habitat fragmentation studies that concluded that continuous forests and large fragments hold more biodiversity than small areas (Laurance *et al.* 2002; Haddad *et al.* 2015). Zipkin *et al.* (2009) for example, used the community occupancy model to find that fragment area was a good predictor of bird richness; of 15 forest interior birds, nine species had their occupancy estimates positively impacted by fragment area, while five species had the opposite trend. Similarly, bats in a fragmented landscape of Atlantic Forest in Paraguay were more abundant in larger sites (Gorresen & Willig 2004), in a scenario similar to my study. In general, area is correlated with species diversity and at least for some species, with abundance (Laurance *et al.* 2002; Gorresen & Willig 2004; Zipkin *et al.* 2009; Haddad *et al.* 2015). Although fragment area has a positive impact on species occupancy, the responses to fragment size is very similar for every species in this metacommunity and, therefore, is not a good predictor of differential species responses to fragmentation.

The bat metacommunity had heterogeneous responses to the degree of isolation of fragments in the landscape. Although the posterior confidence intervals were wide and overlapped with zero for all species, and we cannot be certain of the real influence of these parameters, the mean values still hold some indication of the impact of isolation on different species. A brief examination of the direction of the

association between fragment isolation and occupancy rates shows that half of the species had negative associations, while the other half, positive associations. The effect of isolation is inversely proportional to a species dispersal ability and body size (Cosson *et al.* 1999), and although bats are mobile species, not all species are able to cross open spaces to reach new isolated areas (Meyer 2007; Rocha *et al.* 2017). Most of the species to which isolation had a negative impact includes small or forest specialist species like *Anoura geoffroyi, Dermanura cinerea, Glossophaga soricina, Micronycteris minuta, Peropterix macrotis* and *Vampyressa pusilla.* A notable exception is *Desmodus rotundus*, the vampire bat, that although abundant in most fragments, apparently had its occupancy estimates negatively impacted by isolation, but again, with such large confidence intervals, this result must be assessed with caution. In Mexico, abundance of bats in isolated trees immersed in a pasture matrix was inversely proportional to the distance of the tree to the nearest fragment (Galindo-González & Sosa 2003). In French-Guiana, Cosson *et al.* (1999) found that the response of bats to isolation was variable among species. Although no rare canopy frugivores were found in any fragment, there was no increase in abundance of any of the taxa observed in these sites after the fragmentation event. The degree of isolation of fragments might be a good predictor of the effect of habitat fragmentation on bats, as different species have different thresholds of tolerance to the isolation of a fragment, but more detections are needed in order to get more reliable information.

Habitat Structure as a Predictor of Occupancy

I found that the bat metacommunity responded to the two habitat structure principal components in different ways. For the first axis of variation (PCA1), the

metacommunity occupancy estimates were negatively associated with an increase in the abundance of *Cecropia* trees and a decrease on liana abundance. Although *Cecropia* trees can indicate abundance of food for some bat species (Mello *et al.* 2011b), it is also associated with areas in early successional stages (Brokaw & Busing 2000; Pearson *et al.* 2003). On the second axis (PCA2), the metacommunity mean occupancy estimates crossed zero and therefore I can't identify if the community had a positive or negative association with increased overstory, understory and decreased frequency of fallen logs. One of the impacts of fragmentation is a decrease of the overstory and understory vegetation density, and although this covariate should not be used as a proxy for disturbance, there are species that thrive at both ends of this metric (Delciellos *et al.* 2016). For bats, an increase of the overstory and understory vegetation corresponds to increased availability of resources in the form of roosts, fruits and prey abundance. The heterogeneous responses of bat metacommunity suggests that occupancy may be higher in sites with higher structural complexity, which might be related to the availability of food and roosts, but these are mean estimates and might be heavily influenced by the most abundant taxa (i.e. *Carollia perspicillata*, *Artibeus lituratus*) that thrive in disturbed habitat characterised by vegetation edges (Faria *et al.* 2006). On the other hand, when the species-specific responses in the community models are inspected, there is significant variation, as expected in such an ecologically-diverse metacommunity. If these results hold true after accumulation of more data, it would suggest that bat metacommunity diversity could be maximised under a regime of low disturbance level at the landscape-scale (the intermediate disturbance hypothesis) (Roxburgh *et al.* 2004; Shea *et al.* 2004), which would retain enough of the heterogeneous habitat structure for the persistence of most of the species in the community. This is a pattern described for many taxa

(Roxburgh *et al.* 2004), from corals (Aronson & Precht 1995) to birds (Zipkin *et al.* 2009; Banks-Leite *et al.* 2013), and in aquatic (Townsend *et al.* 2014) and terrestrial (Molino & Sabatier 2001) environments. Villard *et al.* (1999) concluded that although fragment area is a better predictor of bird richness in Ontario, Canada, habitat structure influenced the occurrence of half of the species in their study, and thus should be incorporated in conservation planning. In the same region as my study, Delciellos *et al.* (2016) showed that habitat quality was a better predictor of small mammals abundance than landscape and land use metrics, because it captured most of the variability in the responses among different species.

The phyllostomid bat metacommunity in the study area has a nested structure, with the variation following the gradient of fragment isolation (Chapter 2), while other studies in the Atlantic Forest showed that habitat structure is a good predictor of small mammal abundance and occurrence (Pardini *et al.* 2005; Delciellos *et al.* 2016). In my study, the wide posterior estimates do not allow a conclusion about the best predictors of species-specific occupancy estimates, but there is an indication that isolation and habitat structure have more heterogeneous responses of bat species. In the Cerrado, a Neotropical savannah north of my study location in Brazil, Mendes *et. al.* (2017) assessed the effect of landscape configuration and habitat structure in the occupancy of eight bat species using single species occupancy models for each of them. *Myotis nigricans, Platyrrhinus lineatus* and *Sturnira lilium* occurrences were better predicted by landscape configuration, while *Desmodus rotundus, Glossophaga soricina* and *Platyrrhinus incarum* occurrences were better predicted by habitat configuration. These studies used single species models, and only with species that had enough detections in the sampling areas (Mendes *et al.* 2017). In my study, *M. nigricans* was the only species that allowed that kind of inference and it was also better predicted by

landscape properties, but most single species models' results were not different from my community occupancy model as they both did not offer reliable estimates. The occupancy models, be it either at single species or community level) should then be used when there is a large number of sampling occasions with a big dataset of species occurrence, most species with detection rates > 0.2 and at least seven detections (MacKenzie *et al.* 2002). When these conditions are not met, other methods that use presence only might be more reliable (Kéry & Royle 2016). Although single species models don't allow inferences about the whole community, they may be an option for most abundant species, when they can provide estimates that are precise, different than community occupancy models when there are many rare species.

The results of my study indicate that the bat metacommunity is dominated by a few very abundant and easily detected species and many rare and elusive species. Accounting for imperfect detection is useful to obtain better estimates of species occurrence and species richness, but it needs large sampling effort in order to have enough detection of rare and rarely detected species to provide reliable estimates.

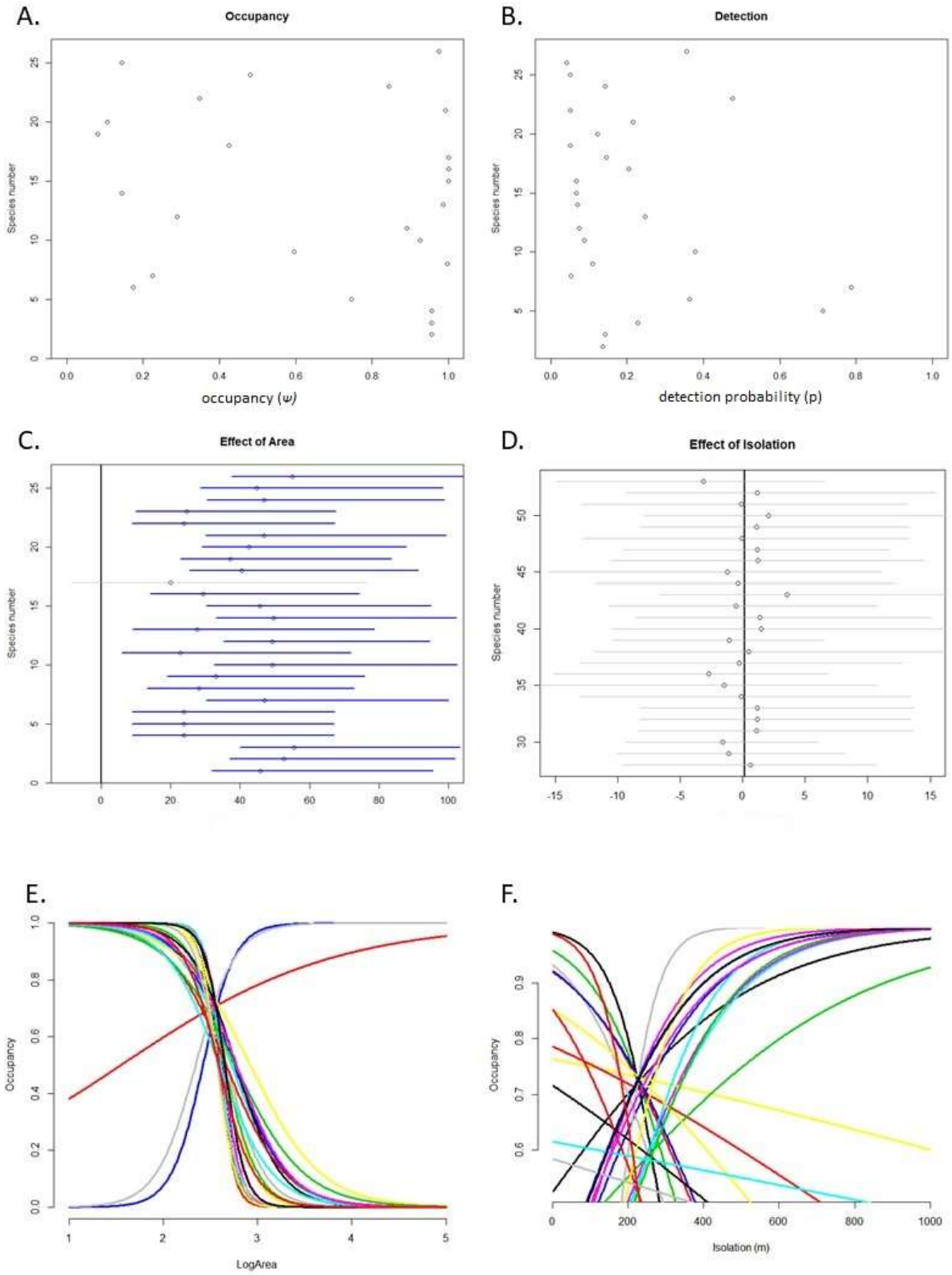


Figure 3.1: Outputs of community model 1 (landscape). 3.1A: Occupancy estimates for model 1. The x-axis represents the mean occupancy of each of the 26 species in the metacommunity. The y- axis correspond to species numbers and follows the ID

number from the tables. 3.2B: Detection probability estimates for Model 1. The x-axis represents the mean detection probability of each of the 26 species in the metacommunity. The y- axis correspond to species numbers and follows the ID number from the tables. 3.1C: Effect of area on occupancy estimates in Model 1, the landscape model. X-axis represents the estimates of parameter β1 on model 1 in the logit scale. Horizontal lines represent the posterior confidence intervals, with the blue lines corresponding to those estimates that do not overlap zero. The y- axis correspond to species numbers and follows the ID number from the tables. 3.1D: Effect of isolation on occupancy estimates in Model 1. X-axis represents the estimates of parameter β2 on Model 1 in the logit scale. Horizontal lines represent the posterior confidence intervals. The y- axis correspond to species numbers and follows the ID number from the tables. 3.1E: Predicted values of occupancy depending on fragment area. Each line corresponds to one species. X-axis correspond to different fragment sizes, log transformed, and y-axis is the expected occupancy. Wide posterior confidence intervals for individual species don't allow inferences about the effect of area in occupancy estimates. 3.1F: Predicted values of occupancy depending on fragment isolation. Each line corresponds to one species. X-axis correspond to different fragment isolation and y-axis is the expected occupancy. Wide posterior confidence intervals for individual species don't allow inferences about the effect of isolation in occupancy estimates.

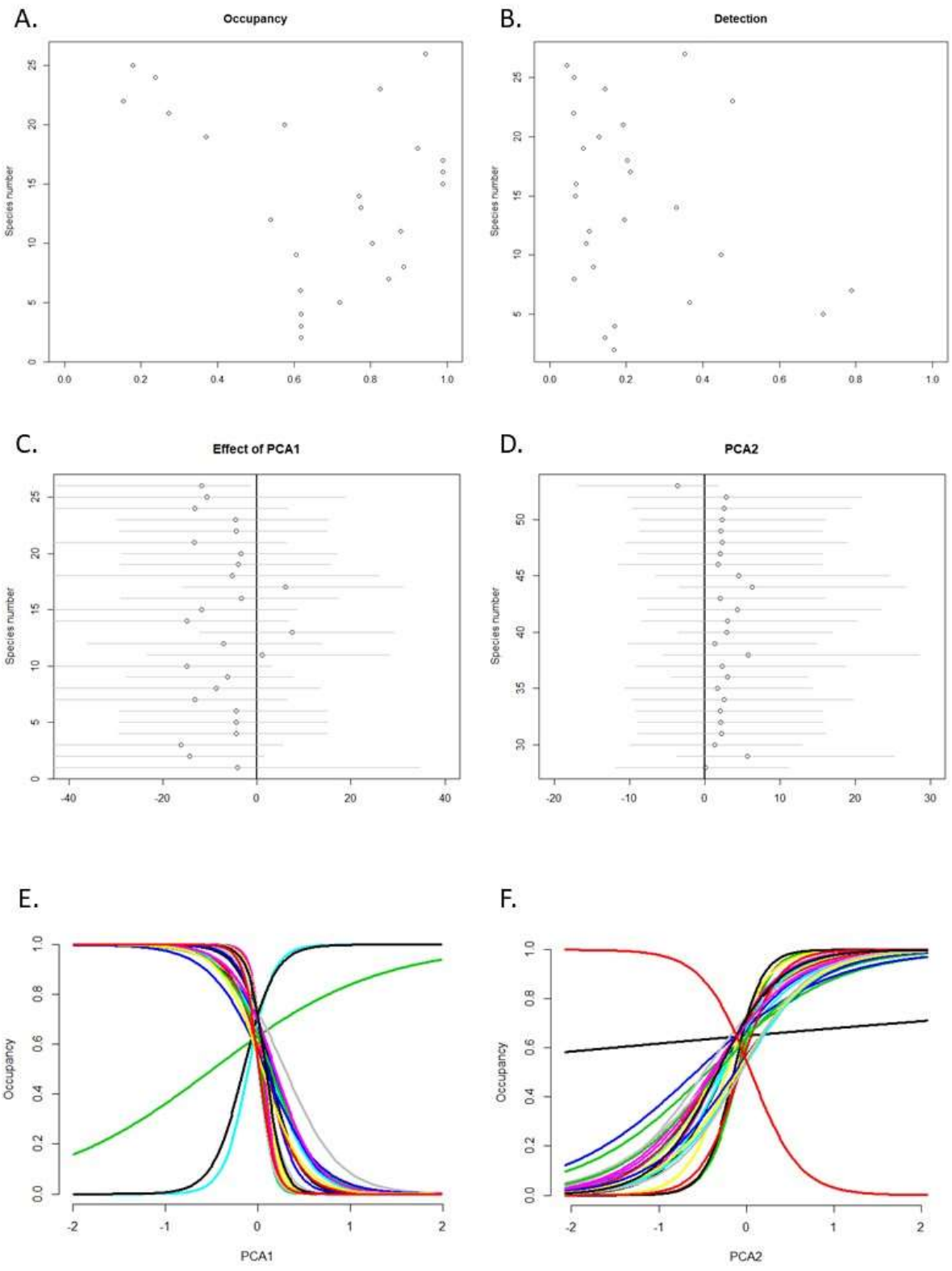

A.
Occupancy
Species number
B.
Detection
Species number
C.
Effect of PCA1
Species number
D.
PCA2
Species number
E.
Occupancy
PCA1
F.
Occupancy
PCA2

Figure 3.2: Outputs of community model 2 (habitat structure). 3.2A: Occupancy estimates for model 2. The x-axis represents the mean occupancy of each of the 26 species in the metacommunity. The y- axis correspond to species numbers and follows the ID number from the tables. 3.2B: Detection probability estimates for model 2. The x-axis represents the mean detection probability of each of the 26 species in the metacommunity. The y- axis correspond to species numbers and follows the ID number from the tables. 3.2C: Effect of PCA1 on occupancy estimates in model 2. X-axis represents the estimates of parameter β1 on model 2 in the logit scale. Horizontal lines represent the posterior confidence intervals. The y- axis correspond to species numbers and follows the ID number from the tables. 3.2D: Effect of PCA2 on occupancy estimates in model 2. X-axis represents the estimates of parameter β2 on model 2 in the logit scale. Horizontal lines represent the posterior confidence intervals. The y- axis correspond to species numbers and follows the ID number from the tables. 3.2E: Predicted values of occupancy depending on PCA1 value. Each line corresponds to one species. X-axis correspond to PCA1 values and y-axis is the expected occupancy. Wide posterior confidence intervals for individual species don't allow inferences about the effect of habitat structure in occupancy estimates. 3.2F: Predicted values of occupancy depending on PCA2 value. Each line corresponds to one species. X-axis correspond to PCA2 values and y-axis is the expected occupancy. Wide posterior confidence intervals for individual species don't allow inferences about the effect of habitat structure in occupancy estimates.

Table 3.1: Mean detection probability estimates with their standard deviation (sd) and posterior confidence interval from community model 1 (landscape). Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	Detection probability - Model 1	mean	sd	2.50%	97.50%	Rhat
	metacommunity	0.13	0.58	0.07	0.22	1
1	*Anoura caudifer*	0.14	0.05	0.06	0.26	1
2	*Anoura geoffroyi*	0.14	0.05	0.05	0.28	1
3	*Artibeus fimbriatus*	0.23	0.06	0.11	0.38	1
4	*Artibeus lituratus*	0.71	0.05	0.61	0.81	1
5	*Artibeus obscurus*	0.36	0.05	0.26	0.47	1
6	*Carollia perspicillata*	0.79	0.04	0.69	0.87	1
7	*Chiroderma doriae*	0.05	0.04	0.01	0.17	1
8	*Dermanura cinerea*	0.11	0.03	0.05	0.19	1
9	*Desmodus rotundus*	0.38	0.06	0.27	0.51	1
10	*Diphylla ecaudata*	0.09	0.06	0.01	0.25	1
11	*Eptesicus brasiliensis*	0.08	0.03	0.03	0.15	1
12	*Glossophaga soricina*	0.25	0.05	0.14	0.37	1
13	*Histiotus velatus*	0.07	0.08	0.02	0.35	1.07
14	*Micronycteris microtis*	0.07	0.04	0.01	0.18	1
15	*Micronycteris minuta*	0.07	0.03	0.02	0.16	1
16	*Myotis nigricans*	0.2	0.04	0.12	0.31	1
17	*Myotis riparius*	0.15	0.04	0.07	0.25	1
18	*Peropteryx macrotis*	0.05	0.04	0.01	0.14	1.01
19	*Phyllostomus hastatus*	0.12	0.04	0.06	0.22	1
20	*Platyrrhinus lineatus*	0.21	0.05	0.12	0.33	1
21	*Pygoderma bilabiatum*	0.05	0.04	0.01	0.17	1
22	*Sturnira lilium*	0.48	0.05	0.37	0.59	1
23	*Sturnira tildae*	0.14	0.03	0.08	0.23	1
24	*Tonatia bidens*	0.05	0.04	0.01	0.17	1
25	*Trachops cirrhosus*	0.04	0.03	0.01	0.13	1
26	*Vampyressa pusilla*	0.36	0.09	0.18	0.56	1

Table 3.2: Mean detection probability estimates with their standard deviation (sd) and posterior confidence interval from community model 2. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	Detection probability - Model 2	mean	sd	2.50%	97.50%	Rhat
	metacommunity	0.15	0.58	0.08	0.25	1.00
1	*Anoura caudifer*	0.17	0.11	0.05	0.47	1.00
2	*Anoura geoffroyi*	0.14	0.06	0.05	0.29	1.00
3	*Artibeus fimbriatus*	0.17	0.06	0.07	0.31	1.00
4	*Artibeus lituratus*	0.71	0.05	0.61	0.81	1.00
5	*Artibeus obscurus*	0.36	0.05	0.26	0.47	1.00
6	*Carollia perspicillata*	0.79	0.05	0.69	0.87	1.00
7	*Chiroderma doriae*	0.06	0.06	0.01	0.24	1.00
8	*Dermanura cinerea*	0.11	0.04	0.05	0.20	1.00
9	*Desmodus rotundus*	0.45	0.08	0.29	0.61	1.00
10	*Diphylla ecaudata*	0.10	0.07	0.01	0.27	1.00
11	*Eptesicus brasiliensis*	0.10	0.05	0.03	0.24	1.00
12	*Glossophaga soricina*	0.19	0.05	0.11	0.32	1.00
13	*Histiotus velatus*	0.32	0.19	0.03	0.71	1.00
14	*Micronycteris microtis*	0.07	0.05	0.01	0.19	1.00
15	*Micronycteris minuta*	0.07	0.04	0.02	0.17	1.00
16	*Myotis nigricans*	0.21	0.06	0.12	0.37	1.00
17	*Myotis riparius*	0.20	0.07	0.09	0.37	1.00
18	*Peropteryx macrotis*	0.08	0.09	0.01	0.38	1.00
19	*Phyllostomus hastatus*	0.13	0.07	0.05	0.33	1.01
20	*Platyrrhinus lineatus*	0.19	0.05	0.11	0.32	1.00
21	*Pygoderma bilabiatum*	0.06	0.06	0.01	0.23	1.00
22	*Sturnira lilium*	0.48	0.06	0.37	0.59	1.00
23	*Sturnira tildae*	0.14	0.04	0.08	0.23	1.00
24	*Tonatia bidens*	0.06	0.06	0.01	0.23	1.00
25	*Trachops cirrhosus*	0.04	0.04	0.01	0.15	1.00
26	*Vampyressa pusilla*	0.36	0.10	0.17	0.56	1.00

Table 3.3: Mean occupancy estimates with their standard deviation (sd) and posterior confidence interval from community model1. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	*Occupancy - Model 1*	mean	sd	2.50%	97.50%	Rhat
	metacommunity	1	0.99	0.99	1	1.02
1	*Anoura caudifer*	0.68	0.26	0.19	1	1.01
2	*Anoura geoffroyi*	0.57	0.21	0.37	1	1.00
3	*Artibeus fimbriatus*	0.5	0.14	0.36	0.76	1.02
4	*Artibeus lituratus*	1	0.02	0.96	1	1.03
5	*Artibeus obscurus*	1	0.02	0.96	1	1.01
6	*Carollia perspicillata*	1	0.02	0.96	1	1.01
7	*Chiroderma doriae*	0.53	0.34	0.23	1	1.00
8	*Dermanura cinerea*	0.96	0.1	0.74	1	1.02
9	*Desmodus rotundus*	0.93	0.09	0.78	1	1.01
10	*Diphylla ecaudata*	0.43	0.3	0.23	1	1.00
11	*Eptesicus brasiliensis*	0.93	0.18	0.55	1	1.01
12	*Glossophaga soricina*	0.71	0.12	0.58	0.99	1.01
13	*Histiotus velatus*	0.83	0.33	0.01	1	1.01
14	*Micronycteris microtis*	0.56	0.31	0.27	1	1.00
15	*Micronycteris minuta*	0.71	0.26	0.39	1	1.02
16	*Myotis nigricans*	0.93	0.13	0.71	1	1.00
17	*Myotis riparius*	0.9	0.2	0.54	1	1.01
18	*Peropteryx macrotis*	0.72	0.31	0.1	1	1.01
19	*Phyllostomus hastatus*	0.87	0.17	0.6	1	1.01
20	*Platyrrhinus lineatus*	0.83	0.14	0.68	1	1.02
21	*Pygoderma bilabiatum*	0.53	0.34	0.23	1	1.01
22	*Sturnira lilium*	1	0.02	0.96	1	1.01
23	*Sturnira tildae*	0.99	0.05	0.86	1	1.01
24	*Tonatia bidens*	0.52	0.34	0.23	1	1.00
25	*Trachops cirrhosus*	0.65	0.36	0.05	1	1.01
26	*Vampyressa pusilla*	0.35	0.1	0.24	0.52	1.02

Table 3.4: Mean occupancy estimates with their standard deviation (sd) and posterior confidence interval from community model 2. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	Occupancy - Model 2	mean	sd	2.50%	97.50%	Rhat
	metacommunity	0.99	0.99	0.71	1	1.02
1	*Anoura caudifer*	0.73	0.37	0.04	1.00	1.01
2	*Anoura geoffroyi*	0.59	0.27	0.26	1.00	1.01
3	*Artibeus fimbriatus*	0.73	0.24	0.33	1.00	1.01
4	*Artibeus lituratus*	0.99	0.03	0.93	1.00	1.02
5	*Artibeus obscurus*	0.99	0.03	0.93	1.00	1.02
6	*Carollia perspicillata*	0.99	0.03	0.93	1.00	1.02
7	*Chiroderma doriae*	0.52	0.39	0.06	1.00	1.01
8	*Dermanura cinerea*	0.93	0.15	0.50	1.00	1.01
9	*Desmodus rotundus*	0.81	0.19	0.43	1.00	1.00
10	*Diphylla ecaudata*	0.44	0.34	0.14	1.00	1.01
11	*Eptesicus brasiliensis*	0.74	0.32	0.20	1.00	1.01
12	*Glossophaga soricina*	0.95	0.13	0.53	1.00	1.03
13	*Histiotus velatus*	0.20	0.31	0.00	1.00	1.04
14	*Micronycteris microtis*	0.60	0.34	0.20	1.00	1.01
15	*Micronycteris minuta*	0.73	0.30	0.25	1.00	1.01
16	*Myotis nigricans*	0.95	0.14	0.47	1.00	1.02
17	*Myotis riparius*	0.68	0.27	0.25	1.00	1.01
18	*Peropteryx macrotis*	0.64	0.42	0.00	1.00	1.00
19	*Phyllostomus hastatus*	0.93	0.19	0.23	1.00	1.03
20	*Platyrrhinus lineatus*	0.96	0.12	0.55	1.00	1.02
21	*Pygoderma bilabiatum*	0.53	0.39	0.06	1.00	1.01
22	*Sturnira lilium*	0.99	0.03	0.93	1.00	1.02
23	*Sturnira tildae*	0.99	0.06	0.84	1.00	1.02
24	*Tonatia bidens*	0.53	0.39	0.06	1.00	1.01
25	*Trachops cirrhosus*	0.68	0.39	0.01	1.00	1.00
26	*Vampyressa pusilla*	0.37	0.18	0.18	0.77	1.01

Table 3.5: Effect of area on occupancy estimates with their standard deviation (sd) and posterior confidence interval from community model 1. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	β1 Model 1	mean	sd	2.50%	97.50%	Rhat
	metacommunity	37.47	14.34	12.62	67.95	1.03
1	*Anoura caudifer*	44.72	26.21	-18.65	93.91	1
2	*Anoura geoffroyi*	51.27	22.15	12.11	98.9	1
3	*Artibeus fimbriatus*	55.02	21.77	18.09	102.76	1
4	*Artibeus lituratus*	23.15	20.17	-10.21	66.13	1
5	*Artibeus obscurus*	23.11	20.15	-10.04	66.15	1
6	*Carollia perspicillata*	23.31	20.2	-10.12	66.3	1
7	*Chiroderma doriae*	45.88	24.22	2.51	97.44	1
8	*Dermanura cinerea*	27.14	20.76	-8.82	70.79	1
9	*Desmodus rotundus*	32.94	20.42	-0.98	76.98	1
10	*Diphylla ecaudata*	49.35	23.97	8.23	100.92	1.01
11	*Eptesicus brasiliensis*	21.35	26.72	-32.56	70.17	1
12	*Glossophaga soricina*	49.03	20.35	13.89	94	1
13	*Histiotus velatus*	27.13	26.29	-24.76	76.57	1.01
14	*Micronycteris microtis*	48.81	24.8	3.48	100.89	1.01
15	*Micronycteris minuta*	44.64	23.48	-0.04	93.31	1.01
16	*Myotis nigricans*	28.47	21.49	-10.72	72.57	1.01
17	*Myotis riparius*	19	31.9	-38.74	75.15	1
18	*Peropteryx macrotis*	39.33	26.65	-17.39	91.16	1
19	*Phyllostomus hastatus*	36.3	21.99	-4.78	81.78	1
20	*Platyrrhinus lineatus*	42	21.47	0.08	87.78	1
21	*Pygoderma bilabiatum*	46.56	24.19	3.38	98.54	1
22	*Sturnira lilium*	23.28	20.22	-10.14	66.25	1
23	*Sturnira tildae*	24.1	20.23	-9.9	67.13	1
24	*Tonatia bidens*	46.63	24.61	3.47	99.69	1
25	*Trachops cirrhosus*	43.04	26.71	-12.79	96.41	1
26	*Vampyressa pusilla*	54.31	23.43	14.99	105.18	1.01

Table 3.6: Effect of isolation on occupancy estimates with their standard deviation (sd) and posterior confidence interval from community model 1. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	β2 - Model1	mean	sd	2.50%	97.50%	Rhat
	metacommunity	0.19	2.86	-5.41	6.21	1
1	*Anoura caudifer*	0.6	5.01	-9.55	10.43	1
2	*Anoura geoffroyi*	-0.94	4.49	-9.4	8.4	1
3	*Artibeus fimbriatus*	-1.49	3.69	-9	5.92	1
4	*Artibeus lituratus*	1	5.05	-8.24	12.64	1
5	*Artibeus obscurus*	1.07	5.17	-8.15	13.03	1
6	*Carollia perspicillata*	1.03	5.08	-8.16	12.67	1
7	*Chiroderma doriae*	-0.05	5.9	-11.94	13.03	1
8	*Dermanura cinerea*	-1.24	6.05	-15.22	10.59	1
9	*Desmodus rotundus*	-2.47	5.18	-14.26	7.19	1.01
10	*Diphylla ecaudata*	-0.33	5.69	-12.14	11.69	1
11	*Eptesicus brasiliensis*	0.47	6.34	-11.17	15.29	1
12	*Glossophaga soricina*	-0.92	4.1	-9.66	6.56	1.01
13	*Histiotus velatus*	1.39	6.6	-10.16	17.62	1
14	*Micronycteris microtis*	1.32	5.71	-8.73	14.47	1
15	*Micronycteris minuta*	-0.44	5.04	-10.2	10.58	1
16	*Myotis nigricans*	3.22	6.07	-6.96	16.77	1.01
17	*Myotis riparius*	-0.25	5.47	-11.04	11.89	1
18	*Peropteryx macrotis*	-1.01	6.11	-14.42	10.57	1
19	*Phyllostomus hastatus*	1.31	6.06	-10.27	14.78	1
20	*Platyrrhinus lineatus*	1.19	4.96	-8.94	11.48	1
21	*Pygoderma bilabiatum*	-0.02	5.91	-11.8	12.63	1
22	*Sturnira lilium*	1.07	5.1	-8.08	12.8	1
23	*Sturnira tildae*	1.85	6	-7.84	16.99	1
24	*Tonatia bidens*	-0.2	5.88	-12.34	12.22	1
25	*Trachops cirrhosus*	1.12	5.73	-9.09	14.48	1
26	*Vampyressa pusilla*	-2.92	5.19	-14	6.86	1

Table 3.7: Effect of PCA hab1 on occupancy estimates with their standard deviation (sd) and posterior confidence interval from community model 2. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	*α1 - Model 2*	mean	sd	2.50%	97.50%	Rhat
	metacommunity	-8.32	6.76	-24.08	0.71	1.04
1	*Anoura caudifer*	-3.73	19.12	-48.72	34.35	1.02
2	*Anoura geoffroyi*	-13.95	14.45	-51.78	1.46	1.01
3	*Artibeus fimbriatus*	-15.72	16.61	-57.29	4.43	1.01
4	*Artibeus lituratus*	-4.07	10.05	-28.85	14.68	1
5	*Artibeus obscurus*	-4.15	10.12	-29.27	14.57	1
6	*Carollia perspicillata*	-4.2	10.09	-28.97	14.48	1
7	*Chiroderma doriae*	-12.67	14.54	-50.72	5.09	1.01
8	*Dermanura cinerea*	-8.31	13.73	-43.1	13.12	1
9	*Desmodus rotundus*	-6.14	8.26	-27.28	5.58	1.01
10	*Diphylla ecaudata*	-14.25	14.45	-51.59	1.71	1
11	*Eptesicus brasiliensis*	1.25	11.52	-23.52	28.82	1
12	*Glossophaga soricina*	-6.28	11.35	-34.55	13.67	1
13	*Histiotus velatus*	7.61	9.23	-5.67	29.6	1.01
14	*Micronycteris microtis*	-14.31	16.17	-56.06	5.54	1.01
15	*Micronycteris minuta*	-11.67	14.56	-49.76	7.46	1.01
16	*Myotis nigricans*	-2.79	10.49	-28.08	17.17	1
17	*Myotis riparius*	6.02	10.82	-14.58	31.81	1
18	*Peropteryx macrotis*	-4.72	15.85	-43.72	25.31	1.01
19	*Phyllostomus hastatus*	-3.82	10.03	-28.7	13.99	1
20	*Platyrrhinus lineatus*	-3.13	10.57	-28.88	16.97	1
21	*Pygoderma bilabiatum*	-13.06	15.03	-52.19	5.16	1.01
22	*Sturnira lilium*	-4.26	10.14	-29.1	14.57	1
23	*Sturnira tildae*	-4.2	10.15	-29.34	14.48	1
24	*Tonatia bidens*	-12.57	14.52	-49.98	5.88	1.01
25	*Trachops cirrhosus*	-10.11	16.97	-52.27	18.93	1.01
26	*Vampyressa pusilla*	-11.06	11.15	-42.3	-1.32	1.01

Table 3.8: Effect of PCA hab2 on occupancy estimates with their standard deviation (sd) and posterior confidence interval from community model 2. Rhat is the "potential scale reduction factor", values < 1.1 indicates that the model converged.

ID	*α2 - Model 2*	mean	sd	2.50%	97.50%	Rhat
	community	3.05	3.21	-1.62	10.74	1.02
1	*Anoura caudifer*	0.29	5.18	-11.03	11.85	1.01
2	*Anoura geoffroyi*	5.23	6.99	-3.34	23.43	1.01
3	*Artibeus fimbriatus*	1.38	5.06	-9.46	13.1	1
4	*Artibeus lituratus*	2.13	5.65	-8.56	15.97	1
5	*Artibeus obscurus*	2.18	5.48	-7.88	15.92	1
6	*Carollia perspicillata*	2.07	5.48	-8.5	15.34	1
7	*Chiroderma doriae*	2.52	6.7	-8.8	19.53	1
8	*Dermanura cinerea*	1.74	5.52	-9.46	14.1	1
9	*Desmodus rotundus*	3.03	4.33	-3.02	13.7	1.01
10	*Diphylla ecaudata*	2.06	6.19	-8.77	17.02	1.01
11	*Eptesicus brasiliensis*	5.8	8.42	-4.19	28.84	1.01
12	*Glossophaga soricina*	1.4	5.5	-9.56	14.92	1
13	*Histiotus velatus*	2.58	4.85	-3	14.51	1.02
14	*Micronycteris microtis*	3.04	6.96	-7.61	21.26	1.01
15	*Micronycteris minuta*	4.46	7.14	-5.67	22.9	1
16	*Myotis nigricans*	1.84	5.46	-8.54	15.17	1
17	*Myotis riparius*	5.95	7.94	-3.69	26.67	1
18	*Peropteryx macrotis*	4.25	7.29	-6.3	23	1
19	*Phyllostomus hastatus*	1.5	6.31	-11.55	14.48	1.01
20	*Platyrrhinus lineatus*	2.01	5.4	-8.14	15.11	1
21	*Pygoderma bilabiatum*	2.49	6.84	-8.84	18.99	1
22	*Sturnira lilium*	2.18	5.58	-8.34	15.86	1
23	*Sturnira tildae*	2.18	5.49	-8.18	15.65	1
24	*Tonatia bidens*	2.15	6.42	-9.58	17.89	1
25	*Trachops cirrhosus*	2.55	6.84	-10.03	19.31	1.01
26	*Vampyressa pusilla*	-3.24	4.75	-15.87	1.58	1.01

CHAPTER FOUR

The effects of habitat loss and fragmentation on bat-plant mutualistic networks

ABSTRACT

Network theory offers a robust mathematical framework to characterise ecological systems and predict how they will respond to environmental disturbances. Habitat fragmentation reduces habitat amount available and causes a reorganization of the landscape, resulting in smaller habitat patches and increased isolation between them. These landscape changes have cascading effects on ecological systems and can cause the loss of biodiversity and a reduction in ecological services. Of particular conservation interest is the role of seed dispersal within modified landscapes. Animals are responsible for most of seed dispersal in rainforests, and bats are of notable importance in the Neotropics. One of the challenges of interactions studies is the identification of all the species taking part in the interaction network, as the direct observation of an interaction can be difficult, resulting in a lack of taxonomic resolution. One solution to this problem is the adoption of new methodologies like DNA barcoding, which uses short standardised DNA sequences, or a combination of sequences, to give an unambiguous identification. This method can be used to identify species from traces material, such as hairs, degraded tissues and faecal matter, excluding the need to directly observe an interaction. To assess the changes in network structure caused

by fragment area reduction and increased isolation, I reconstructed mutualistic networks involving bats and plants in a fragmented landscape of Atlantic Forest using DNA barcode to identify plant material contained in bat guano. I found that network structure is largely maintained, but that network nestedness increases with area and isolation. These results show that although smaller fragments have a species poor bat fauna, the seed dispersal process is still ensured by generalist species that persist in these highly altered sites and consume a wide range of fruits.

Introduction

The use of networks in ecological systems was pioneered by Odum and Lindenman, who used the approach to represent food webs in riverine habitats more than 75 years ago (Lindeman 1942; Odum 1956). Network theory has advanced considerably and today provides a robust mathematical framework to study a broad range of subjects. The elements that form a network are represented as nodes and can correspond to a wide variety of biological entities, from genes (Guet *et al.* 2002), proteins, individuals, families and social groups (Bascompte & Jordano 2007) through to biological species (Hagen *et al.* 2012), functional groups (Kratina *et al.* 2014) and habitat fragments in a landscape (Teixeira *et al.* 2014). Interactions between nodes are represented as "links" and nodes and links can be weighted to represent frequencies, abundances, or strengths of the interactions. Networks can be used to measure the structure of a system (Bastolla *et al.* 2009) or monitor changes to the dynamics of the system over time (Olesen *et al.* 2011a; Rasmussen *et al.* 2013).

The use of network theory in ecology can help us understand how complex ecological communities are structured, and networks can be used to predict how these communities will respond to environmental perturbations (Bascompte 2007; Ings *et al.* 2009; Albouy *et al.* 2014). Ecological networks can be separated into three main types; these are "traditional" food webs that usually involve predator-prey interactions (Ings *et al.* 2009), host-parasitoid webs that involve interactions between parasites and their hosts (Ings *et al.* 2009), and mutualistic networks that have interactions that are beneficial for both parties (Bascompte 2009). Mutualistic networks can comprise some of the most important ecological services attributed to natural systems (Costanza *et*

al. 1998; Kunz *et al.* 2011), with the two most commonly studied mutualisms in a network context being pollination and seed dispersal (Bascompte 2009; Ings *et al.* 2009). These networks tend to have a nested structure (Krishna *et al.* 2008), with a few generalist species that dominate the links, forming hubs that connect different parts of the network. Specialists have fewer links, usually a subset of the links from a generalist species (Montoya *et al.* 2006; Ings *et al.* 2009). A long-standing debate in ecology is whether the complexity of interactions imposed by a large number of specialists also brings stability to the ecosystems (McCann 2000) by spreading links among a larger number of species rather than concentrating these among a few central connecting species. This functional redundancy is thought to buffer the system against species loss. In general, the stability of ecosystems, and the services they provide, appears to depend on the preservation of species and functional groups capable of different responses to perturbations (McCann 2000; Ings *et al.* 2009). In this way, the maintenance of specific functional modules is an important measure of an ecosystem.

Until recently most ecological network studies have focused mainly on 'global' (i.e. network-wide) descriptors (Bascompte 2007), such as connectance (Memmott *et al.* 2000), linkage density (Sole & Montoya 2001), modularity (Fortuna *et al.* 2010; Mello *et al.* 2011b) and centrality (Memmott *et al.* 2000; Sole & Montoya 2001; Woodward & Hildrew 2002), with less emphasis on node-specific characteristics. One of the main criticisms of network ecology is the lack of resolution and the related taxonomic biases in the identification of nodes included in the network (Symondson 2002; Ings *et al.* 2009). For example, Hemprich-Bennett et al. (2018) recently demonstrated that even small changes in node resolution can have drastic effects on network quantification with most common network metrics showing strong

dependency on the degree of network resolution. In this study the authors also suggest that absolute values for most network metrics are likely more dependent on node resolution than on actual network and biological properties, and advocate for relative quantification instead (Hemprich-Bennett *et al.* 2018). Connectance, for example, is a metric that can be heavily influenced by the node resolution, with the clustering of a node changing the number of possible links and the strength of interactions (Hemprich-Bennett *et al.* 2018). Another known issue in network ecology studies is how networks are sampled and reconstructed. Many studies were based on unrepilcated designs, with data aggregated from different points in time and space or just based on the presence or absence of species in an area. Replicated networks along an environmental gradient can advance our understanding of community change and ecosystem function in face of disturbances (Ma *et al.* 2018). The challenge then is to provide well resolved and replicated networks that can be scaled up to study landscape level processes.

Habitat loss and fragmentation are major processes affecting landscapes across the globe, and typically involve loss of suitable habitats and the breaking apart of once-continuous habitats, respectively. When co-occurring, these processes lead to a decrease in absolute habitat area, while simultaneously increasing the number of patches, their degree of isolation, and the proportion of edges (Fahrig 2003). These dual impacts have become a major issue in conservation due to their predominantly negative impacts on biodiversity (Fahrig 2003; Fletcher *et al.* 2018). Although we can assess the relative impacts of these two processes separately in mathematical models and controlled experiments (Fahrig 1997), in the real world habitat loss and fragmentation are usually correlated (Fletcher *et al.* 2018). In a meta-analysis of the relationship of habitat loss and population decline, Bender *et al.* (1998) predict that

populations of edge specialists and generalist species that use both edge and forest interior habitats will be affected by habitat loss but when habitat loss is associated with fragmentation, the impact on forest specialists populations will be greater, than the impact on edge specialists.

A few studies argue that when fragmentation is decoupled from habitat loss it may have positive effects on biodiversity (Fahrig 2017; Fahrig *et al.* 2018), but Fletcher *et al.* (2018) refuted these arguments and suggest that habitat fragmentation can directly impact diversity (genetic diversity, species' abundance or richness), and also lead to alterations to ecological dynamics (species interactions, population growth, predation rates, and reductions in ecological services) (Fahrig 2003; Struebig *et al.* 2011; Hagen *et al.* 2012; Haddad *et al.* 2015). Long-term studies of habitat fragmentation have revealed that intact forest tends to host higher levels of biodiversity than fragmented and altered areas (Laurance *et al.* 2002; Laurance 2008). Results from the Biological Dynamics of Forest Fragments Project in the Brazilian Amazon show that many large mammals, primates, understory birds and even several species of highly mobile insects are significantly affected by the fragmentation processes (Laurance *et al.* 2002). In this study many species were absent even in the largest fragments studied while others persisted even in the smaller fragments demonstrating species-specific responses to fragmentation with a tendency towards survival of only edge and matrix habitats specialists (Laurance *et al.* 2002; Martensen *et al.* 2008). In the Argentinean Chaco, a study assessing the vulnerability of plants, leaf-miners and parasotoids found that habitat loss and fragmentation had different effects in species with different ecological niche breadth (specialists and generalists), rarity (common and rare) and in species from different trophic levels. Specialists, rare species and

species from higher trophic levels were more affected by habitat loss than generalists, common species and species from lower trophic levels (Cagnolo *et al.* 2009).

While changes in species composition and abundance due to fragmentation will certainly have an impact on the interaction between species (Valiente-Banuet *et al.* 2015), it is not always clear how network structure changes in the face of habitat loss and fragmentation (Evans *et al.* 2013).

In a study assessing the effect of habitat loss on the structure of plant-animal mutualistic networks, Fortuna & Bascompte (2006) found that real communities decline faster in face of habitat loss than random communities, but real communities have a tendency to persist longer than random ones because they contain a few species with a disproportionate number of connections which contribute to the robustness of real networks. Evans *et al.* (2013) studied how interaction networks change in a heterogenous farmland landscape and concluded that networks are robust to habitat loss, but different habitat types may have a disproportionate contribution to regional network structure. Pollinator-plant networks in sandhill habitats in north Florida showed that habitat loss may affect network architecture by changing species richness, composition and abundance within habitat patches, with reduced species richness and abundance being correlated with reduced nestedness and increased modularity (Spiesman & Inouye 2013).

In a study in a fragmented area of the Atlantic Forest of northeast Brazil Girão *et al.* (2007) concluded that fragmentation led to a decline in the number of pollinator-plant interactions, and in some cases the complete disappearance of some of the modules of the mutualistic networks present in the control area. A study in a fragmented aquatic ecosystem using stable isotopes to measure niche breadth of top

predators showed a collapse of niche breadth related to a significant reduction of prey availability (Layman *et al.* 2007). In another case involving herbivores, parasitoids and plants, fragmentation and patch size reduction led to impoverished plant-herbivore and host parasitoid food webs and changes in network properties, most notably an increase in connectance due to the loss of specialists, and an increase in generalism with fewer links in the network concentrated around a few generalist species. These changes in network properties were mostly driven by species loss in smaller fragments (Valladares *et al.* 2012).

The Atlantic Forest of Brazil was once one of the largest rainforests in the world, with highly heterogeneous environmental conditions (Myers *et al.* 2000; Ribeiro *et al.* 2009). Because of its exceptional biodiversity and endemism levels the Atlantic Forest was classified as a global hotspot for biological conservation (Myers *et al.* 2000). However, this forest has a long history of large-scale clearance and only 11-16% of forest cover is left, distributed over 200,000 fragments, with 97% of the forest patches smaller than 250 ha and 83.4% smaller than 50 ha (Ribeiro *et al.* 2009). Many of these fragments are several decades old and, in a few cases, date from the early 1800s (Ribeiro *et al.* 2009). As a result, the Atlantic Forest can provide insights into the long-term impacts of habitat loss and fragmentation on biodiversity and ecosystem function, which in turn have important implications for understanding the consequences of current clearance in Amazonia and SE Asia. In addition to the history of land-use modification, the loss of Atlantic Forest continues today, in particular, due to the expansion of agricultural land and pasture, and illegal logging (Dean 1996). As such, there is an urgent need to understand the impact of on-going fragmentation on this unique biome, which will help to guide conservation efforts.

Of particular conservation interest is the status of seed dispersal within modified landscapes, including those that are highly fragmented, such as the Atlantic Forest. Seed dispersal is a fundamental process in forest ecology and the most common way for plants to colonize new areas and is thus seen as critical for the maintenance of biodiversity (Wunderle 1997; Wright 2002). (Zahawi *et al.* 2013). Moreover, seed dispersal ensures the movement of progeny away from the mother plant into suitable areas for plant recruitment, thus also facilitating gene flow (Ricklefs 1977; Traveset *et al.* 2014). Animals are responsible for the seed dispersal of the majority of plant species (Traveset *et al.* 2014), and this is particularly important in wet tropical forests, where humidity is high and wind is often light. These animals - which range from insects to vertebrates - are thus important agents in the process of forest regeneration, such as following tree falls or larger-scale disruptions(Holl *et al.* 2000), and in the context of ecological restoration (Holl *et al.* 2000; Zahawi *et al.* 2013).

The Chiroptera (bats) is one of the most ecologically-diverse orders of mammals, consuming small vertebrates, arthropods, fruits, nectar, pollen, grains, leaves and blood (Reis et al. 2013; Emmons and Feer 1997). Bats provide critical ecological services, acting as pollinators and primary seed dispersers in forest restoration (Kunz *et al.* 2011; Mello *et al.* 2011a) and they may also provide biological control of invertebrates pests (Kunz *et al.* 2011). Roles in pollination and seed dispersal are likely to be particularly important in the Neotropics due to the rapid diversification of the New World leaf-nosed bats (family Phyllostomidae) (Shi & Rabosky 2015) and of critical importance in fragmented landscapes as bats are often the keystones species in Neotropical forest regeneration (Duncan & Chapman 1999; Kunz *et al.* 2011; Neuschulz *et al.* 2016). Although some studies have shown that a few bat species may benefit from the fragmentation process (Bianconi 2005), other

species may suffer negative impacts (Meyer 2007). Struebig et al. (2011) showed that the bat species most negatively impacted by fragmentation were the forest interior specialists.

Despite the importance of bats for forest regeneration, and their potential for mitigating fragmentation-effects, the mechanisms that control these responses are not clear and there are significant gaps in our knowledge of how these animals are affected by habitat loss and fragmentation (Martins *et al.* 2007; Willig *et al.* 2007) and subsequently how their ecosystem services are affected. Yet significant challenges exist in resolving the mutualistic interactions among bats and plants. A particular difficulty for identifying the plants is that bats are nocturnal, and visits are rarely seen. Instead, we can examine plant material that has been egested in faecal samples, which is sometimes possible for seeds, but is more problematic for pollen or pulp.

Recent technological advances have suggested a solution to the problem. DNA barcoding (Hebert *et al.* 2003) is a tool developed to help identify species using short standardized gene regions including the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene for animals (Hebert *et al.* 2003), the internal transcribed spacer for fungi (Schoch *et al.* 2012) and a variety of gene regions for plant life (CBOL Plant Working Group *et al.* 2009). The ability to identify and differentiate species using DNA is extremely useful in ecology (Yoccoz 2012) especially when morphological traits are not enough to identify species, or the only evidence available is composed of trace material such as hairs or degraded tissues (Deiner *et al.* 2017). DNA barcoding with short standardized sequences (or sets of sequences) has the potential to discriminate among species if sequences are more similar within than between species. Under this condition, DNA barcoding can permit the unambiguous identification of even the most degraded materials when compared to a reference collection of known barcoded

materials (Hebert *et al.* 2003; Hajibabaei *et al.* 2006). Indeed this method has been successfully applied in a large range of organisms and environments such as mammals (Clare *et al.* 2007; Hajibabaei *et al.* 2007; Haarsma *et al.* 2016), birds (Hebert *et al.* 2004; Kerr *et al.* 2007; Ward 2009), reptiles (Jeong *et al.* 2013; Murphy *et al.* 2013), fishes (Ward *et al.* 2009; Pereira *et al.* 2013), insects (Gan *et al.* 2015; Bittleston *et al.* 2016) and plants (Gonzalez *et al.* 2009; Kuzmina *et al.* 2012; Fazekas *et al.* 2013) among many other taxonomic groups where active reference library building is on-going.

Over the last decade DNA barcoding has been transformed from a taxonomic tool to a method in applied ecological analysis through the assessment of diet (Symondson 2002; Pompanon *et al.* 2012; Clare 2014) and has been widely used to identify the diets of bats, and to characterise their associated ecological niches. For example Salinas-Ramos *et al.* (2015) used DNA barcodes to describe the diet of three sympatric mormoopids bats in a tropical dry forest in Mexico. These three bats showed significant dietary overlap, indicating a resource driven use of the dietary niche (Salinas-Ramos *et al.* 2015). While most such molecular dietary studies of bats to date have focused on insectivorous lineages, other feeding guilds are now being targeted. Lim *et al.* (2018) assessed the impact of urbanisation and agriculture on the diet of *Cynopterus brachyotis*, a fruit bat in Peninsular Malaysia, using DNA barcodes for plants. These authors identified plants that were not previously reported as part of the diet of this species and revealed the tremendous capacity for foraging flexibility of this bat in the face of landscape conversion.

Despite the increasingly wide use of DNA barcoding by researchers as a standard tool in dietary studies, only a few studies have started to broaden the scope of analysis to communities and ecological networks. The first case to strongly

demonstrate the power of resolving nodes with DNA barcodes was the use of this method to clarify parasite networks. In this study, Wirta *et al.* (2014) found that the number of interactions recovered surpassed other traditional methods leading to much higher resolution networks and fundamentally different measurements of network properties. For example, the presumed host specificity of parasitoids and the parasitoid load of host species were both significantly altered with the use of molecular methods (Wirta *et al.* 2014). Many others have advocated for the integration of DNA into ecological networks (Toju 2015; Evans *et al.* 2016; Roslin *et al.* 2016), although few ecological network studies have employed DNA technologies. One of the most comprehensive examples of this integration was the study of seed dispersal by birds, where González-Varo *et al.* (2014) used DNA barcode sequences to accurately identify and estimate the strength of interactions between seed dispersers and four plant species in a Mediterranean woodland.

In this study I use plant DNA barcodes (ITS2 and *rbcL*) to build interaction networks among bats and the fruits they consumed across the highly fragmented landscape of the Atlantic Forest in southeast Brazil. The use of DNA barcode allows the identification of seeds and pulp consumed by bats to the level of genus, while using morphological traits, seeds can be usually identified up to families (Barroso 1999) and pulp are often not even detected and thus larger fruits may not be detected as dietary items. I built separate networks for 13 sites, which included both fragments and control zones of continuous habitat. I assessed how three key network metrics (connectance, modularity and nestedness) change with area reduction and increased isolation. I made several predictions. First, I predicted that connectance would not be affected, because the loss of interactions will occur together with the loss of species. Second, I predicted that nestedness would decrease with area and increased

isolation, because specialist tend to be the first ones to disappear after environmental disturbance such as fragmentation (Haddad *et al.* 2015). Third, I expected modularity to not be affected, because of the strong genus-to-genus relationship between bats and their preferred fruits.

Methods

Bat captures

Sampling fragments and control sites, times and methods are described in Chapter 2. In brief, I captured individual bats across 10 forest fragments and at 3 sites in a control area of intact forest (hereafter fragments and control sites). I identified all bats to species and allocated each bat to an individual cotton bag for 2-6 hours in order to give them time to defecate. I placed guano (faecal) pellets from each bat in a separate tube of ethanol and stored these at -20 degrees Celsius.

Seed and pollen identification

To identify the plants visited by bats, I examined each faecal sample under magnification and separated out those containing seeds and fruit pulp. From each of these I selected 3 seeds of each species or a piece of pulp. This material was placed in tubes for molecular analysis and sent to the Canadian Centre for Biodiversity Genomics, Biodiversity Institute of Ontario (BIO) at the University of Guelph, Canada where all molecular protocols were performed. DNA extraction, PCR and sequencing followed established protocols from the Canadian Centre for DNA barcoding (CCDB) (Kuzmina *et al.* 2012). All protocols were carried out by the CCDB staff. In brief seeds were ground using stainless steel beads and DNA was extracted in 96 well glass fibre plates using CTAB and eluted in ddH2O (Kuzmina et al. 2012, CCDB Protocols Glass Fiber Plate DNA Extraction Protocol, see appendix 1). I selected the regions ITS2 and *rbcL* for amplification, recommended for plant DNA barcoding for species identification

(Kuzmina *et al.* 2012). For the amplification of ITS2 the CCDB used primers ITS_S2F (Chen *et al.* 2010) and ITS 4 (White et al. 1990) and for *rbcL* they used primers *rbcL*a-F (Levin *et al.* 2003) and *rbcL*a-R (Kress & Erickson 2007). PCR amplification followed Kuzmina et al. (2012) and was assessed using 96-well precast E-gels (Invitrogen) and samples producing a single clear band were sequenced using the same primers and following the protocols outlined by Prosser *et al.* (2013). The samples were consolidated into 384 well plates and cleaned using the ALINE PureSEQ (Aline Biosciences) following manufacturer's instructions and sequenced on an ABI 3730 capillary sequencer following standard barcode protocols for plants (Fazekas *et al.* 2013). Forward and reverse sequences were aligned and assembled, primers were removed and ambiguous bases were resolved manually using CodonCode Aligner v. 2.7.1 (CodonCode Co, USA) and the MUSCLE algorithm (Edgar 2004) as implemented within CodonCode Aligner. See Kuzmina *et al*. (2012) for further details on sequence editing. All sequences, collection and protocol details were uploaded to the project BCRS REGUA Seed Dispersal in the BOLD database (barcodinglife.org) for further analysis at QMUL.

Data processing

I compared all sequences with the reference databases in the Barcode of Life Data System (BOLD) and GenBank to retrieve an identification. I followed the same identification protocol described by Lim *et al.* (2018) with some modifications for this dataset as follows. All the matches above 95% similarity were recorded and a decision is made depending on the match percentage. First, I checked if any sequence returned a 100% match with any species and I excluded any match to a species not known

from the Atlantic Forest of southeast Brazil. The next step was to record the subsequent highly similar matches and check if they had any record for the Atlantic Forest of southeast Brazil. Again, any species without any record were excluded. With the matches remaining for each gene region sequenced (ITS2 and *rbcL*) I checked if they were assigned to one or more genera present in the study area. If all the matches were in one genus only, the samples were assigned to this genus. If more than one genus were present in the top matches, I did not assign this sample to any genus, as I could not be certain of the match. I then compared the identification for both genes and if they were the same, I would register only one interaction. If the gene matches did not match, I assumed that each gene amplified different plant DNA and registered two interactions for that sample (See a decision tree schematic for matching in Figure 4.1). Plant identifications were kept at genus-level to minimize problems related to different taxonomic resolution in the network (Hemprich-Bennett *et al.* 2018) and because species within several genera (*Ficus, Piper, Cecropia*) cannot be reliably differentiated by DNA barcoding.

Network construction

For each forest fragment or control site, I recorded every plant genus identified in each faecal sample as one interaction and the number of times this interaction was found in each fragment or control site as the interaction strength. This generated a frequency-based matrix of bat species and the genera of seeds that they dispersed. I then built 13 bipartite interaction networks (one for each fragment or control site) using the *bipartite* package (Dormann *et al.* 2008) for R v. 3.4.1 (R Development Core Team 2018) with bats as the higher level and plants as the lower level of the bipartite

network. For each network I calculated the following metrics with the function *networklevel* from the *bipartite* package (Dormann *et al.* 2008) for R v. 3.4.1. (R Development Core Team 2018), unless noted otherwise:

- Weighted connectance: calculated as the number of realised links divided by the number of possible links in the network.

- Nestedness: this is a measure of how much of the interactions of the least connected nodes are a subset of the links of the most connected nodes (Dormann *et al.* 2009). I measured nestedness with two different metrics, as they have different responses to sample size. Nestedness temperature (T) was proposed by Atmar & Patterson (1993) and it measures the "temperature" (*T*) of an interaction matrix as the departure from a perfectly nested matrix. *T*=0 is defined as maximum nestedness and *T*=100 correspond to no nestedness. This index of nestedness is reasonably consistent between small and large-sized networks (Fründ *et al.* 2016). Weighted NODF was proposed by Almeida-Neto *et al.* (2008) and it considers the decreasing fill of the interaction matrix and the paired overlap between the interactions. This metric has the advantage of being theoretically less sensitive to sample size than the alternative metrics of nestedness (Almeida-Neto *et al.* 2008). Ecologically, a community with high nestedness (T) and one with high NODF should have similar structures though the approaches to the measurements are different.

- Modularity: It is calculated using the fast algorithm for Modular Maximization (Leger *et al.* 2015) with the function *fast.greedy* from the package *igraph* for R v 3.4.1. (R Development Core Team 2018). This metric estimate how many modules are present in the network. A module is a group of species

that interact more with other members of the module than with members of another module (Olesen *et al.* 2007).

- Niche overlap: I examined the overlap of the dietary dimension of the ecological niche of bats using Pianka's index (Pianka 1974) with the function *niche.overlap.boot* from package *spaa* (Zhang 2016) for R v.3.4.1 (R Development Core Team 2018). I recorded the niche overlap between the three most common species of bats (*Artibeus lituratus*, *Carollia perspicillata* and *Sturnira lilium*), each of which had enough capture records to make meaningful comparisons across all fragments and control sites, and between *A. lituratus* and other ecologically similar bats from Stenodermatini tribe (Table 2.3, Table 4.1).

Similarity between networks

To help visualize the differences between the networks, I generated an NMDS plot using the selected network metrics (weighted connectance, NODF and modularity) with the *vegan* (Oksanen *et al.* 2013) package for R. v. 3.4.1. (R Development Core Team 2018) which measures the pairwise distance between every fragment or control site. I used these metrics to generate Figure 4.4, that shows the pairwise distance of the network metrics between all sampling areas.

Statistical analysis

To test the effects of fragmentation and landscape configuration on mutualistic networks among bats and the plants they consumed, I performed linear

regressions between the selected metrics and the same landscape and habitat complexity metrics (area, isolation and the principal components of habitat complexity (Delciellos *et al.* 2016) as the ones used in Chapter 2 (Table 2.1). I used the function *step* from R v.3.4.1 (R Development Core Team 2018) to build models starting with the simplest (no covariate) and adding one covariate at a time until the most complex model (all covariates). I compared these models using the Akaike information criterion (AIC) to select the model with the best fit.

Results

Sample collections and sequence data

I collected a total of 843 seed dispersing and pollinating bats. REGUA 2 was the site with most captures of seed dispersers (100 bats), and *C. perspicillata* the most abundant species in my study area, with 382 captures across all sites. From these I collected in total 653 faecal samples, with *C. perspicillata* contributing 348 samples (53% of all faecal samples). In total, 475 seed samples were processed for DNA barcoding. Of these, ITS2 sequences were recovered for 253 (53%) and *rbcL* sequences were recovered for 335 (70%). By comparing my sequences to those on GenBank and BOLD, I was able to assign a genus-level identification to 227 ITS2 sequences (89% of samples successfully sequenced, 47% of total). I was able to assign a genus-level identification to 327 *rbcL* sequences (97% of the samples sequenced, 68% of total). In total I was able to assign a plant genus identification to 367 samples (77% of collected material), of which 23 samples were assigned by ITS2 only, 123 samples by *rbcL* only, and 205 samples by both genes. Of the latter, there were 7 cases where the genes produced different genus-level identifications; in these cases, I assumed that two plant DNA sources were present. For a decision tree of identifications see Figure 4.1.

Seed disperses and pollinator diversity

Seed disperser and pollinator richness ranged from five species in fragments F01 and F03 to ten species in fragment F08 (Table 4.2). Control site REGUA 2 had

the highest number of bat species with successful plant identifications (8 species, 53 samples with plant identification) (Table 4.1). The smallest networks recorded had 6 nodes (F02 and F03) and the largest had 13 nodes (REGUA 2, F07 and F09) (Table 4.2, Figure 4.2). Network metrics are presented in Table 4.2. Figure 4.4 shows the pairwise distance between all sampling areas, and fragments F1, F2, F3, F4 and F5 are the most divergent fragments in their network structure and also the smallest fragments in this study. It is interesting to note that these fragments are more different to each other than with medium-large areas (Figure 4.4).

Network characteristics across fragments

To determine which landscape characteristics explained network properties I used linear models comparing network properties to fragment area and isolation. I determined that weighted connectance, modularity and niche overlap are not explained by any of the landscape metrics. Isolation explained a significant amount of the variation in nestedness (T) (Figure 4.5); nestedness increases with increased fragment isolation (R^2 = 0.33 p= 0.04, with f-value = 5.445 in 1 and 11 DF). Weighted NODF, was also significantly explained by forest cover amount and isolation (Figure 4.6), with nestedness increasing with forest cover (R^2 = 0.52, p= 0.2) and also with isolation (R^2 = 0.52, p= 0.04). Nestedness (T) is measured from 0 (perfect nestedness) to 100 (no nestedness), while NODF is interpreted with the opposite values (0= no nestedness, 100 = perfect nestedness).

Niche overlap between species was typically low, with *C. perspicillata* and *S. lilium* showing the highest rates of overlap. *A. lituratus* and *C. perspicillata* presented low levels of niche overlap, except in the case of fragment T13 where they had a large

overlap (0.94) (Table 4.3). *A. lituratus* showed large overlap with most of the other species from the genera *Artibeus, Chiroderma, Dermanura, Platyrrhinus* and *Vampyressa*, whenever they were present in the same area (Table 4.3).

Discussion

In this study I used DNA barcoding to resolve the seed dispersal relationship of bats and the plants they visit across a matrix of fragmented landscape in the Brazilian Atlantic Forest. I was able to identify 77% of the seed samples to genus which represents a substantial increase in resolution compared to the reported rate of assignments in a traditional morphological analyses which is often limited to family in hyper diverse tropical forests (Barroso 1999). DNA barcoding also made it possible to identify fruit pulp from the gut system and record seed dispersal of plants such as *Sygidium spp.*, that usually are not recorded in faecal samples through morphological analysis because only the pulp, nectar or pollen are eaten, and the seeds are discarded (Mello *et al.* 2005).

Connectance and modularity of fragmented networks

In the networks that I constructed I observed low connectance in all fragments and control sites, ranging from 0.16 to 0.29, and found that connectance was not correlated with area, isolation or habitat complexity. One explanation for this is that with the expected loss of biodiversity in smaller and isolated areas, the number of possible links in the network decreases proportionally with the decrease in interactions, thus the values do not show much variation despite significant changes in network content. The low values of connectance are consistent with other studies where mutualistic networks have been found to be less connected than expected by chance (Olesen *et al.* 2011b; Vidal *et al.* 2014). It is interesting that for all fragments, the constructed networks comprised 2-4 modules, even when those networks had

been reduced to only a few species. In most fragments and control sites bats from the genus *Artibeus* fed on *Cecropia* or *Ficus* fruits, *C. perspicillata* was the most generalist species, but mostly fed on *Piper* fruits, while bats from the *Sturnira* genus consumed mostly *Solanum* fruits. Previous work has also revealed strong genus-level relationships between neotropical frugivorous bats and their preferred plants (Mello *et al.* 2011b), and this pattern has also been observed in other communities, such as figs-wasps mutualisms or in the Galapagos finches (Abbott *et al.* 1977; Machado *et al.* 2005). It is particularly interesting that these relationships are maintained even in the most depauperate communities. One plausible explanation is that there may be functional constraints on the foraging behaviour of these species, for example in relation to bite force required to carry and consume certain fruits and seeds (Santana & Dumont 2009; Santana *et al.* 2011), and it is this which limits the flexibility of species to change to novel fruit and seed types.

Nestedness of fragmented networks

I observed that nestedness (T) was negatively correlated with isolation, with more isolated fragments having the most nested networks (Figure 4.5). Weighted NODF increased with fragment isolation and forest cover (Figure 4.6). Note that these metrics are interpreted with alternative scales, so the results are consistent. Previous observations have suggested that nestedness decreases with isolation and increases with area (Hagen *et al.* 2012). This lack of consistency with my own findings could stem from aspects of the network topology and species composition in my focal fragments. Specifically, networks were mostly represented by extremely generalist species, with *C. perspicillata* representing the most abundant species in my study

area. Although this taxon shows marked preference for *Piper spp.* fruits, it is also the most generalist or flexible of all the focal species, eating most of the resources available and overlapping in this function with the few other frugivorous species left in these small and isolated fragments. This results in high nestedness in these areas. In larger areas, we might expect more bat richness, with the additional presence of specialists that feed on a subset of plants consumed by the generalists, thus generating high values of nestedness. This is a similar conclusion to the one obtained by Lewinsohn *et al.* (2006) in a study of the structure of plant-animal networks in which the authors observed that in nested assemblages, plants with few interactions will be associated with generalist consumers, while specialist consumers will be connected to plants linked to many consumers. It is apparent that many of these bats can make use of novel food sources, within some functional constraints, and when species do make this switch, nestedness increases. For example, the most nested fragment is also the smallest and most isolated fragment, which is surrounded by guava (*Psidium spp.*) plantation, which was widely consumed by many bats in this fragment (Figure 4.2M, network F1), which increased nestedness values and indicates that local conditions and fruit availability play an important role in determining network structure. Similarly, in small fragments, and in those sites that are surrounded by cattle ranching pastures, I observed very small values of nestedness, possibly because there was no access to novel food sources to supplement the natural resources of the fragment (Table 4.2) and that functional constraints may dominate these communities.

Loss of specialists and niche overlap in small fragments

When subject to environmental stresses, specialists are known to disappear from species assemblages more rapidly than the generalists (Davies *et al.* 2004; Struebig *et al.* 2011). In my study, this observed trend may be directly linked to the structure of the phyllostomid bat metacommunity, which was determined to be nested along a gradient of increased isolation (results from Chapter 2). The observed loss of specialists that I reported in Chapter 2 causes the loss of redundant interactions in the networks. These changes in the community structure may have implications for network stability and the seed dispersal processes (McConkey *et al.* 2012). Generalists usually have more interactions with a variety of species, but weaker interactions with any one plant consumed (Bascompte *et al.* 2003). Because of the generalists feeding behaviour and movement inside forest fragments, they may not deposit all the seeds in favourable places for seed germination (Jordano 2014). Within small isolated fragments, the smallest networks were characterized by the maintenance of the same distinctive modules but less redundancy of interactions, with only the generalist species surviving in these fragments. This community structure maintains the ecological services of seed dispersal in these highly altered environments with a combination of moderate nestedness and modularity suggesting a highly resilient network structure as also demonstrated by Mello *et al.* (2011a), however, the loss of all redundancy of function makes these networks vulnerable to any further plant or bat species loss.

Niche overlap was typically low between the most abundant species, and this can also be related to the modular structure of the networks, as each of these species was placed in a different module of the interaction network. On the other hand, members of the tribe Stenodermatini showed high niche overlap across all fragments and control sites, implying greater flexibility and potentially more resilience to the loss

of plant species. This result is similar to other studies with Neotropical bats (Heithaus *et al.* 1975; Marinho-Filho 1991; Willig *et al.* 1991; Lopez & Vaughan 2007). For example, in Costa Rica, bats from different genera showed low niche overlap, while congeners showed much higher levels of niche overlap (Lopez & Vaughan 2007). These results support the predictions of niche theory and resource partitioning, where niche theory predicts that the maximal tolerable niche overlap decreases with increasing intensity of competition, and that in order to coexist species need to exploit different resources to avoid competition (Pianka 1974). If niche overlap is inversely proportional to competition (Pianka 1974), then my results suggests that food in these habitats is not a limiting factor (as many species can feed on the same resources and not be excluded by competition) and that closely related species have traits that allow them to survive in smaller and altered fragments (Chapter 2) and are likely to differ in other aspects of their ecological niches that allows them to coexist (Tamsitt 1967; Pianka 1974).

Habitat Loss and fragmentation are threats to biodiversity, mostly causing the local extinction of more sensitive and specialist species (Fortuna & Bascompte 2006; Hagen *et al.* 2012; Haddad *et al.* 2015) and increasing the abundance of generalist and edge-loving taxa (Laurance *et al.* 2002). In order to fight the biodiversity crisis of our time (Ripple *et al.* 2017), it is necessary to conserve not only certain species, but also the interactions between them (Forup *et al.* 2008; Ribeiro da Silva *et al.* 2015) if we want to keep ecosystem services such as seed dispersal and pollination at sustainable levels. Habitat reduction can lead to species poor communities (Haddad *et al.* 2015) and small networks (Valladares *et al.* 2012), while increased isolation will affect dispersal between habitat patches, which may magnify this effect (Hagen *et al.* 2012). Low species richness and changes in species abundance may lead to networks

with reduced nestedness and increased modularity (Fortuna & Bascompte 2006). In our study, bat-plant interaction networks are resilient to habitat loss and fragmentation, as even with the loss of specialists and increased abundance of generalists, networks retain most of their modular and nested structure, which will maintain the ecological dispersion of most groups of plants that depend on bats. This finding highlights the importance of bats in forest regeneration. Not only do these species disperse pioneer plants into areas following disturbance (De La Peña-Domene *et al.* 2014) but they are also able survive and perform roles in seed dispersal in small and isolated fragments. Therefore, even with reduced species richness, small fragments still have conservation and strategic value, as they can serve as stepping stones for the initiation of forest regeneration.

However, it is also apparent that while basic dispersal of common plants by resilient generalist bats is maintained on these fragments, specialists of both plants and bats have been lost. Although network structure is largely maintained even in the most disturbed habitats, vital redundancy of functions and specialist interactions are missing. This trend of network robustness was also observed in other fragmented systems and shows the potential of fragmented landscapes to the conservation of biodiversity (Resasco *et al.* 2017). To mitigate the effects of habitat loss and fragmentation on biodiversity, I suggest that it is important to maintain and protect the largest areas of forest, which contain most of the diversity and also the interactions mediated by specialist bats, as well as increase the connectivity between forest patches. This approach will allow larger areas to act as a source of sensitive species to move across the landscape and add redundant interactions to the networks of small fragments, buffering the whole system against local extinctions. Because of the ability of some bats to survive in degraded habitats in small fragments and their role

dispersing pioneer plants, restoration projects should consider nucleation strategies to attract bats to forests in early stages of development (Zahawi *et al.* 2013). This is supposed to enhance seed dispersal processes and the diversity of plant recruitment in these areas, accelerating the forest recovery.

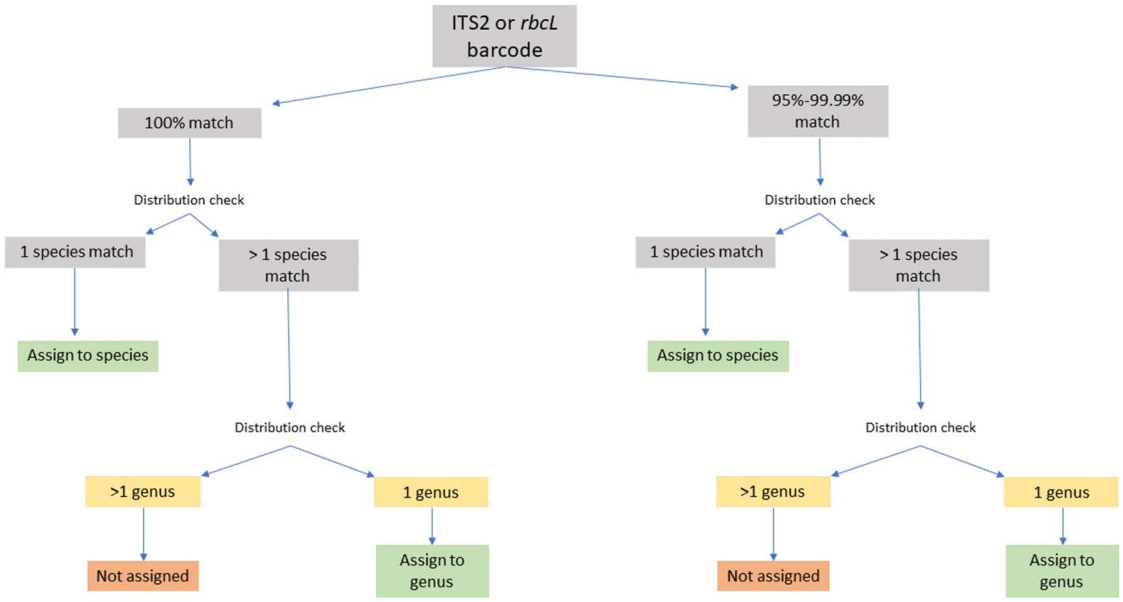
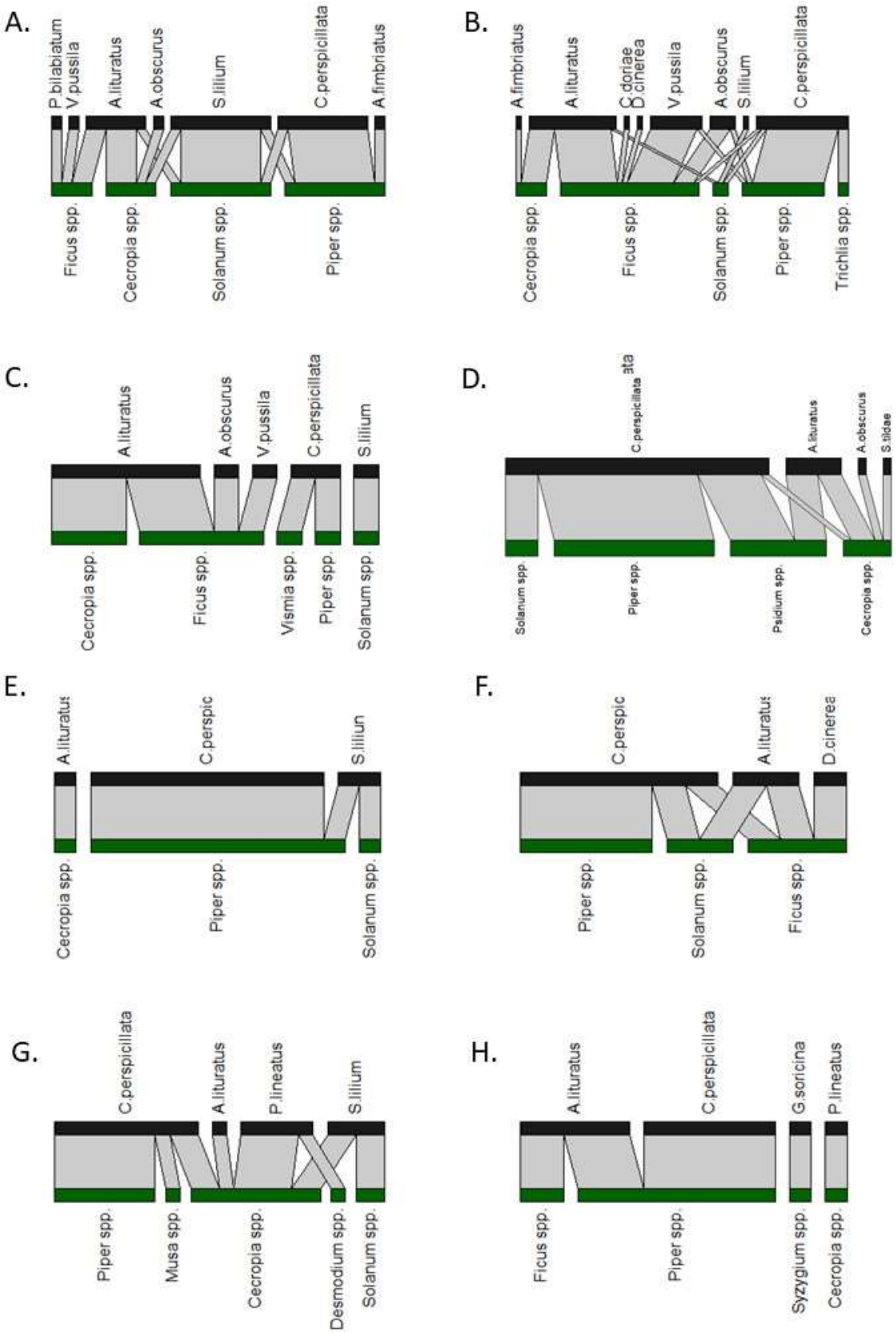


Figure 4.1: Decision tree for assigning plant DNA barcode sequences based on matches returned by BLAST searches on Genbank, NCBI database and BOLD database.


A.
P.bilabiatum
V.pussila
A.lituratus
A.obscurus
S.lilium
C.perspicillata
A.fimbriatus
Ficus spp.
Cecropia spp.
Solanum spp.
Piper spp.
B.
A.fimbriatus
A.lituratus
C.doriae
D.cinerea
V.pussila
A.obscurus
S.lilium
C.perspicillata
Cecropia spp.
Ficus spp.
Solanum spp.
Piper spp.
Trichilia spp.
C.
A.lituratus
A.obscurus
V.pussila
C.perspicillata
S.lilium
Cecropia spp.
Ficus spp.
Vismia spp.
Piper spp.
Solanum spp.
D.
C.perspicillata
A.lituratus
A.obscurus
S.lilidae
Solanum spp.
Piper spp.
Psidium spp.
Cecropia spp.
E.
A.lituratus
C.perspic
S.lilium
Cecropia spp.
Piper spp.
Solanum spp.
F.
C.perspic
A.lituratus
D.cinerea
Piper spp.
Solanum spp.
Ficus spp.
G.
C.perspicillata
A.lituratus
P.lineatus
S.lilium
Piper spp.
Musa spp.
Cecropia spp.
Desmodium spp.
Solanum spp.
H.
A.lituratus
C.perspicillata
G.soricina
P.lineatus
Ficus spp.
Piper spp.
Syzygium spp.
Cecropia spp.

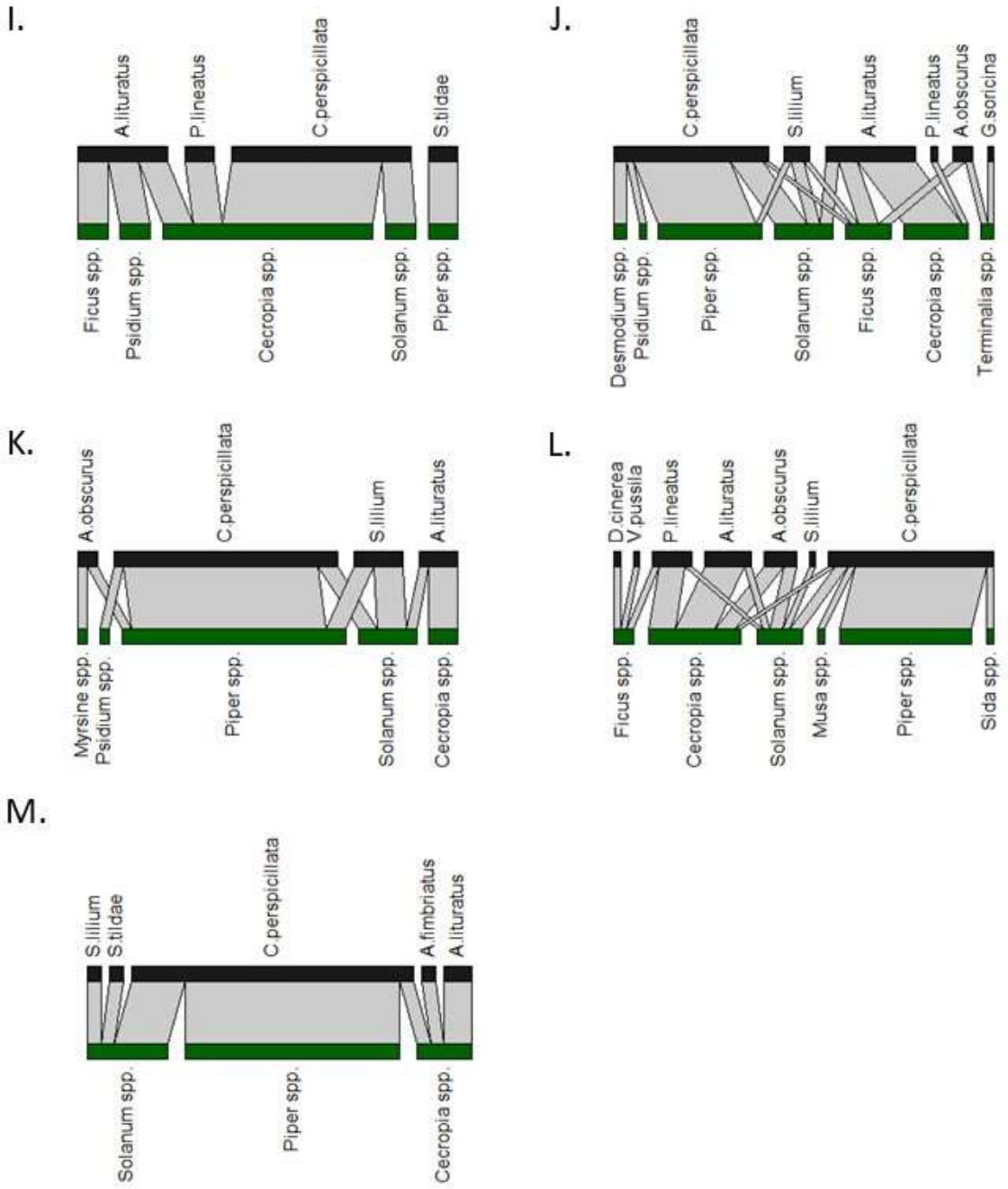


Figure 4.2: Bipartite networks for sites: A. REGUA1; B. REGUA2; C. REGUA 3; D. F1; E. F2; F. F3; G. F4; H. F5, I. F6; J. F7; K. F8; L. F9; M. F10. Black bars represent bat nodes and green bars plant nodes. The width of nodes is proportional to abundance while the width of grey connecting lines is proportional to interaction frequency. Network from smaller fragments are simpler than networks from larger fragments and

inside the reserve, but all networks show a modular and nested structure, driven mostly by the most generalist species, *C. perspicillata*.

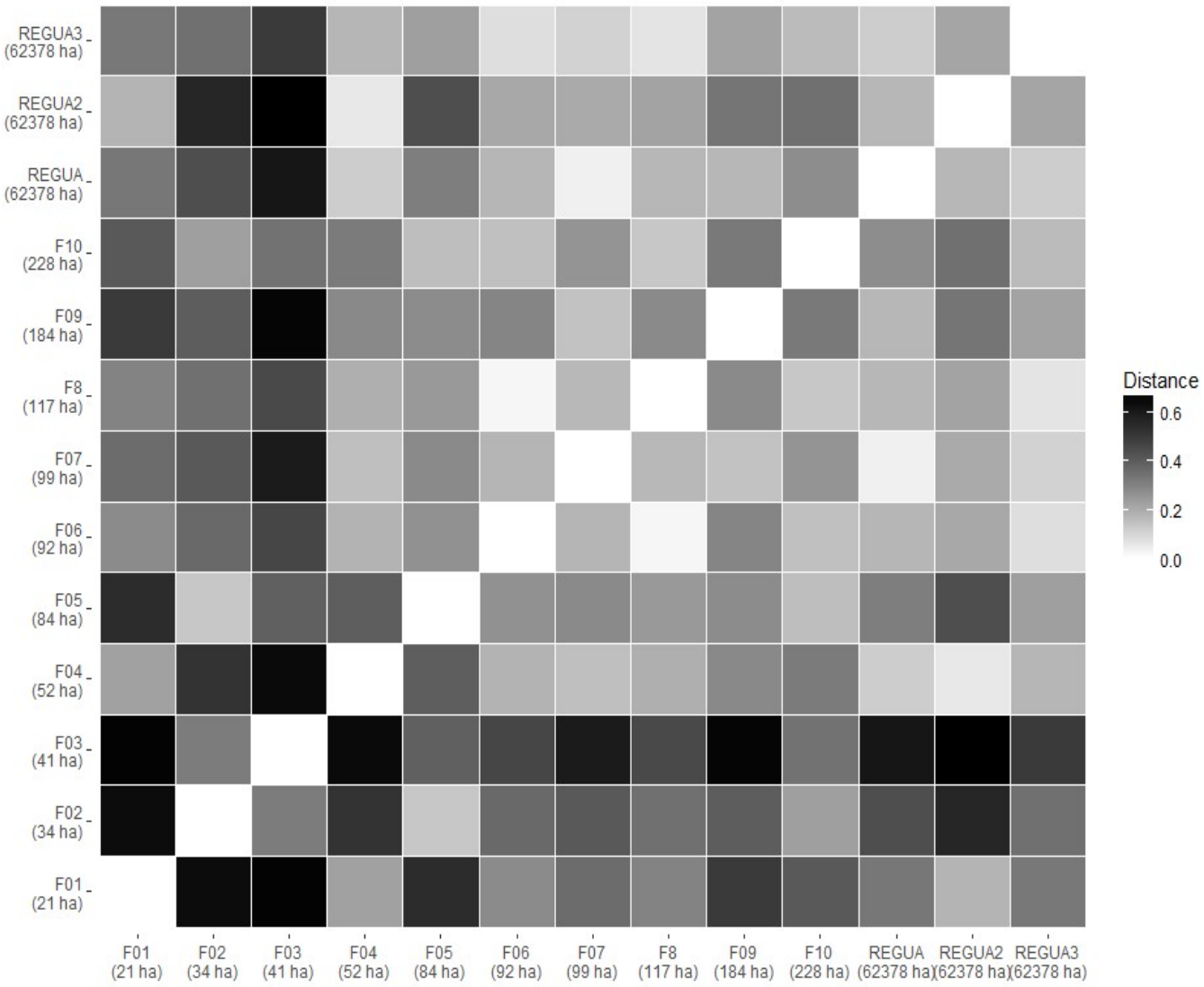


Figure 4.4: Similarity between networks based on the pairwise distance of weighted connectance, NODF and modularity between any two fragments. Fragment area is given under each fragment name in hectares. In this case, smaller fragments (e.g. F01 and F02) are more dissimilar between themselves than with larger fragments, showing that stochastic events can lead to very different network structures in face of habitat loss and fragmentation.

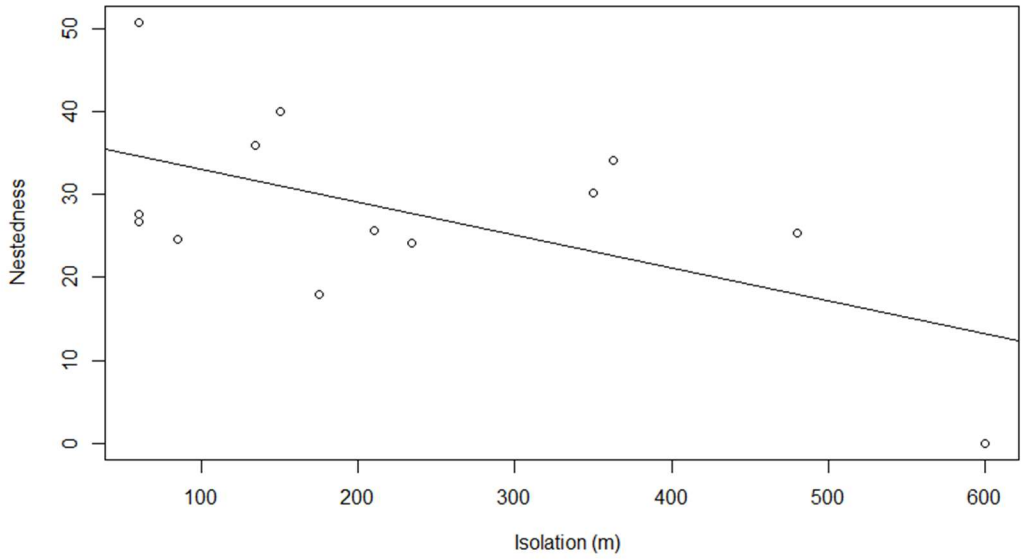


Figure 4.5: Relationship between nestedness (T) and isolation. R^2 = 0.46; p= 0.01. From this analysis, as fragments become more isolated from each other and the remaining preserved habitats, nestedness increases (T=0 perfect nestedness, T= 1 no nestedness) This suggest that isolated communities may be dominated by super generalist species that consume most of the resources available in these areas, creating a highly nested network.

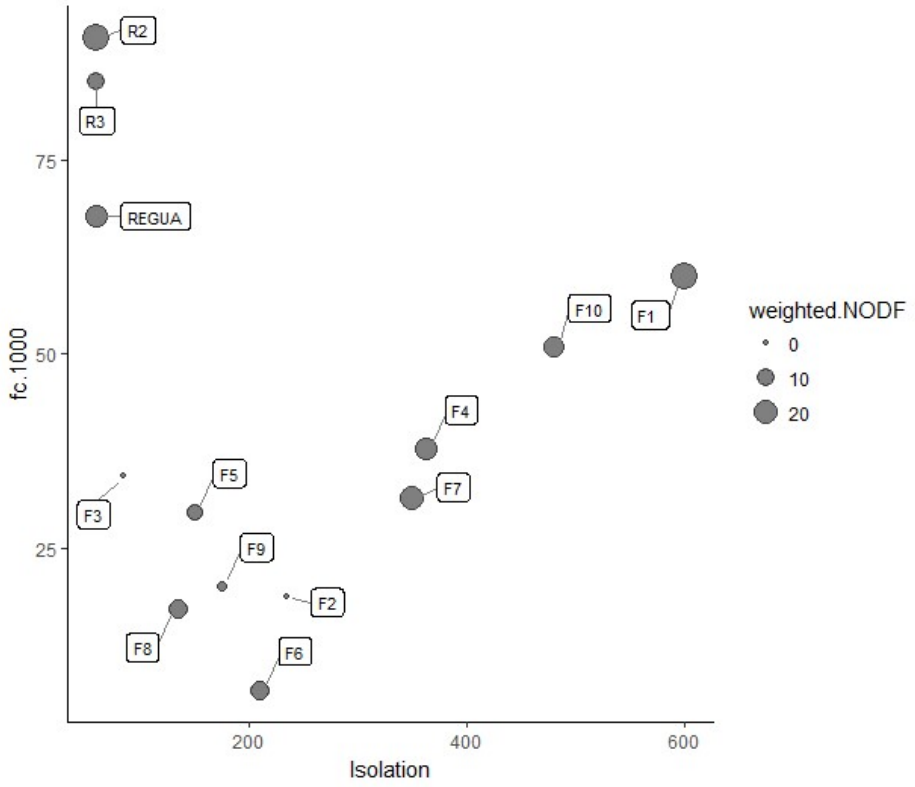


Figure 4.6: Relationship between forest cover (fc.1000), isolation and weighted NODF. The x-axis represents the fragment isolation, the y-axis represents fragment forest cover percentage in a radius of 1km surrounding the fragment and the circle diameter is scaled by the NODF value. This analysis shows that nestedness (NODF) increases both with fragment isolation and with surrounding forest cover. In isolated fragments networks may become dominated by a generalist species in a generalist community, leading to high nestedness as one species (e.g. *Carollia perspicillata)* consumes most of the resources. Similarly, an increase in suitable habitat in the surrounding landscape, may cause communities to be more diverse through immigration, and the addition of specialists that consume a subset of generalists diet will increase redundancy and thus nestedness.

Table 4.1: Species richness (R), number of herbivores, number with seeds identified and numbers of sequences identified.

	R	Herbivores	Sps with seeds Id	Samples sent for sequencing	ITS recovered	*RBCL recovered*	Seeds identified
REGUA	15	10	7	30	10	*28*	29
REGUA2	12	10	8	55	45	*52*	53
REGUA3	10	8	5	12	6	*9*	10
F01	6	5	4	46	19	*42*	42
F02	7	5	3	8	4	*8*	8
F03	11	10	7	44	26	*36*	42
F04	12	6	4	21	11	*19*	19
F05	14	11	4	37	27	*31*	32
F06	8	6	3	14	11	*13*	14
F07	13	9	6	52	29	*46*	47
F08	11	7	4	11	6	*11*	11
F09	8	6	4	12	9	*9*	12
F10	12	7	5	29	15	*25*	26

Table 4.2: Network metrics calculated for three control areas (REGUA, REGUA2 and REGUA3) and 10 fragments and their landscape characteristics.

	number of nodes	weighted connectance	nestedness	weighted NODF	modules	modularity	Area	logArea	Isolation
REGUA	11	0.18	50.68	16.67	3	0.52	62378.6	4.79	60
REGUA2	13	0.16	26.64	27.19	3	0.43	62378.6	4.79	60
REGUA3	10	0.19	27.54	10	2	0.44	62378.6	4.79	60
F01	9	0.26	0	29.17	3	0.49	21.15	1.32	600
F02	6	0.2	24.21	0	3	0.23	34.11	1.53	234
F03	6	0.29	24.63	0	3	0.28	41.04	1.61	84.85
F04	9	0.18	34.08	18.75	3	0.51	52.11	1.71	362.49
F05	8	0.18	40.03	8.33	4	0.3	84.33	1.92	150
F06	9	0.2	25.58	12.5	3	0.38	92.34	1.96	210
F07	14	0.18	30.1	21.76	4	0.41	99.99	1.99	349.85
F08	9	0.18	35.89	12.5	3	0.33	117.27	2.06	134.16
F09	13	0.16	17.92	1.39	3	0.49	184.77	2.26	174.92
F10	8	0.21	25.34	15.38	3	0.26	228.78	2.35	480

Table 4.3: Niche overlap between most abundant species (*Artibeus lituratus*, *Carollia perspicillata* and *Sturnira lilium*) and *Artibeus lituratus* and other bats in the Stenodermatini tribe.

	C. perspicillata - S. lilium	*A. lituratus -*	*A. lituratus - S. lilium*	*A. lituratus - A. fimbriatus*	*A. lituratus - A. obscurus*	*A .lituratus - C. doriae*	*A. lituratus - D. cinerea*	*A. lituratus - P. lineatus*	*A. lituratus-*	*A. lituratus - S. tildae*	*A. lituratus - V. pusilla*
		C. perspicillata							*P. bilabiatum*		
	0.24	*0.03*	*0.362*	*0*	*0.8*	*NA*	*NA*	*NA*	*0.53*	*NA*	*0.535*
REGUA	*0.07*	*0.006*	*0.08*	*0.412*	*0.9*	*0.907*	*0.907*	*NA*	*NA*	*NA*	*0.902*
REGUA2	*0.577*	*0*	*0*	*NA*	*0.7*	*NA*	*NA*	*NA*	*NA*	*NA*	*0.7*
REGUA3	*NA*	*0.56*	*NA*	*NA*	*NA*	*NA*	*NA*	*0.577*	*NA*	*0*	*NA*
F01	*NA*	*0.319*	*NA*	*NA*	*0.6*	*NA*	*NA*	*NA*	*NA*	*0.6*	*NA*
F02	*NA*	*0.236*	*NA*	*NA*	*NA*	*NA*	*0*	*NA*	*NA*	*NA*	*NA*
F03	*NA*	*0.052*	*0.164*	*NA*	*0.988*	*NA*	*0*	*0.969*	*NA*	*NA*	*0*
F05	*0.595*	*0.01*	*0.263*	*NA*	*0*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
F06	*0.707*	*0*	*0*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
F07	*0*	*0*	*0.707*	*NA*	*NA*	*NA*	*NA*	*0.97*	*NA*	*NA*	*NA*
F08	*0.663*	*0.08*	*0.295*	*NA*	*0.277*	*NA*	*NA*	*0.928*	*NA*	*NA*	*NA*
F09	*NA*	*0.949*	*NA*	*NA*	*NA*	*NA*	*NA*	*0*	*NA*	*NA*	*NA*
F10	*0.242*	*0.06*	*0*	*1*	*NA*	*NA*	*NA*	*NA*	*NA*	*0*	*NA*

CHAPTER FIVE

General Discussion

The ecological impacts of human activity are severe (Ripple *et al.* 2017) and one of the most obvious effects is deforestation and habitat fragmentation caused by urban expansion and land conversion for pastures and monoculture farming (Fahrig 2003; Haddad *et al.* 2015; Ripple *et al.* 2017). In this thesis I have investigated the effects of habitat loss and fragmentation on the bat metacommunity in a highly fragmented landscape of Atlantic Forest.

My study is based in the Macacú River Basin, an area of lowland Atlantic Forest, composed mainly of small- to medium-sized fragments that show different levels of isolation. These forest patches are in close proximity to a large area of protected continuous forest that stretches across three different reserves. The private reserve Reserva Ecológica de Guapiaçú (REGUA) connects with Três Picos State Park and Serra dos Órgãos National Park to form the third largest area of the Atlantic Forest (Ribeiro *et al.* 2009). For my study of the impacts of forest fragmentation on bat communities, I surveyed bats and collected their guano at three control sites inside the continuous forest of REGUA and 10 adjacent fragments, visiting each of these for six nights. I used the “elements of metacommunity structure” (Leibold & Mikkelson 2002; Presley *et al.* 2010) and a mix of phylogenetic and functional diversity measures (Faith 1992; Webb *et al.* 2002; Cadotte & Davies 2016) to characterize the metacommunity structure and investigate the drivers of species assembly. With the community occupancy model (Dorazio & Royle 2005), I evaluated the use of landscape properties and habitat structure as predictors of species occurrence and

the species-specific responses to changes in the landscape, while accounting for the imperfect detection of bats. Using DNA barcoding (Hebert *et al.* 2003) and network theory (Bascompte 2007), I described the mutualistic networks involving bats and plants to assess the impacts and consequences of habitat fragmentation on network topology and niche overlap (Pianka 1974).

The bat metacommunity in my study area was found to have a random structure (Leibold & Mikkelson 2002), but when meta-ensembles were considered, the Phyllostomidae and animalivorous groups showed a nested and quasi-nested structure, respectively (Leibold & Mikkelson 2002; Presley *et al.* 2010), while the herbivores showed a random structure. The nested and quasi-nested structures are distributed along an isolation gradient, with communities in smaller fragments composed of a subset of the species in larger fragments. Other studies evaluating metacommunity structure have been conducted on a broad regional scale and have reported that mammal metacommunity in the Atlantic Forest (de la Sancha *et al.* 2014), bat metacommunity in the Caribbean (Presley & Willig 2010) and vertebrate metacommunity along an elevational gradient in the Andes (Presley *et al.* 2012) have a Clementsian structure, with distinct communities substituting each other along an environmental gradient. My study used a unique approach by focussing on a smaller spatial scale, at which the abiotic conditions such as temperature, precipitation and seasonality were relatively uniform. It is interesting then that patterns of metacommunity structure exist at this scale suggesting that meta-ensemble structures may be scale dependent.

In general my results were similar to those of other studies of habitat fragmentation (Laurance *et al.* 2002; Haddad *et al.* 2017; Rocha *et al.* 2017), where larger and connected fragments harbour more biodiversity than small and isolated

fragments. The non-significant values of phylogenetic diversity (PD), mean pairwise phylogenetic distance (MPD) and functional diversity (FD) in all fragments suggest that at these sites the species assembly is driven by stochastic events. When I examine the sites inside the reserve, REGUA1 and REGUA2 had lower scores of PD and MPD, indicating that the species assembly is driven by an ecological filter and survival is mediated by inherited traits.

This is one of the first attempts to model bat community occupancy in fragmented landscape using the community occupancy model and although estimates of occupancy (MacKenzie *et al.* 2006; Kéry & Royle 2016) were not precise and they allowed few inferences about the bat metacommunity. Detection probability estimates for most bats were low, and a few more detections (>7) (MacKenzie *et al.* 2002) of rare species should allow for better predictions. Confidence intervals for occupancy estimates and the effects of covariates were so wide that they do not allow any conclusion about the importance of landscape metrics and habitat structure for bat communities. Only the accumulation of data, with many more sampling occasions could improve these estimations, and for communities with many rare species this may be a drawback in the use of the community occupancy. Area had a positive association with species occurrence for the whole metacommunity and all of the species within it. Other studies with birds in the Neotropics showed different results, with area having a positive effect on species persistence and isolation having a less obvious effect, with some species responding positively and others negatively (Ferraz *et al.* 2007). Habitat structure is important in determining the species occurring in a site of interest for birds (Pardini *et al.* 2005; Zipkin *et al.* 2009, 2010) and mammals (Vieira *et al.* 2009; Pfeifer *et al.* 2017).

Beyond simple presence and absence of species on a landscape, understanding the consequences of habitat fragmentation on ecosystem functioning and services is vital to understanding a community level response to this disruption. This project is one of the first network-based studies of the impacts of fragmentation on mutualistic interactions among frugivorous vertebrates and plants, and the first such study focused on bats. In my study, the use of DNA barcoding (Hebert *et al.* 2003) provided the means to uncover the interactions between bats and the plants that they consume, as well as reveal how these interactions are affected by the fragmentation process. Overall bat-plant interaction networks were seen to be resilient to habitat fragmentation, and even in the smaller and defaunated fragments, network structure appears to be maintained with no detectable change in its modules and connectance. Isolation and area positively impacted network nestedness, caused by the presence of specialists in larger fragments and a species-poor community dominated by generalists in smaller fragments. This resilience of bat-plant interaction networks (Mello *et al.* 2011a) suggests that even in the smallest and most isolated fragments, bats act as active agents of seed dispersal and promote forest regeneration. Thus, managing landscapes for bats should be considered an important element in any programme of forest restoration.

In this study, I concluded that habitat fragmentation has a profound effect on the bat metacommunity via its impacts on taxa within two dominant Neotropical meta-ensembles. Area reduction along with increased fragment isolation disrupts the species assembly process, leading to a domination of generalist bats such as *Artibeus lituratus*, *Carollia perspicillata* and *Sturnira lilium* and the loss of sensitive and rare species like *Chiroderma doriae, Diphylla ecaudata, Histiotus velatus*, *Micronycteris microtis*, *Micronycteris minuta*, *Peropteryx macrotis* and *Pygoderma bilabiatum*. Each

of these species was detected at only one site and, as exemplified by the heterogeneous species-specific responses to isolation and habitat structure, it is possible that they need specific conditions (roosts, prey, specific fruits or flowers, presence of water) to persist in a specific site. In the reserve, which represents the original condition of the habitat in terms of landscape configuration, vegetation structure and resource availability, the assembly process appears to be driven by competition and character displacement. The most abundant species in my study area, *A. lituratus, C. perspicillata* and *S. lilium*, showed little overlap in the dietary dimension of their ecological niche, which is expected by their membership in different modules of the bat-plant interaction network. On the other hand, *A. lituratus* showed greater niche overlap with related species from the Stenodermatini tribe. This suggest that food is not necessarily a limiting factor, as niche overlap should be negatively associated with the intensity of competition (Pianka 1974). As the community is expected to be shaped by inherited traits, and this could explain the coexistence of closely related species in natural conditions of landscape configuration and habitat structure. With the maintenance of network structure, seed dispersal by bats is an ecosystem service that is maintained even in the most small, isolated and species poor fragments which is a critically important factor in conservation management of these areas and any attempt at habitat restoration.

Although habitat fragmentation is a serious threat for biodiversity, we are still far from understanding all of its longer-term consequences (Laurance *et al.* 2002, 2018; Haddad *et al.* 2017). Future studies should consider the role of environmental filters and the traits that allows the coexistence of closely related and ecologically similar species, and the consequences of the disruption of the assembly process in small fragments. The metacommunity concept is a useful tool for linking different

scales in ecology and comparing how metacommunity structure differs across these scales may help to explain the changes caused by habitat fragmentation. Similarly, the use of DNA is a useful tool, and offers an accessible way to identify taxa in the diets of animals that would be extremely difficult to achieve using more traditional approaches based on morphological examination. The creation of a local DNA barcode library could enhance the resolution of plant identification, but this is an expensive and time-consuming task, and unlikely to help resolve some of the rapidly radiating and common taxa (e.g. *Ficus*) where taxonomy remains a problem for any identification system. Applying DNA barcoding more widely in the context of habitat fragmentation, to investigate pollinator-plant networks, host-parasitoid networks, and food webs, would likely allow a better understanding of the status of ecosystem function and services in fragmented landscapes.

The impacts of habitat fragmentation occur at multiple dimensions and scales (Banks-Leite *et al.* 2013). While fragment area is expected to be a good predictor of species richness, it does not capture all the heterogeneous responses of species in a metacommunity that are seen in relation to isolation and habitat structure. Although small fragments in a severely threatened and fragmented biome such as the Atlantic Forest do not harbour a diverse bat fauna, these remaining generalist species still act as active agents of seed dispersal and contribute to the processes of forest regeneration (Reid 2013; De La Peña-Domene *et al.* 2014). Fragmented landscapes are composed of sites that represent different levels of disturbance and habitat structure, which collectively have the potential to host a rich and diverse regional fauna (Townsend *et al.* 2014). To ensure this, large areas should be protected and expanded whenever possible, to permit the persistence of those species that are sensitive to the changes caused by habitat fragmentation. These areas could function as sources for

smaller fragments, as long they are connected or are sufficiently near to allow dispersal. My study traces the impact of forest fragmentation from the drivers of the metacommunity assembly process to the individual species responses through to the impact on ecological functions related to forest regeneration. The results of my study will contribute to the growing body of research of habitat fragmentation and provide directions to help us mitigate the impacts of large-scale habitat fragmentation that is ongoing in other parts of the world such as the Amazon, Africa and Southeast Asia.

CHAPTER SIX

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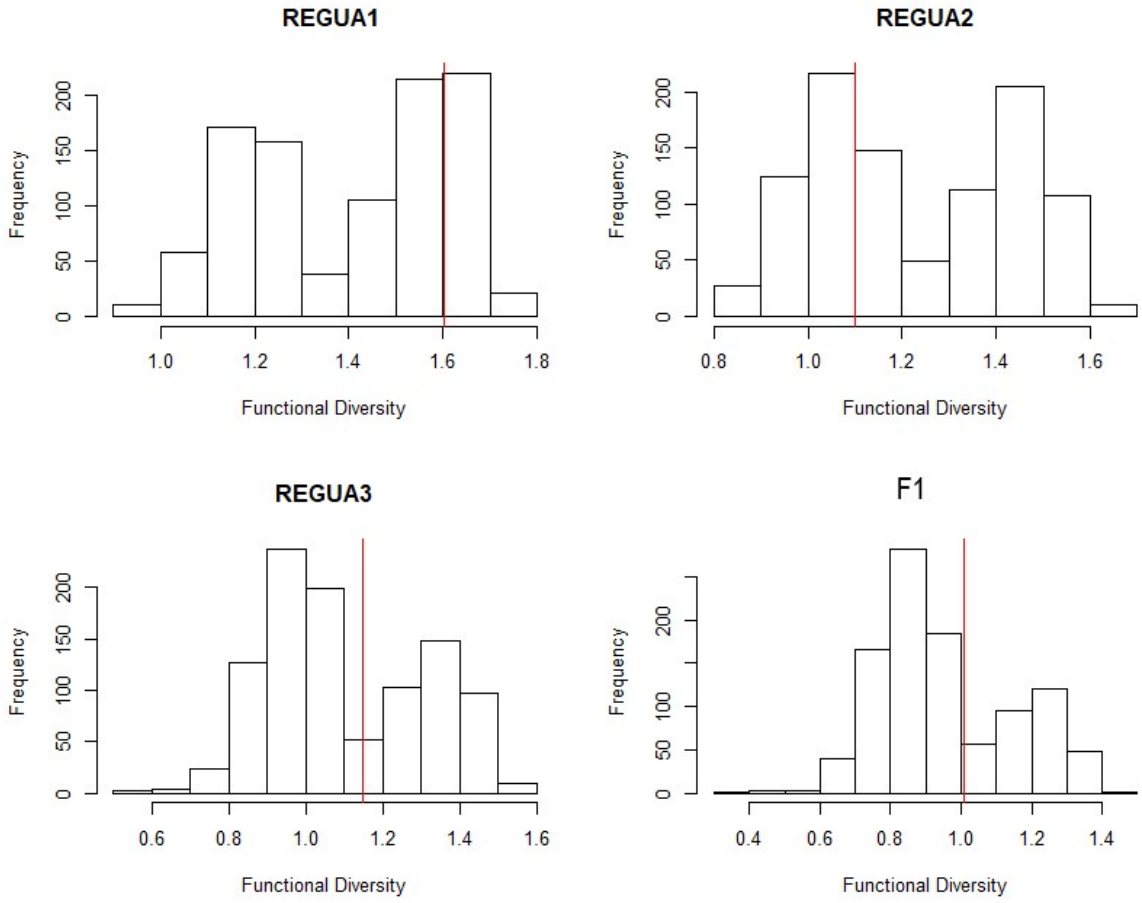
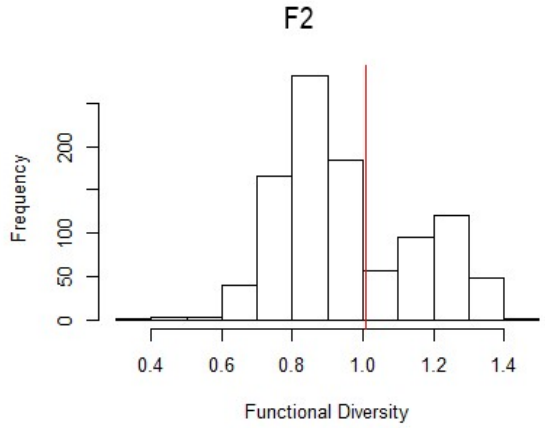
SUPPLEMENTARY MATERIALS

Figure S2.1: Histograms showing the observed value of functional diversity against 1000 null values.

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Frequency
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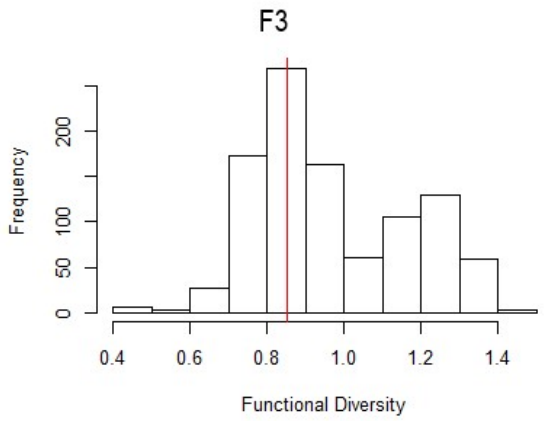
50
100
200
0.4
0.6
0.8
1.0
1.2
1.4
Functional Diversity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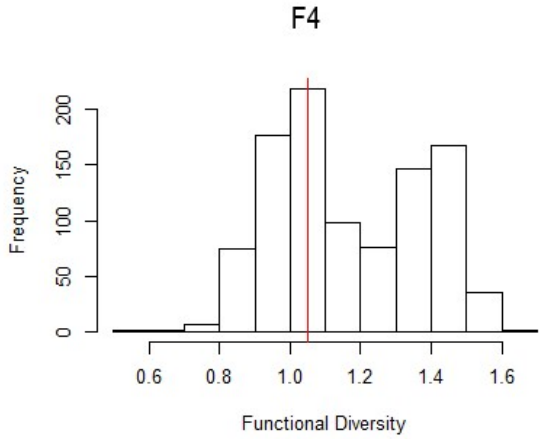
Frequency
0
50
100
200
0.4
0.6
0.8
1.0
1.2
1.4
Functional Diversity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Frequency
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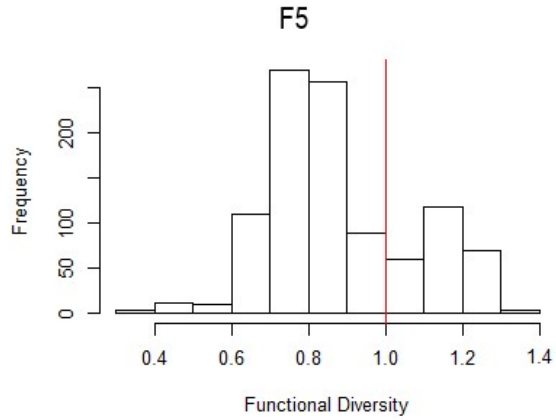
100
150
200
0.6
0.8
1.0
1.2
1.4
1.6
Functional Diversity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Frequency
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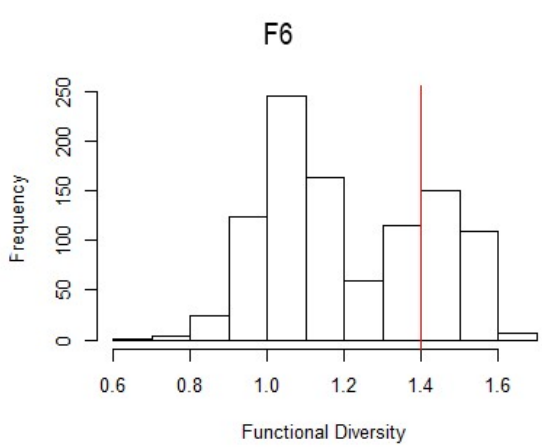
50
100
200
0.4
0.6
0.8
1.0
1.2
1.4
Functional Diversity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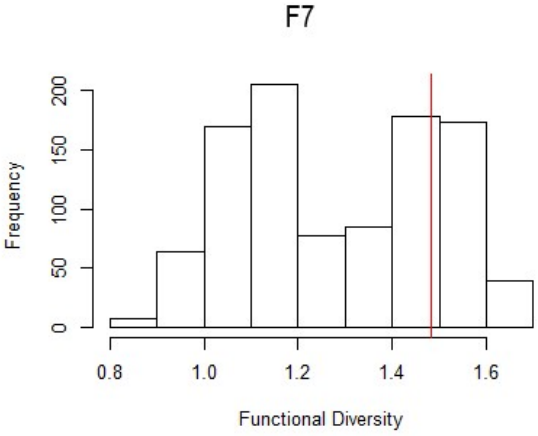
Frequency
0
50
100
150
200
250
0.6
0.8
1.0
1.2
1.4
1.6
Functional Diversity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Frequency
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1.2
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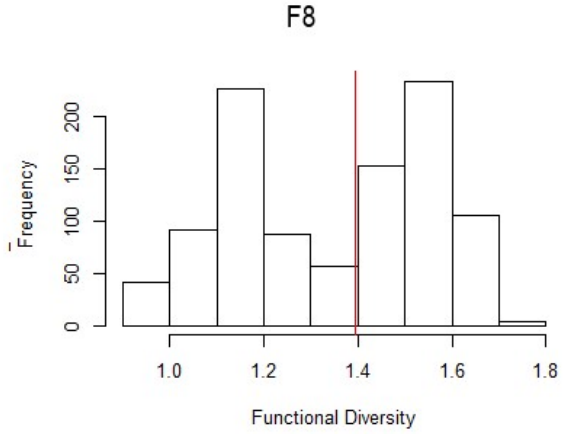
1.6
Functional Diversity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Frequency
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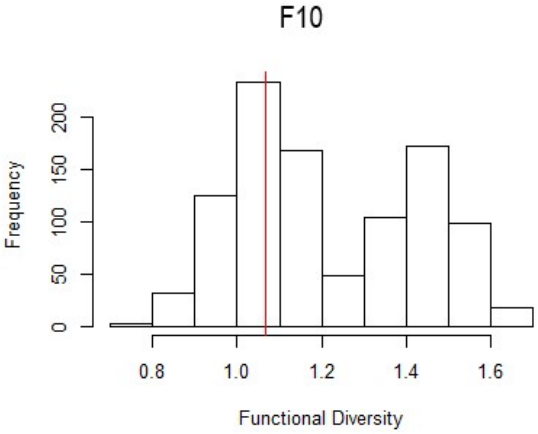
1.2
1.4
1.6
1.8
Functional Diversity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200
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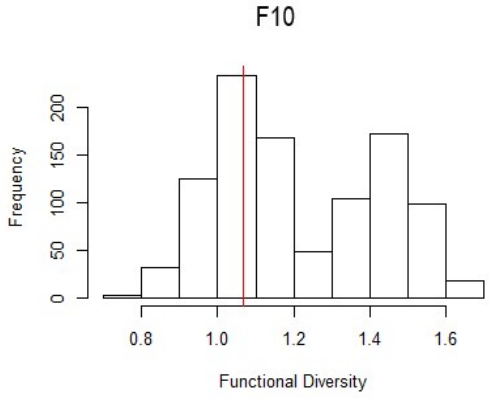
1.0
1.2
1.4
1.6
Functional Diversity


F10
Frequency
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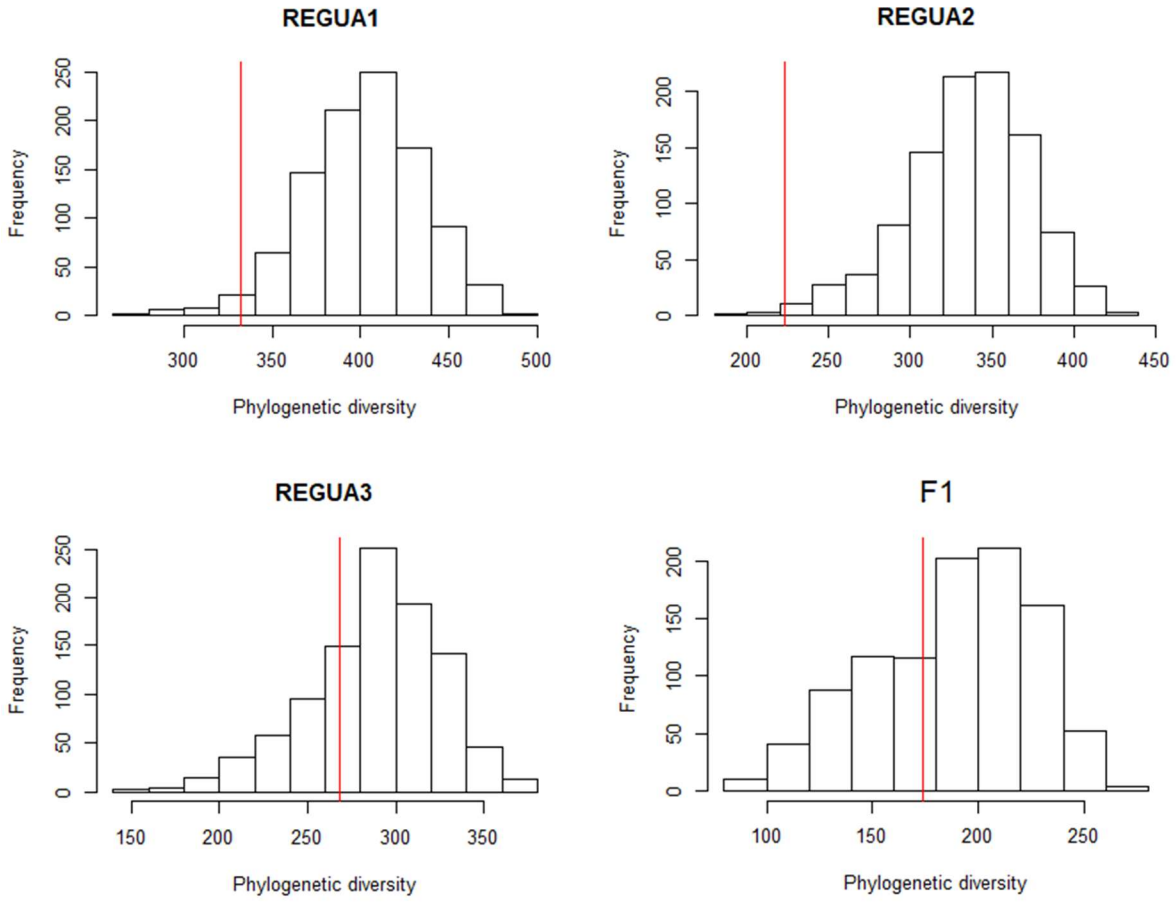
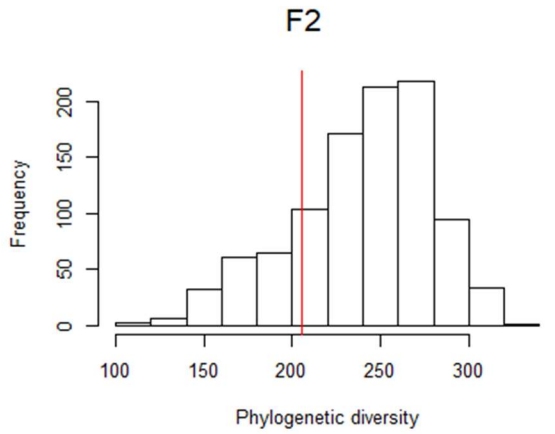
50
100
150
200
0.8
1.0
1.2
1.4
1.6
Functional Diversity

Figure S2.2: Histograms showing the observed value of phylogenetic diversity against 1000 null values.

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Frequency
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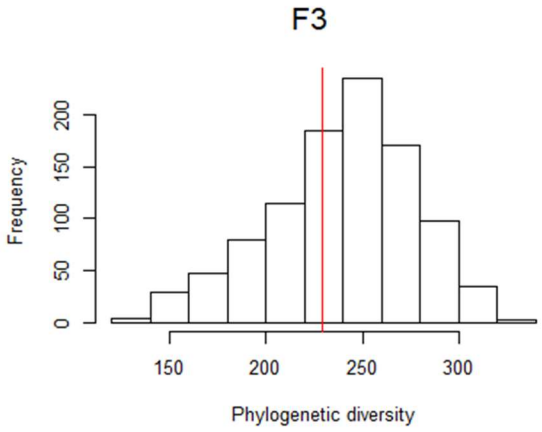
50
100
150
200
100
150
200
250
300
Phylogenetic diversity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Frequency
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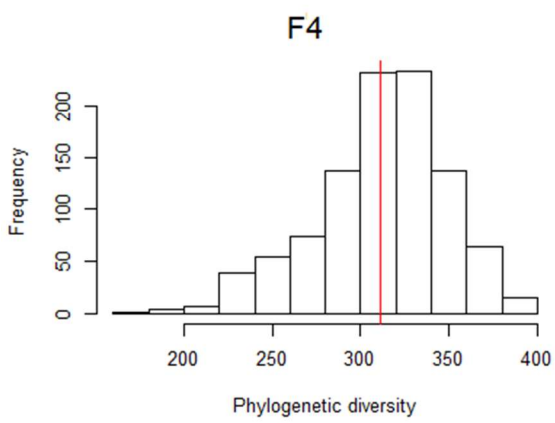
50
100
150
200
150
200
250
300
Phylogenetic diversity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Frequency
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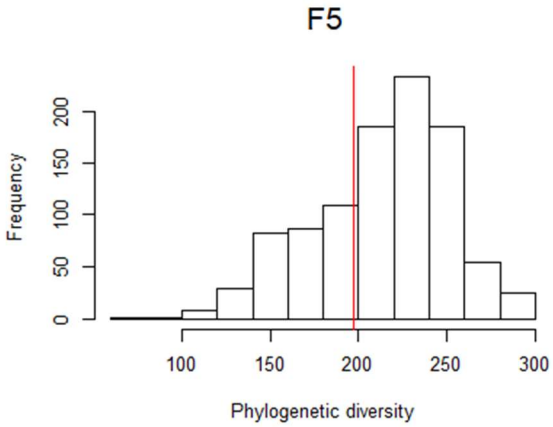
100
150
200
200
250
300
350
400
Phylogenetic diversity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Frequency
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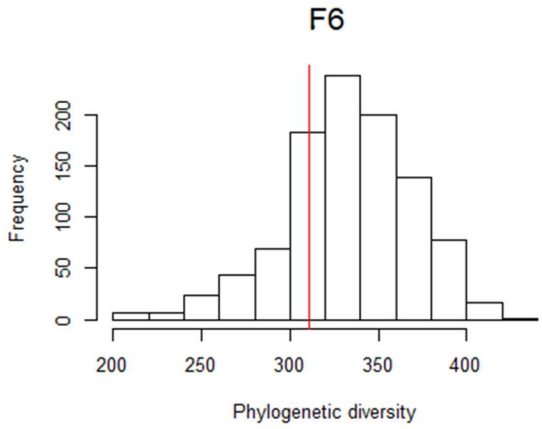
100
150
200
100
150
200
250
300
Phylogenetic diversity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Frequency
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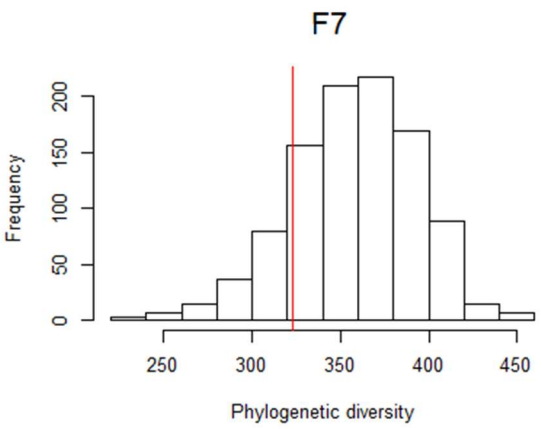
400
Phylogenetic diversity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Frequency
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250
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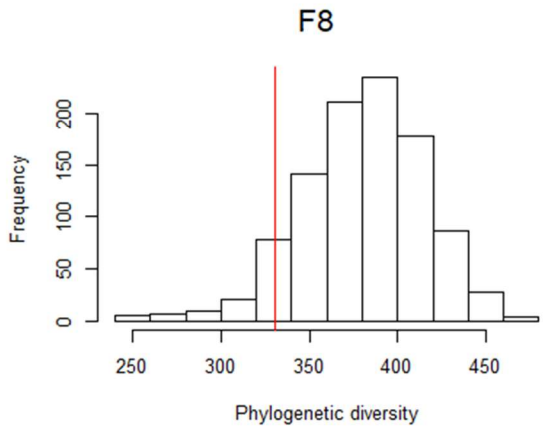
350
400
450
Phylogenetic diversity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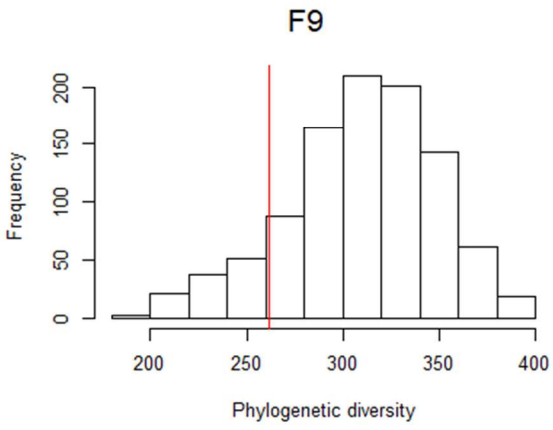
450
Phylogenetic diversity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400
Phylogenetic diversity

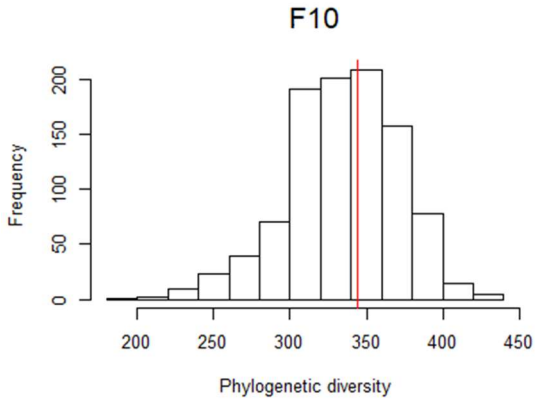
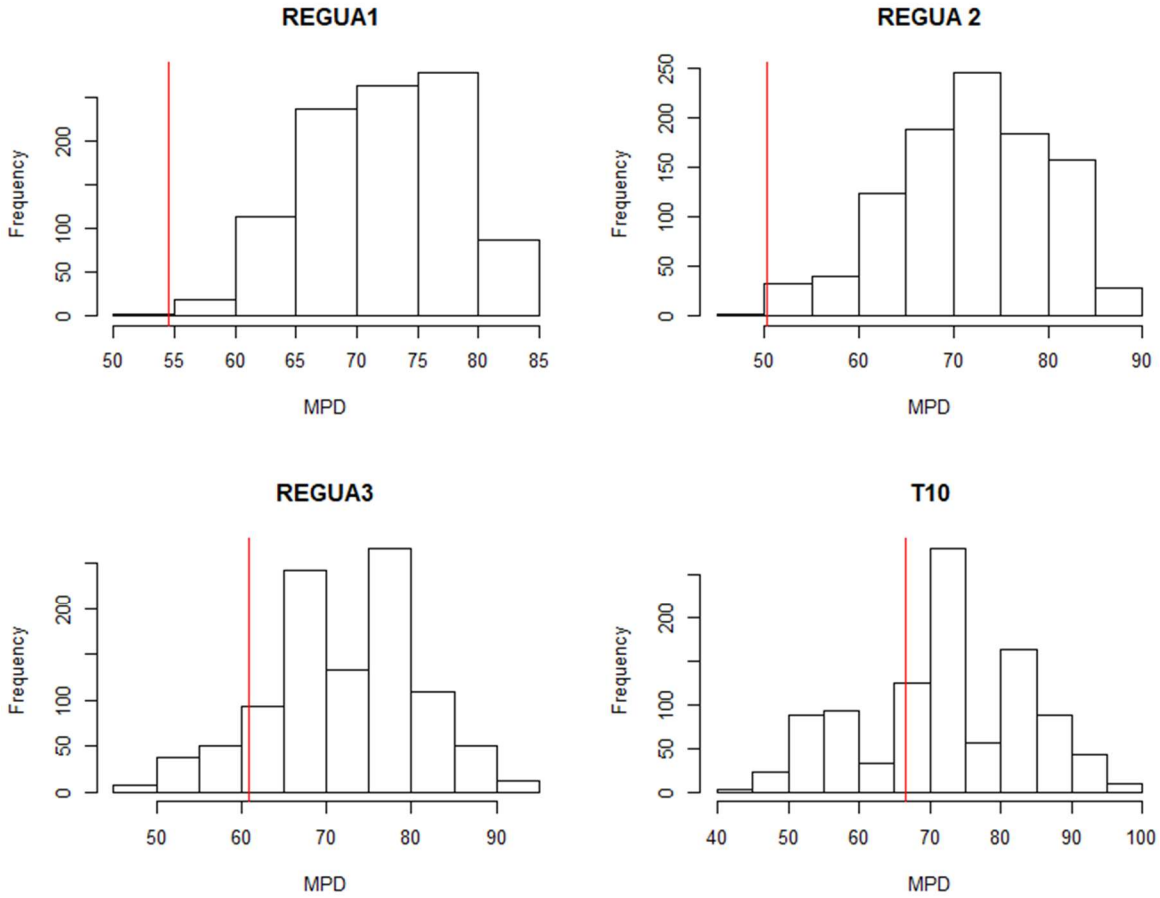
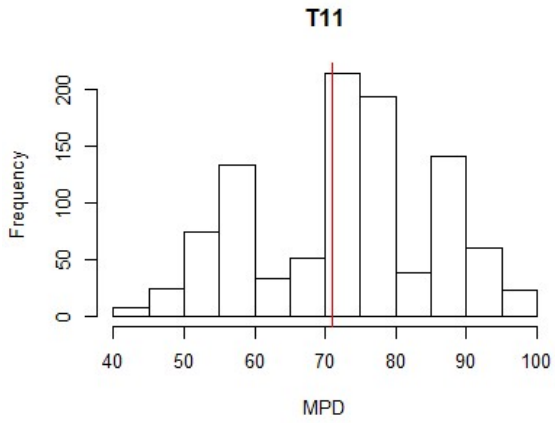

F10
Frequency
0
50
100
150
200
200
250
300
350
400
450
Phylogenetic diversity

Figure S2.3: Histograms showing the observed value of mean pairwise phylogenetic distance against 1000 null values.

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Frequency
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100
150
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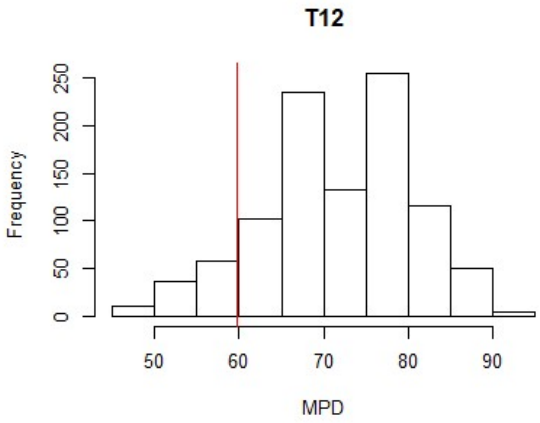
40
50
60
70
80
90
100
MPD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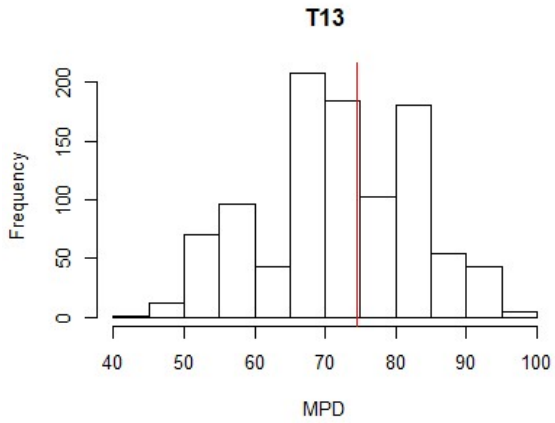
MPD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50
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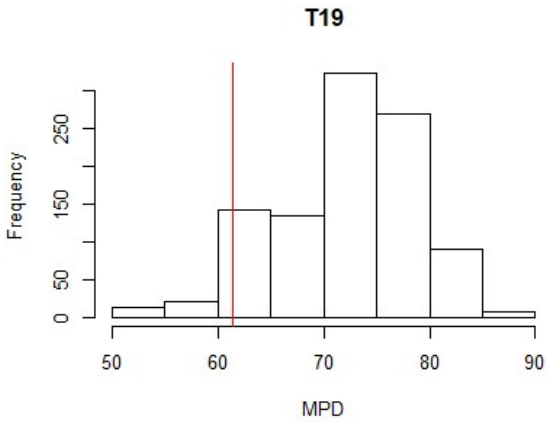
90
100
MPD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Frequency
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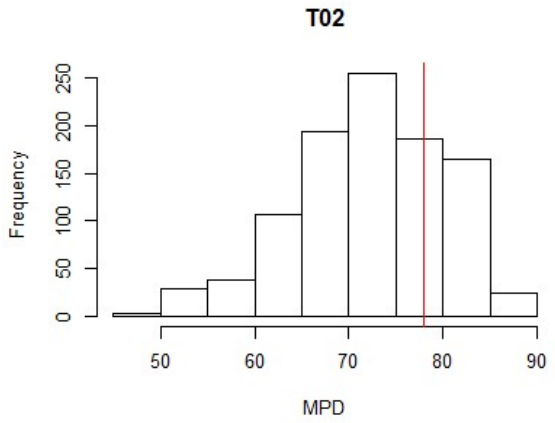
70
80
90
MPD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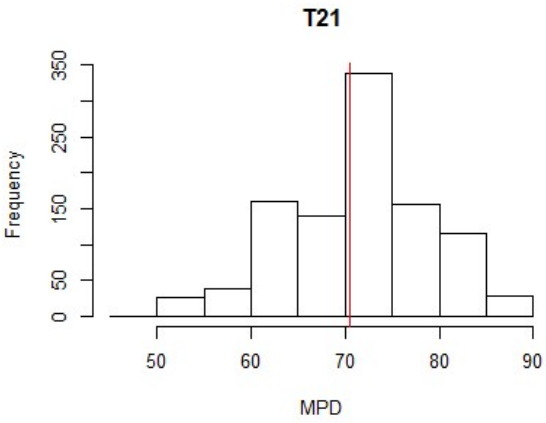
90
MPD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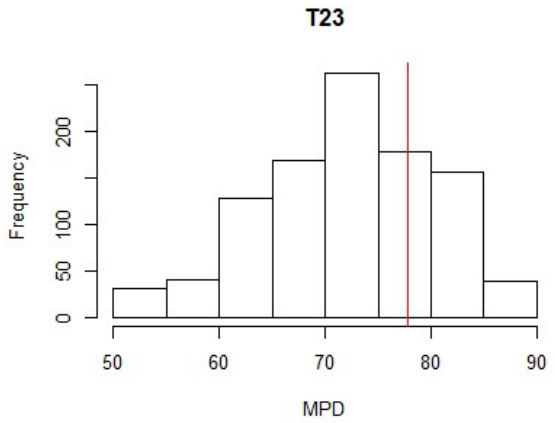
90
MPD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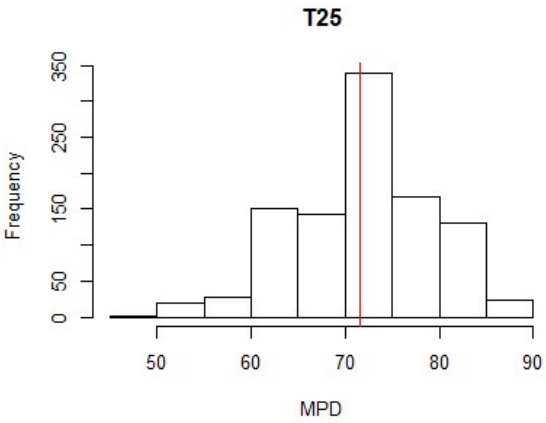
80
90
MPD


T25
Frequency
0
50
150
250
350
50
60
70
80
90
MPD

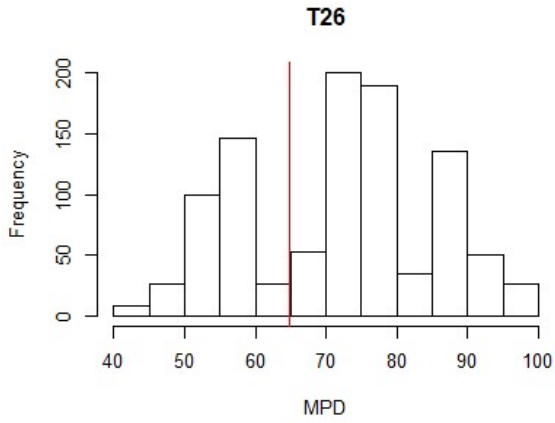

T26
Frequency
0
50
100
150
200
40
50
60
70
80
90
100
MPD

Table S3.1: Presence (1) and absence (0) of bats in the sampled sites on each of the sampling occasions. All fragments use the same codes as used through this thesis, except for: R1 = REGUA1, R2 = REGUA2, R3 = REGUA3. Numbers after the fragment code corresponds to the sampling night.

Species	R1_1	R1_2	R1_3	R1_4	R1_5	R1_6	R2_1	R2_2	R2_3	R2_4	R2_5	R2_6	R3_1	R3_2	R3_3	R3_4	R3_5	R3_6
Anoura caudifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anoura geoffroyi	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Artibeus fimbriatus	0	1	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0
Artibeus lituratus	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Artibeus obscurus	0	0	1	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1
Carollia perspicillata	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Chiroderma doriae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Dermanura cinerea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Desmodus rotundus	1	1	1	1	0	1	0	1	1	0	1	1	1	0	1	1	0	0
Diphylla ecaudata	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Eptesicus brasiliensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Histiotus velatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronycteris microtis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronycteris minuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myotis nigricans	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Myotis riparius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peropteryx macrotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllostomus hastatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platyrrhinus lineatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pygoderma bilabiatum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	0	1	1	1	1	0	0	1	1	0	0	0	1	1	0	1	1	0
Sturnira tildae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Tonatia bidens	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Trachops cirrhosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vampyressa pusilla	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1

Species	T2_1	T2_2	T2_3	T2_4	T2_5	T2_6	T10_1	T10_2	T10_3	T10_4	T10_5	T10_6	T11_1	T11_2	T11_3	T11_4	T11_5	T11_6
Anoura caudifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anoura geoffroyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus fimbriatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artibeus lituratus	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	0
Artibeus obscurus	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Carollia perspicillata	1	1	0	1	1	0	1	1	1	1	1	1	1	0	1	0	1	1
Chiroderma doriae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dermanura cinerea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0
Desmodus rotundus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Diphylla ecaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus brasiliensis	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Glossophaga soricina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Histiotus velatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronycteris microtis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronycteris minuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myotis nigricans	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Myotis riparius	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Peropteryx macrotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllostomus hastatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platyrrhinus lineatus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygoderma bilabiatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	1	1
Sturnira tildae	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tonatia bidens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachops cirrhosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vampyressa pusilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	T12_1	T12_2	T12_3	T12_4	T12_5	T12_6	T13_1	T13_2	T13_3	T13_4	T13_5	T13_6	T19_1	T19_2	T19_3	T19_4	T19_5	T19_6
Anoura caudifer	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1
Anoura geoffroyi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
Artibeus fimbriatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Artibeus lituratus	1	1	0	1	1	1	1	1	0	0	0	1	0	1	1	1	0	0
Artibeus obscurus	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0
Carollia perspicillata	1	0	0	1	1	0	1	1	0	1	0	0	1	1	1	1	1	1
Chiroderma doriae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dermanura cinerea	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Desmodus rotundus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diphylla ecaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus brasiliensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glossophaga soricina	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1
Histiotus velatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronycteris microtis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micronycteris minuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Myotis nigricans	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Myotis riparius	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Peropteryx macrotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Phyllostomus hastatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Platyrrhinus lineatus	1	0	0	1	1	0	1	0	0	1	0	0	0	0	1	0	0	1
Pygoderma bilabiatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	1	1
Sturnira tildae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Tonatia bidens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachops cirrhosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vampyressa pusilla	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	T21_1	T21_2	T21_3	T21_4	T21_5	T21_6	T23_1	T23_2	T23_3	T23_4	T23_5	T23_6	T25_1	T25_2	T25_3	T25_4	T25_5	T25_6
Anoura caudifer	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anoura geoffroyi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Artibeus fimbriatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Artibeus lituratus	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1
Artibeus obscurus	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1
Carollia perspicillata	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1
Chiroderma doriae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dermanura cinerea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Desmodus rotundus	1	1	0	1	0	0	1	1	1	1	1	1	1	1	0	0	1	1
Diphylla ecaudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eptesicus brasiliensis	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Glossophaga soricina	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Histiotus velatus	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0
Micronycteris microtis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Micronycteris minuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myotis nigricans	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Myotis riparius	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Peropteryx macrotis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllostomus hastatus	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Platyrrhinus lineatus	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Pygoderma bilabiatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sturnira lilium	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	1	1
Sturnira tildae	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Tonatia bidens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachops cirrhosus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Vampyressa pusilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	T26_1	T26_2	T26_3	T26_4	T26_5	T26_6
Anoura caudifer	0	0	0	0	0	0
Anoura geoffroyi	0	0	0	0	0	0
Artibeus fimbriatus	0	0	0	0	0	0
Artibeus lituratus	1	1	1	1	1	1
Artibeus obscurus	0	0	1	0	0	0
Carollia perspicillata	1	1	1	1	1	1
Chiroderma doriae	0	0	0	0	0	0
Dermanura cinerea	0	0	0	0	0	0
Desmodus rotundus	0	0	0	0	0	0
Diphylla ecaudata	0	0	0	0	0	0
Eptesicus brasiliensis	0	0	0	0	0	0
Glossophaga soricina	0	0	0	0	0	0
Histiotus velatus	0	0	0	0	0	0
Micronycteris microtis	0	0	0	0	0	0
Micronycteris minuta	0	0	0	0	0	0
Myotis nigricans	0	0	0	1	0	0
Myotis riparius	0	0	0	0	0	0
Peropteryx macrotis	0	0	0	0	0	0
Phyllostomus hastatus	0	0	0	0	0	0
Platyrrhinus lineatus	0	0	0	0	0	0
Pygoderma bilabiatum	0	0	0	0	0	0
Sturnira lilium	1	1	1	0	0	0
Sturnira tildae	1	0	0	0	0	0
Tonatia bidens	0	0	0	0	0	0
Trachops cirrhosus	0	0	0	0	0	0
Vampyressa pusilla	0	0	0	0	0	0

Table S3.2: Single species occupancy model. The models are named for the covariates used in it. I present the AIC, delta AIC, AIC weight and cumulative weight. Models with delta AIC < 2 have their parameter estimates shown.

Anoura caudifer	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
PCAhab2	3	40.03	0	0.471	0.47	PCAhab2	0.323	0.09	-1.54	0.1	0.4	0.31
none	2	41.74	1.71	0.2	0.67							
Area	3	43.19	3.16	0.1	0.77							
PCAhab1	3	43.56	3.53	0.08	0.85							
Prox500	3	43.68	3.65	0.07	0.93							
Isolation	3	43.73	3.7	0.07	1							
Anoura geoffroyi						model	occupancy	z	covariate (α)	z	detection	z
Prox500	3	36.04	0	0.6	0.6	Prox500	0.001	0.63	37.6	0.66	0.2	0.002
PCAhab1	3	38.45	2.41	0.18	0.79							
Area	3	38.51	2.46	0.17	0.96							
PCAhab2	3	42.18	6.14	0.02	0.99							
none	2	44.85	8.81	0.01	1							
Isolation	3	46.49	10.45	0.003	1							
Artibeus fimbriatus						model	occupancy	z	covariate (α)	z	detection	z
PCAhab1	3	46.5	0	0.5	0.5	PCAhab1	1	0.68	-72	0.66	0.25	0.004
Area	3	46.56	0.06	0.48	0.99	Area	1	0.45	148.8	0.45	0.25	0.004
Prox500	3	55.51	9.01	0.005	1							
none	2	59.15	12.65	0.001	1							
Isolation	3	59.71	13.21	0.001	1							
PCAhab2	3	61.03	14.53	0.001	1							

Artibeus lituratus	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
none	2	96.8	0	0.35	0.35	none	1	0.79	*	*	0.72	0.0002
Isolation	3	98.8	2	0.13	0.48							
Prox500	3	98.8	2	0.13	0.61							
Area	3	98.8	2	0.13	0.74							
PCAhab1	3	98.8	2	0.13	0.87							
PCAhab2	3	98.8	2	0.13	1							
Artibeus obscurus						model	occupancy	z	covariate (α)	z	detection	z
none	2	107.94	0	0.35	0.35	none	1	0.79	*	*	0.39	0.04
PCAhab2	3	109.94	2	0.13	0.48							
Isolation	3	109.94	2	0.13	0.61							
PCAhab1	3	109.94	2	0.13	0.74							
Area	3	109.94	2	0.13	0.87							
Prox500	3	109.94	2	0.13	1							
Carollia perspicillata						model	occupancy	z	covariate (α)	z	detection	z
none	2	80.337	0	0.35	0.35	none	1	0.86	*	*	0.8	0.001
Isolation	3	82.37	2	0.13	0.48							
Prox500	3	82.37	2	0.13	0.61							
PCAhab2	3	82.37	2	0.13	0.74							
Area	3	82.37	2	0.13	0.87							
PCAhab1	3	82.37	2	0.13	1							

Dermanura cinerea	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
Prox500	3	53.14	0	0.37	0.37	prox500	1	0.6	35	0.6	0.13	0.001
Isolation	3	53.19	0.04	0.364	0.74	Isolation	1	0.49	-104	0.5	0.13	0.001
none	2	55.53	2.39	0.112	0.85							
PCAhab2	3	56.78	3.64	0.06	0.91							
Area	3	57.28	4.13	0.04	0.95							
PCAhab1	3	57.35	4.2	0.04	1							
Diphyla ecaudata						model	occupancy	z	covariate (α)	z	detection	z
Isolation	3	16.92	0	0.4		Isolation	0.01	0.45	-238	0.45	0.16	0.03
Area	3	18.56	1.64	0.18		area	0.01	0.94	11.65	0.03	0.11	0.005
PCAhab1	3	18.56	1.64	0.18		PCAhab1	0.01	0.92	-10.96	0.88	0.11	0.005
Prox500	3	18.57	1.65	0.18								
PCAhab2	3	22.08	5.17	0.03								
none	2	22.6	5.69	0.02		model	occupancy	z	covariate (α)	z	detection	z
Desmodus rotundus						area	0.74	0.34	2.04	0.28	0.56	0.41
Area	3	85.38	0	0.34	0.34	PCAhab	0.69	0.31	-1.5	0.19	0.56	0.41
PCAhab1	3	85.74	0.36	0.28	0.62	none	0.62	0.39	*	*	0.55	0.43
none	2	87	1.62	0.15	0.77							
PCAhab2	3	88.06	2.68	0.08	0.86							
Prox500	3	88.35	2.96	0.07	0.74							
Isolation	3	88.72	3.34	0.06	1							

Epitesicus brasiliensis	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
Isolation	3	35.02	0	0.67	0.67	Isolation	1	0.73	58.8	0.7	0.13	0.001
PCAhab2	3	38.47	3.45	0.12	0.79							
Prox500	3	39.34	4.32	0.08	0.87							
PCAhab1	3	40.22	5.2	0.05	0.98							
Area	3	40.42	5.4	0.04	0.97							
none	2	41	5.98	0.03	1							
Glossophaga soricina						model	occupancy	z	covariate (α)	z	detection	z
Area	3	67.83	0	0.67	0.67	area	1	0.53	67	0.59	0.26	0.001
PCAhab1	3	70.03	2.2	0.22	0.89							
Isolation	3	73	5.18	0.05	0.94							
none	2	73.87	6.04	0.03	0.97							
Prox500	3	35.68	7.85	0.01	99							
PCAhab2	3	35.81	7.98	0.01	1							
Histiotus velatus						model	occupancy	z	covariate (α)	z	detection	z
Prox500	3	14.33	0	0.78	0.78	PROX500	0.01	0.66	-41.7	0.66	0.5	0.99
none	2	19.34	5.01	0.06	0.85							
PCAhab1	3	19.74	5.41	0.05	0.9							
Area	3	20.49	6.16	0.036	0.93							
PCAhab2	3	20.63	6.3	0.03	0.97							
Isolation	3	20.71	6.38	0.03	1							

Micronycteris minuta	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
Prox500	3	25.51	0	0.41	0.41	PROX500	0.001	0.77	45.7	0.77	0.1	0.001
PCAhab1	3	26.66	1.15	0.22	0.64	PCAhab1	1	0.71	-69.9	0.7	0.08	0.001
Area	3	27.01	1.5	0.19	0.83	Area	1	0.4	73.2	0.4	0.08	0.001
PCAhab2	3	28.45	2.94	0.09	0.92							
none	2	29.43	3.92	0.05	0.98							
Isolation	3	31.43	5.92	0.02	1							
Myotis nigricans						model	occupancy	z	covariate (α)	z	detection	z
Prox500	3	70.66	0	0.76	0.76	PROX500	0.63	0.54	-2.2	0.05	0.34	0.05
none	2	75.5	4.83	0.06	0.83							
Isolation	3	76.19	5.53	0.04	0.88							
PCAhab1	3	76.35	5.68	0.04	0.92							
PCAhab2	3	76.54	5.88	0.04	0.96							
Area	3	76.81	6.15	0.03	1							
Pygoderma bilabiatum						model	occupancy	z	covariate (α)	z	detection	z
Isolation	3	12.92	0	0.27	0.27	Isolation	0.001	0.57	-293	0.57	0.08	0.02
Area	3	13.72	0.8	0.18	0.45	Area	0.001	0.92	8.61	0.9	0.05	0.005
PCAhab1	3	13.72	0.8	0.18	0.63	PCAhab1	0.001	0.91	-10.31	0.89	0.05	0.005
Prox500	3	13.74	0.82	0.18	0.81	Prox500	0.001	0.73	31	0.73	0.05	0.008
none	2	14.7	1.78	0.11	0.92	none	0.32	0.23	*	*	0.39	0.35
PCAhab2	3	15.45	2.53	0.076	1							

Pyllostomus hastatus	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
none	2	49.72	0	0.35	0.35	none	0.35	0.36	*	*	0.29	0.08
Area	3	51.68	1.97	0.13	0.48	Area	0.35	0.67	0.12	0.85	0.29	0.08
PCAhab1	3	51.71	1.99	0.13	0.61	PCAhab1	0.35	0.36	-0.005	0.93	0.29	0.08
PCAhab2	3	51.72	2	0.13	0.74							
Isolation	3	51.72	2	0.13	387							
Prox500	3	51.72	2	0.13	1							
Platyrrhinus lineatus						model	occupancy	z	covariate (α)	z	detection	z
none	2	73.87	0	0.29	0.29	none	0.61	0.5	*	*	0.29	0.02
Prox500	3	74.37	0.5	0.23	0.52	Prox500	0.64	0.5	-0.95	0.3	0.29	0.02
Isolation	3	15.56	1.7	0.13	0.65	Isolation	0.62	0.5	-0.42	0.59	0.29	0.02
Area	3	75.6	1.73	0.13	0.65	Area	0.62	0.5	-0.3	0.6	0.29	0.02
PCAhab1	3	75.71	1.84	0.12	0.89	PCAhab1	0.62	0.5	0.29	0.69	0.29	0.02
PCAhab2	3	75.86	1.99	0.11	1	PCAhab2	0.62	0.5	-0.06	0.92	0.29	0.02
Peropteryx macrotis						model	occupancy	z	covariate (α)	z	detection	z
none	2	18.47	0	0.3	0.3	none	1	0.7				0.82
Prox500	3	19.28	0.78	0.2	0.5	Prox500						
Isolation	3	20.02	1.56	0.14	0.64	Isolation						
PCAhab2	3	20.25	1.78	0.12	0.77	PCAhab2						
Area	3	20.28	1.181	0.12	0.89	Area						
PCAhab1	3	20.42	1.96	0.11	1	PCAhab1						

Sturnira lilium	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
none	2	112	0	0.35	0.35	none	1	0.7	*	*	0.48	0.82
PCAhab1	3	114.08	2	0.13	0.48							
Prox500	3	114.08	2	0.13	0.61							
Isolation	3	114.08	2	0.13	0.74							
PCAhab2	3	114.08	2	0.13	0.87							
Area	3	114.08	2	0.13	1							
Sturnira tildae						model	occupancy	z	covariate (α)	z	detection	z
none	2	67.46	0	0.35	0.35	none	1	0.85	*	*	0.14	0.001
Isolation	3	69.35	1.89	0.14	0.49	Isolation	0.96	0.42	1.82	0.58	0.15	0.001
PCAhab1	3	69.46	2	0.13	0.61							
Prox500	3	69.46	2	0.13	0.74							
Area	3	69.46	2	0.13	0.87							
PCAhab2	3	69.46	2	0.13	1							
Tonatia bidens						model	occupancy	z	covariate (α)	z	detection	z
Isolation	3	13.7	0	0.2	0.2	Isolation	0.001	0.69	-40.6	0.68	0.06	0.03
Area	3	13.72	0.02	0.2	0.4	Area	0.001	0.92	8.61	0.9	0.05	0.005
PCAhab1	3	13.72	0.02	0.2	0.6	PCAhab1	0.001	0.91	-10.3	0.89	0.05	0.005
Prox500	3	13.14	0.03	0.2	0.8	Prox500	0.001	0.73	31	0.73	0.05	0.008
none	2	14.7	1	0.12	0.92	none	0.93	0.93	*	*	0.01	0.001
PCAhab2	3	15.45	1.75	0.08	1	PCAhab2	0.32	0.23		0.93	0.39	0.35

Trachops cirrhosus	number of parameters	AIC	delta	AIC weight	cummulative weight	model	occupancy	z	covariate (α)	z	detection	z
Isolation	3	12.89	0	0.41	0.41	Isolation	0.001	0.83	22	0.83	0.08	0.02
none	2	14.7	1.82	0.17	0.58	none	0.99	0.93	*	*	0.01	0.001
Prox500	3	14.77	1.89	0.16	0.74	Prox500	0.001	0.8	43.9	0.79	0.03	0.001
PCAhab2	3	2.84	2.84	0.1	0.84							
PCAhab1	3	3.29	3.29	0.08	0.92							
Area	3	3.29	3.29	0.08	1							
Vampyressa pusila						model	occupancy	z	covariate (α)	z	detection	z
PCAhab1	3	38.72	0	0.86	0.86	PCAhab1	1	0.41	-199	0.4	0.4	0.41
Area	3	42.6	3.88	0.12	0.98							
Isolation	3	47.31	8.59	0.01	1							
Prox500	3	50.89	12.17	0.001	1							
none	2	52.29	13.57	0.001	1							
PCAhab2	3	54.83	15.57	0.0001	1							

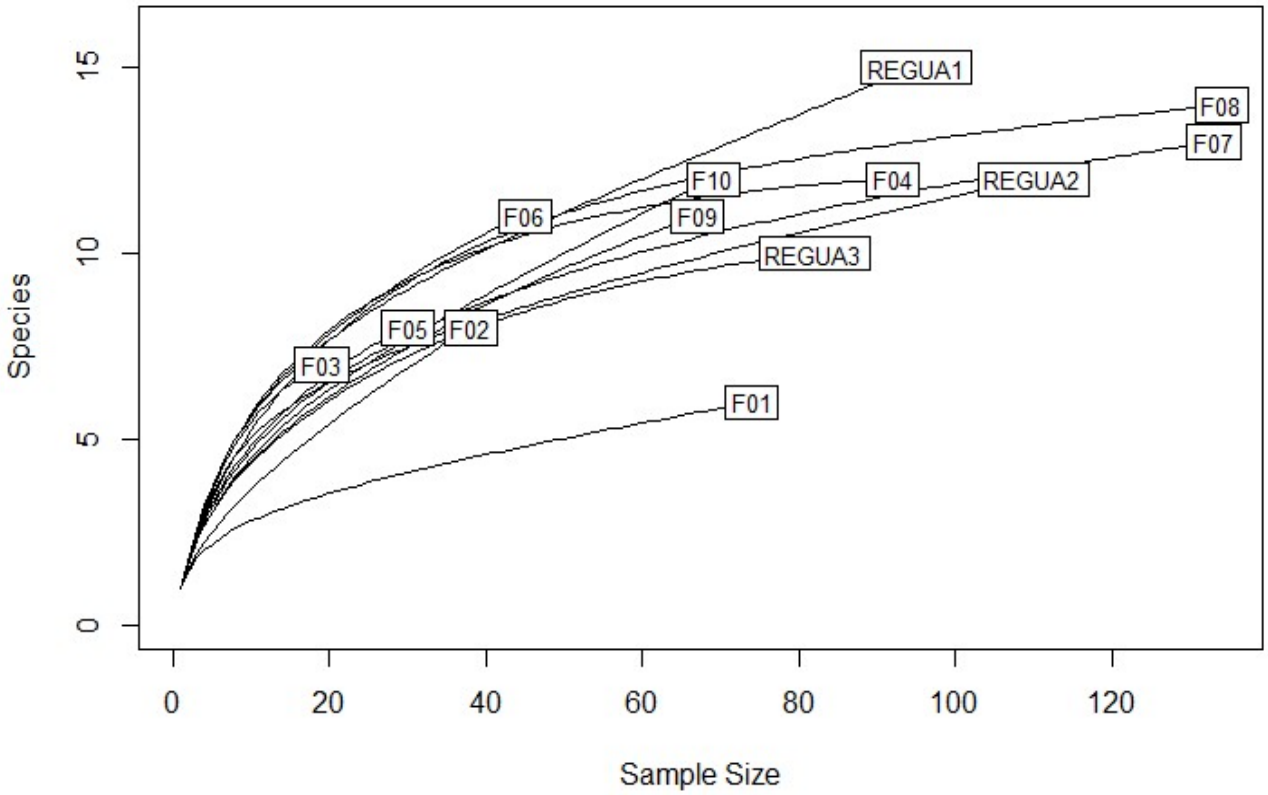


Figure S4.1: Rarefaction curves for each of the sampled sites, showing that most of curves reached a plateau of diversity.

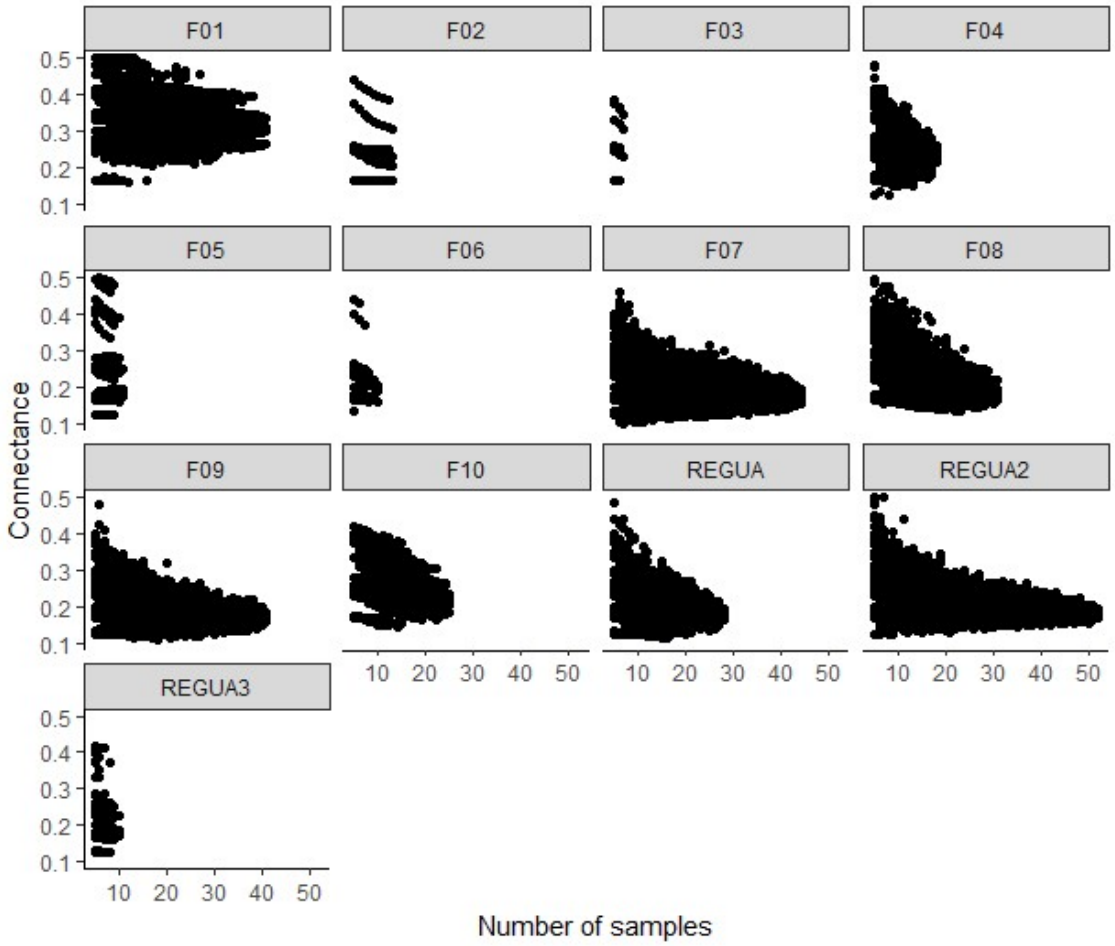


Figure S4.2: Changes in connectance metric according to sample size. Each metric was simulated with a subset of the data of each site 500 times. This shows that small sample sizes can lead to different estimations of connectance, but with increased sample size estimations are more precise.

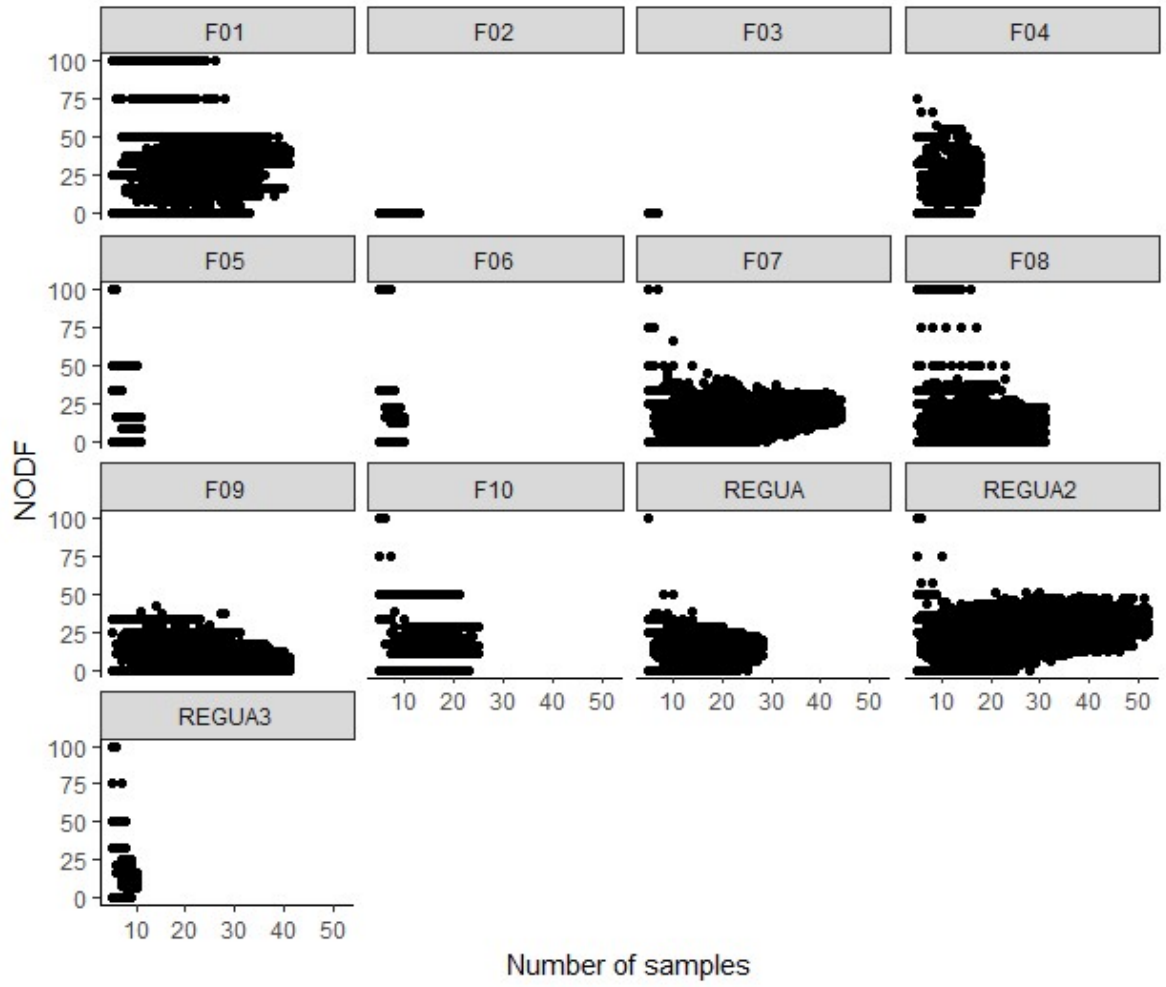


Figure S4.3: Changes in NODF metric according to sample size. Each metric was simulated with a subset of the data of each site 500 times. This analysis shows that NODF values are highly dependent of network structure and that random network structures can give a wide range of values for this metric.

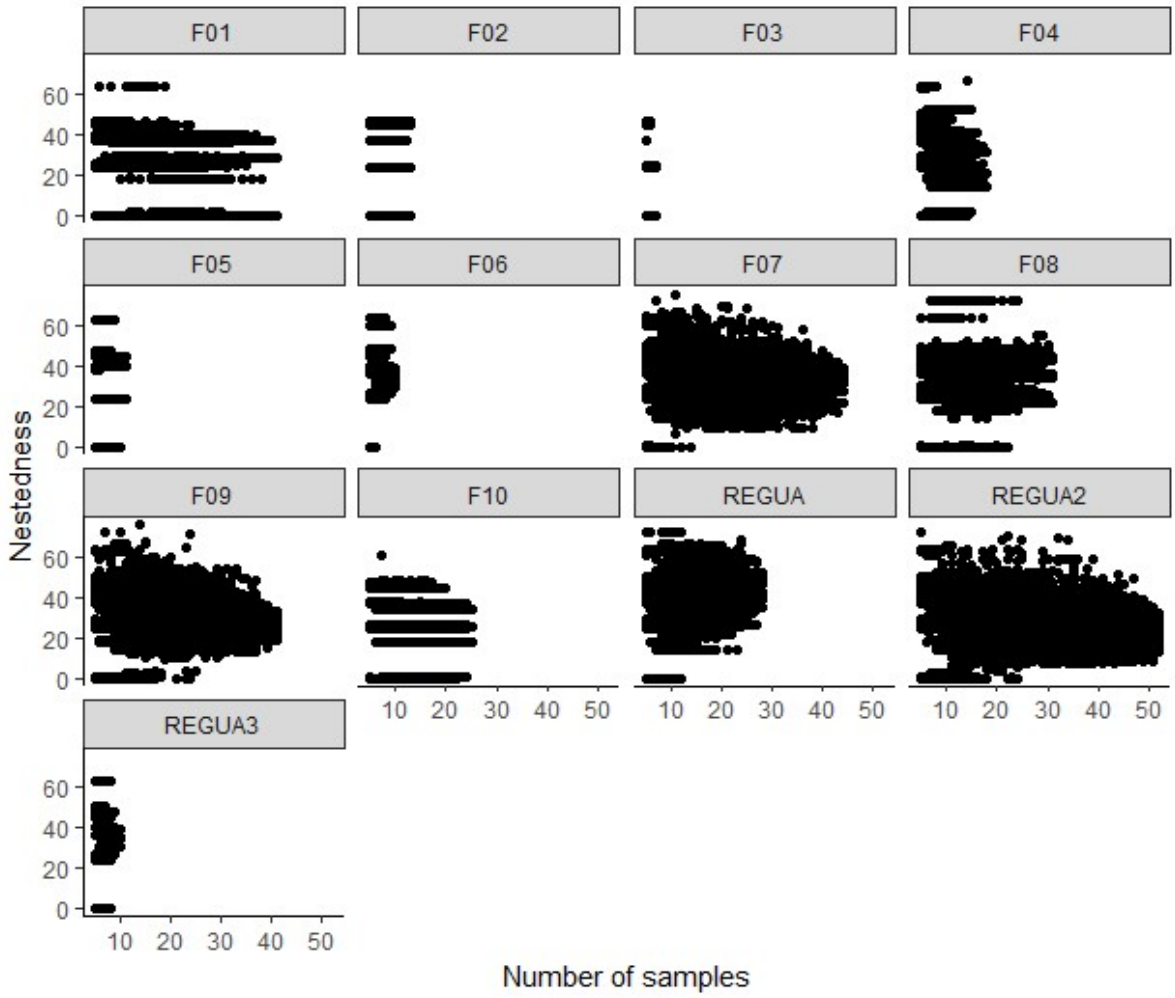


Figure S4.4: Changes in nestedness (T) metric according to sample size. Each metric was simulated with a subset of the data of each site 500 times. This analysis shows that nestedness values are highly dependent of network structure and that random network structures can give a wide range of values for this metric.

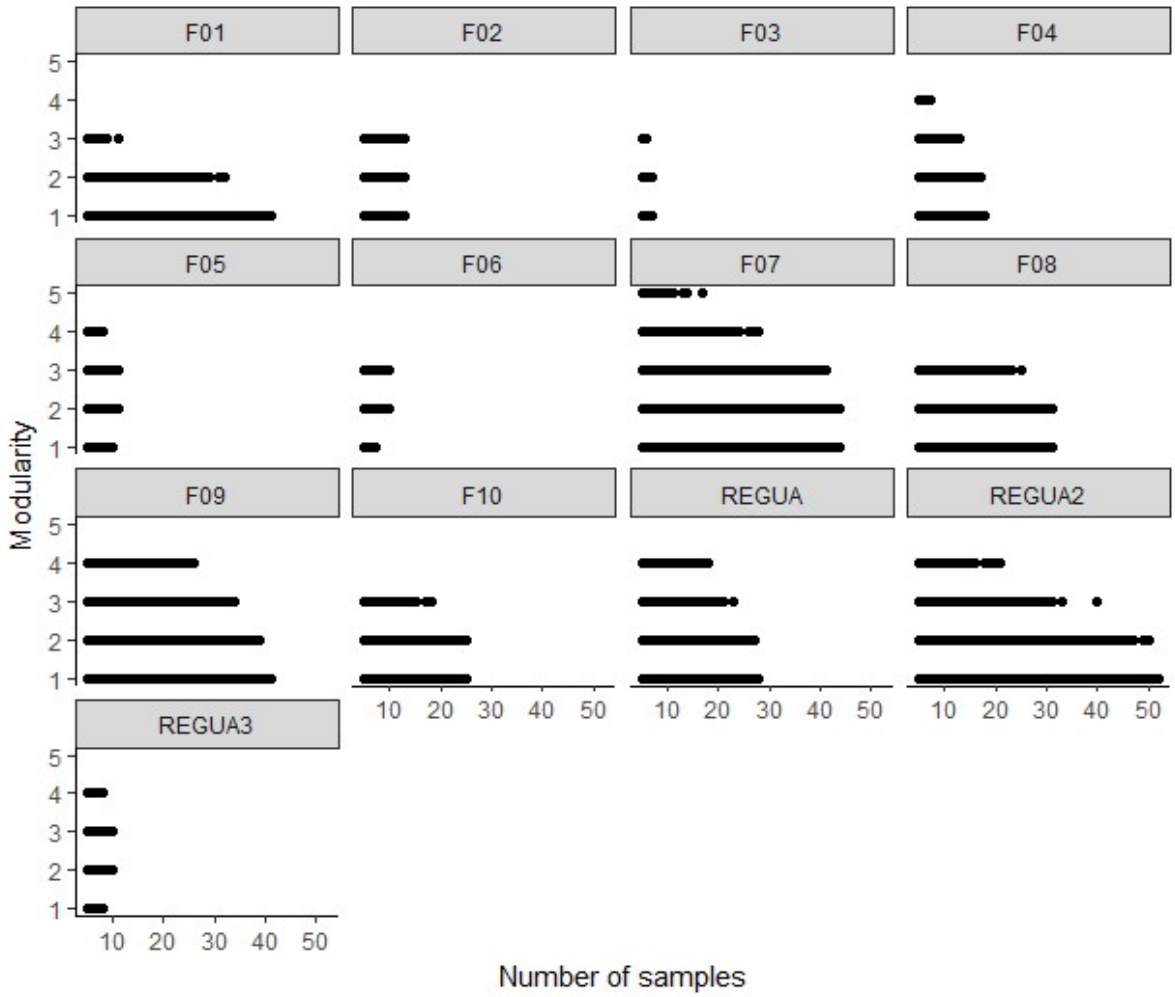


Figure S4.5: Changes in modularity metric according to sample size. Each metric was simulated with a subset of the data of each site 500 times. This analysis shows that modularity values are highly dependent of network structure and that random network structures can give a wide range of values for this metric.