Matrix-mitigated edge and area effects on Neotropical bats in a fragmented landscape

Milou Groenenberg
00701889
September 2012

A thesis submitted in partial fulfilment of the requirements of the degree of Master of Science and the Diploma of Imperial College London.
I declare that this thesis:

‘Matrix-mitigated edge an area effects on Neotropical bats in a fragmented landscape’

is entirely my own work and that where material could be construed as the work of others, it is fully cited and referenced, and/or with appropriate acknowledgement given.

Name of student: Milou Groenenberg

Signature:

Name of Supervisors: Dr. Cristina Banks-Leite
Dr. Christoph F.J. Meyer
# Table of Contents

List of figures 4  
List of tables 4  
List of acronyms 5  
Abstract 6  
Acknowledgements 7  

1. Introduction 8  
1.1 Deforestation 8  
1.2 Fragmentation 8  
1.3 Edge effects 9  
1.4 Area and edge effects 9  
1.5 The matrix matters 10  
1.6 Bats as a model 10  
1.7 Edge effects on bats 10  
1.8 Aims and objectives 11  

2. Background 12  
2.1 Edge effects on bats 12  
2.2 Underlying mechanisms 13  
2.3 Species composition 14  
2.4 The impact of patch size and the interaction between patch size and edge effects 16  
2.5 Vegetation 17  
2.5.1 The matrix 17  
2.5.2 Vegetation characteristics 18  
2.6 Expectations 18  

3. Methods 20  
3.1 Study site 20  
3.2 Methodological framework 21  
3.3 Field methods 23  
3.3.1 Bat sampling 23  
3.3.2 Vegetation sampling 24  
3.4 Analytical methods 25  

4. Results 29  
4.1 Completeness of the bat inventory 29  
4.2 Species richness, diversity, evenness and abundance at the assemblage level 30  
4.3 Species composition 31  
4.4 Differences in vegetation structure and composition between habitat types 34  
4.5 The influence of vegetation characteristics on bats 35  

5. Discussion 36  
5.1 Edge effects 36  
5.2 Area effects 39  
5.3 Caveats 40  
5.4 Conservation Implications 42  

References 44  
Appendix 1. Bat inventory 58
The page contains a list of figures and a list of tables. Here are the details:

**List of figures**

- **Figure 3.1** An experimentally fragmented 1ha forest patch of the BDFFP.
- **Figure 3.2** Map of the ‘biological dynamics of forest fragmentation project’-research area.
- **Figure 3.3** Schematic overview of the sampling design.
- **Figure 4.1** Species accumulation curve for the complete bat inventory.
- **Figure 4.2** Species accumulation curves for the interior-, edge- and matrix habitat.
- **Figure 4.3** Rank Abundance curves for the interior-, edge- and matrix habitat.
- **Figure 4.4** Mean capture rate in the interior-, edge- and matrix habitats in each fragment size category.
- **Figure 4.5** The first two PCOA vectors of the principle coordinate analysis based on bat capture rates.
- **Figure 4.6** Mean and standard errors of the first vector of the PCOA analysis based on bat capture rates in interior-, edge- and matrix habitats.
- **Figure 4.7** Mean capture rates of the guilds and four most abundant species.
- **Figure 4.8** First two PCA vectors of vegetation characteristics in interior-, edge- and matrix habitat.
- **Figure 4.9** Capture rate of bats in relation to the first PCA vector of vegetation characteristics.

**List of tables**

- **Table 2.1** Overview of all recent (>1995) scientific literature on edge effects on bats.
- **Table 3.1** Properties of the study sites and sampling effort per treatment.
- **Table 4.1** Mean values of the attributes of the bat assemblage and vegetation data and p-values for RM-ANOVA model 1, 2 and 3.
- **Table 4.2** Vegetation characteristic with the most influence on the first vegetation PCA-1.
<table>
<thead>
<tr>
<th>Acronym</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>AGB</td>
<td>Above Ground Biomass</td>
</tr>
<tr>
<td>ANI</td>
<td>Gleaning animalivores</td>
</tr>
<tr>
<td>ANOVA</td>
<td>Analysis of Variance</td>
</tr>
<tr>
<td>BDFFP</td>
<td>Biological Dynamics of Forest Fragmentation Project</td>
</tr>
<tr>
<td>CF</td>
<td>Cabo Frio</td>
</tr>
<tr>
<td>CO</td>
<td>Colosso</td>
</tr>
<tr>
<td>DBH</td>
<td>Diameter at Breast Height</td>
</tr>
<tr>
<td>DI</td>
<td>Dimona</td>
</tr>
<tr>
<td>FL</td>
<td>Florestal</td>
</tr>
<tr>
<td>FR</td>
<td>Frugivores</td>
</tr>
<tr>
<td>FR CN</td>
<td>Canopy frugivores</td>
</tr>
<tr>
<td>FR OPP</td>
<td>Opportunistic frugivores</td>
</tr>
<tr>
<td>FR SH</td>
<td>Shrub frugivores</td>
</tr>
<tr>
<td>GEE</td>
<td>Geometric Edge Effects</td>
</tr>
<tr>
<td>GLM</td>
<td>Generalized Linear Model</td>
</tr>
<tr>
<td>IBT</td>
<td>Island Biogeographic Theory</td>
</tr>
<tr>
<td>INS</td>
<td>Aerial insectivores</td>
</tr>
<tr>
<td>K41</td>
<td>KM-41</td>
</tr>
<tr>
<td>mnh</td>
<td>Mist Net Hours</td>
</tr>
<tr>
<td>NEC</td>
<td>Nectarivores</td>
</tr>
<tr>
<td>PA</td>
<td>Porto Alegre</td>
</tr>
<tr>
<td>PCoA</td>
<td>Principle Coordinate Analysis</td>
</tr>
<tr>
<td>RM-ANOVA</td>
<td>Repeated Measures Analysis of Variance</td>
</tr>
<tr>
<td>SAN</td>
<td>Sanguivores</td>
</tr>
<tr>
<td>SAR</td>
<td>Species Area Relation</td>
</tr>
<tr>
<td>SE</td>
<td>Standard Error</td>
</tr>
</tbody>
</table>
Abstract

Deforestation and forest fragmentation are a major conservation concern in the tropical forests of the Brazilian Amazon. Edge effects are important determinants of both physical and biological responses to fragmentation, yet major gaps of knowledge exist on the extent of these effects and their underlying mechanisms for many animal groups. This study contributes to the existing knowledge by exploring edge effects and their interaction with patch size and matrix vegetation, using bats (Chiroptera) as a model group, in the experimentally fragmented research area of the Biological Dynamics of Forest Fragmentation Project in the Brazilian Amazon. We captured members of the Phyllostomidae family and Pteronotus parnellii (Mormoopidae) using ground-level mist nets in fragments of different size categories (1, 10, 100 ha and control plots in the continuous forest) and in three different habit types: interior-, edge- and matrix habitat and conducted vegetation sampling at the same sites.

We found that neither edge- nor area effects had an impact on species richness, diversity and evenness. However, species composition and abundance differed in fragment interior habitat compared to edge- and matrix habitat. These results were primarily caused by a steep increase in the capture frequency of understory frugivores and the most abundant species (Carollia perspicillata) in edge- and matrix habitat compared to the fragment interior. No other guilds or species appeared to be impacted by edge effects. However, the capture rate of gleaning animalivores was negatively associated with decreasing patch size. I conclude that the relative mature age and tall canopy of the matrix habitat attenuates edge effects on bats, which confirms the important role of matrix management in conservation. I furthermore recommend the preservation of sufficiently large forest fragments and their habitat attributes (e.g. large trees which may serve as roost-sites) to mitigate the impact of forest fragmentation on sensitive animalivorous bat species.

(Word count: 11,617)
Acknowledgements

I am most thankful to my two wonderful supervisors. Dr. Cristina Banks-Leite, I would not have been able to do this without your never ending support, insight, patience and enthusiasm, the hours, days, weeks (years?) I spend in your office. Thanks for guiding me through the mysterious ways of “R” and for keeping me motivated and enthusiastic right when I needed it the most. Dr. Christoph F.J. Meyer, I am indebted to the amazing opportunity you gave me to work on such an interesting topic in a worldwide renowned ecological project. Thanks as well for your insightful comments and suggestions, for sharing your knowledge on ecology in general and bats in specific and for the entertaining field nights with you and Joana.

Major thanks to the one and only Català batman: Adrià López Baucells for your unwearrying support with the ‘vegetação’, for saving me when I was lost in Dimona and for your never ending enthusiasm and optimism. I don’t know if I have ever met someone as altruistic and hard working as you.

Big ‘obrigada’ to Ricardo Rocha for introducing me to the fascinating world of bats and for all your hard work that contributed to an impressive dataset an which helped me get through so many obstacles along the way.

I would like to express my gratitude to Paulo Estefano Dineli Bobrowiec for support in the field as well as during our ‘brainstorming’ sessions on the project. Thanks to Julia Treitler and Solange Farias for helping us catch those hundreds of bats.

A warm thanks for our wonderful field assistants Leo and Junior, thanks for keeping me safe and alive during the long nights in the mighty jungle.

Thanks to the Brazilian government, polícia federal and Brazilian embassy in London for issuing my research visa. Major thanks to the Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia and Smithsonian Tropical Research Institute (C.P. 478, Manaus, AM 69011-970, Brazil) for logistical support.
1. Introduction

Tropical forests are the most biologically diverse ecosystems on earth (Dirzo & Raven 2003; Laurance 2007). They sustain at least 50% of all species (Myers 1992; Pimm 2001) and far more endemics than all other biomes combined (MEA 2005). The Amazon basin contains ~60% of remaining tropical rain-forest (Fearnside 1999) and contributes to numerous ecosystem services such as the global carbon- (Dixon et al. 1994) and hydrological cycles (Avissar 2005; Davidson et al. 2012) and provisioning of fuel, food, and water for many of the world’s poorest people (MEA 2005).

1.1 Deforestation

Despite their recognized value, tropical forests are disappearing at an alarming rate (Butchart et al. 2010; Laurance 2007). The Brazilian Amazon has the world’s highest absolute deforestation rates (Laurance et al. 2002), with 1.8 million hectares of forest being lost every year between 2001 and 2010 (Aide et al. 2012; INPE 2011) although deforestation rates have stopped accelerating and are even decreasing in some regions (Wright 2010). Furthermore, Brazil has the highest reforestation rate of the Neotropics: 1.5million ha from 2001 to 2010 (Aida et al. 2012). However, reforestation and deforestation do not always occur in the same regions or even biomes and the conservation value of secondary regrowth remains a topic of debate (Dent & Wright 2009; Dent 2010; Gibson et al. 2011; Herrera-Montes & Brokaw 2010).

Increasing global industrialization and per-capita consumption will accelerate the synergistic pressures on tropical forests (Asner et al. 2005; Davidson et al. 2012; Finer et al. 2008; MEA 2005; Nepstad et al. 2001). Although extinctions in the Brazilian Amazon have been minimal so far, a recently developed model by Wearn et al. (2012) projects average losses of 2-3 mammals (5.5%), 3-7 birds (5.3%) and 1-2 amphibians (4.5%) for every 2500km² by 2050, leaving an ‘extinction debt’ of 60-70% for the years thereafter.

1.2 Fragmentation

One of the main consequences of deforestation is habitat fragmentation, which is a primary concern in conservation biology and perhaps the most alarming trend in the Amazon (Franklin & Noon 2002; Gascon 2000; Peres 2001; Laurance et al. 2011). A key study by Skole & Tucker (1993)
estimated the area of fragmented forest (<100km$^2$) in the Brazilian Amazon to be more than 150% larger than the area deforested.

Island Biogeography Theory (IBT) is the foundation of landscape ecology. It is based on two main pillars: the species-area relationship (SAR) and isolation (MacArthur & Wilson 1967). Although this theory has provided many useful insights, it ignores some essential determinants of species responses to fragmentation, most importantly: matrix- and edge effects (Koh et al. 2010; Kupfer et al. 2006; Laurance 2004; Watling et al. 2011).

1.3 Edge effects
Edge effects are ‘physical and biological alterations that occur along a gradient between a border of one habitat type with another’ *(combined from:* Kupfer et al. 2006; Laurance 2008) and can be either natural or anthropogenic. Edge effects are dominant drivers of fragment dynamics and a major determinant of species composition, structure and ecological processes (Banks-Leite et al. 2010; Laurance et al. 2011; Ries et al. 2004). Better understanding the consequence of edge effects can bring important contributions to conservation planning and management, for example through the design of nature reserves (Collinge 1996; Laurance 1991) and mitigation of the impacts of habitat loss (Laurance et al. 2002). Despite decades of research, much remains to be discovered especially considering the mechanisms behind edge effects and the interaction of factors that modulate edge effects such as patch size and matrix vegetation (Didham et al. 1988; Murcia 1995).

1.4 Area & edge effects
Reduction in patch size generally leads to a decrease in suitable habitat with consequent decreases in species richness and abundance (Fahrig 2003; Watlin & Donnelly 2006).

Small and irregularly shaped fragments have a high perimeter:area ratio, which means edge effects extend over a relatively large area and multiple edge may synergistically impact fragment interiors (Ewers & Didham 2007; Laurance et al. 2006; Laurance 2008). The core-area model of Laurance and Yensen (1991) (and revised version: Didam & Ewers 2012) incorporates patch size and shape to predict the extend of edge- and matrix affected area and found that below a certain threshold the impacts of edge effects increase almost exponentially with decreasing fragment size.
Edge- and area-effects are confounding factors and it is a challenging task to distinguish between them (Didham et al. 1998; Ewers et al. 2007; Laurance 2008). For example, a study in the Brazilian Atlantic forest found that the change in bird species composition from interior to edges was similar to the change from large fragments to small ones, but after controlling for edge effects, area effects were no longer apparent (Banks-Leite et al. 2010).

1.5 The matrix matters
The strength of edge effects is further influenced by matrix quality (Laurance et al. 2011). Several models on diverse animal assemblages demonstrated that matrix habitat was the strongest predictor of occupancy in fragmented landscapes, even stronger than the combined effects of isolation and size (Koh & Ghazoul 2010; Koh et al. 2010; Prugh et al. 2008; Watling et al. 2011). In general, edge effects weaken as the contrast between fragment- and matrix habitat becomes less pronounced (Didham & Lawton 1999; Kupfer at al. 2006; Laurance et al. 2008; Prugh et al. 2008). For example, over time edges become ‘sealed’ and wind, light and heat fluxes become less intense with subsequent buffering impacts on biota (Kapos et al. 1997; Matlack 1994).

1.6 Bats as a model
Bats (Chiroptera) are a promising model group for studies on fragmentation and edge effects because they are abundant both in terms of species and individuals (Voss & Emmons 1996), they are readily detected with cost-efficient sampling methods (Kalko & Handley 1996; Kunz & Parsons 2009) and they represent a high diversity of life-strategies with subsequent differential vulnerability to disturbances (Kunz & Fenton 2006).

Bats are also important from a conservation perspective: they are the most species-rich mammal group after rodents and can represent up to 40% of the mammal species in Neotropical rainforests (Voss & Emmons 1996). Bats perform numerous ecosystem functions and services, including seed- and pollen dispersal; arthropod and pest suppression, fertilizing guano, protein and cultural services (e.g. mythology, tourism, traditional medicine) (Kunz et al. 2011). Bats play a key role in forest restoration because they are primary dispersers of pioneer species and reduce leaf damage to regrowth vegetation by predating on herbivorous insects (Kalka et al. 2008; Morrison & Lindell 2012; Muscarella & Fleming, 2007).

1.7 Edge effect on bats
Bats are sometimes considered to be less affected by fragmentation due to their high mobility and ability to exploit certain matrix habitats (Estrada et al. 1993; Lesinski et al. 2011). However,
evidence is mounting that fragmentation can have profound impacts on bat species richness (Faria 2006; Gorresen & Willig 2004), abundance (Bernard & Fenton 2003; Ethier & Fahrig 2011), activity patterns (Presley et al. 2009; Willig et al. 2007) and species composition (Faria et al. 2006; Meyer & Kalko 2008; Schulze et al. 2000).

Meyer et al. (2008) found that edge-sensitivity was the single most important trait in determining bat vulnerability to fragmentation. Despite this, relatively few studies on bats have been explicitly designed to assess edge effects. The interaction of patch size with edge effects on bats has never been addressed and most other studies rely on rather vague dichotomous descriptions (e.g. disturbed vs. undisturbed, Fenton et al. 1992; interior vs. edge, Lesinski et al. 2011), but without clear descriptive information on the differences in vegetation structure of the habitats under consideration, interpretation and extrapolation of the findings becomes more subjective.

1.8 Aims and objectives
This study intends to fill some of the gaps of knowledge discussed above, with the ultimate aim to ‘assess the impacts of edge effects on bats and its implications for conservation in the Central Amazon’.

The focus of the study is threefold and can be subdivided into the following three specific objectives:

1. To evaluate how bats are influenced by edge effects, looking into differences in species richness, abundance patterns and species composition between forest edge-, interior- and matrix habitat at the assemblage, guild and species level.

2. To assess whether the strength of edge effects is influenced by the size of forest patches.

3. To assess differences in vegetation structure and composition between interior-, edge- and matrix habitat and to evaluate how changes in vegetation characteristics influence the bat assemblage and the strength of edge effects.
2. Background

2.1 Edge effects on bats

Few studies on bats have assessed the impacts of edges and a minority of these studies was set in a tropical context (Table 2.1).

There is no consistent evidence for an edge effect on species richness (table 2.1). Delaval and Charles-Dominique (2006) found a positive effect of edges on species richness, but only for the frugivorous and nectarivorous guild. A decrease in species richness was recorded for edges of fragments (Faria 2006) and continuous forest (Meyer & Kalko 2008). Apparent idiosyncratic responses of species richness to habitat edges have also been found for birds, plants and invertebrates (Ries et al. 2004).

Richness, diversity and evenness are often not statistically different at edges compared to interior habitats (table 2.1) because they reflect the sum of all species responses. Bat assemblages contain a high functional diversity and the multifarious responses may cancel each other out (Ewers & Didham 2006; Klingbeil & Willig 2009). Despite an increase in richness, Delaval and Charles-Dominique (2006) report lower diversity at the edge compared to interior habitat, which was caused by lower evenness at the edge due to a demographic explosion of a few opportunistic species.
Almost all studies that consider bat assemblage abundance report increases at the edge compared to interior habitat (table 2.1). Many other taxa have shown abundance increases at forest edges, including termites; aphids (Fowler et al. 1993); light-loving butterflies (Brown and Hutchings 1997) and generalist or gap-specialist birds (Stouffer & Bierregaard 1995).

Similar to the reports on abundance, all studies in temperate zones using acoustic surveys consistently report higher activity at forest edges compared to the forest interior or matrix habitat at the assemblage- and guild level (table 2.1). However, acoustic detectability is higher in edge-habitats compared to forest interiors (Walsh et al. 2004) and most of the acoustic studies were set in heavily managed and altered landscape which may have already lost edge-sensitive species (Hayes & Loeb 2007).

2.2 Underlying mechanisms

Differential patterns in bat abundance and richness related to edges may be explained by four principal mechanisms.

Access to spatially separated resources

Species abundance may increase at edges when habitats at both side of the edge provide complementary resources to a species (Dunning et al. 1992) so that the edge-habitat provides maximum access to both resources (Law & Dickman 1998). For example, bat species that forage in open areas but roost in forest habitat increase in abundance at the forest borders because they constantly cross borders to access both resources (Ethier & Fahrig 2011; O’Keefe et al. 2009).

Resource mapping

Resource mapping occurs when the abundance of a species follows the abundance of its resources. Bats may prefer edges as flyways over structurally complex and dense interior vegetation (Hogberg et al. 2002; Kusch et al. 2004), find protection from predation and wind (Verboom & Spoelstra 1999) and use edges as a landmark for orientation (Law & Chidel 2002). However, the latter two arguments only apply to edges in comparison to open areas, not to interior habitats.

When resources of the matrix- and interior habitat come together at the edge, ‘species mixing’ may occur. In that case distinct matrix- and interior species map onto resources at the edge and richness increases (Ingham & Samways 1996; Magura 2002).
**Species interactions**

The increase or decrease of certain species may indirectly cascade to the community level through species interactions such as parasitism (Chalfoun et al. 2002; Wolf & Batzli 2001), predation (Andren & Angelstam 1988), mutualism (Fleming & Heithaus 1981; Jules & Rathcke 1999) and competition (Remer & Heard 1998; Youngentob et al. 2012). Bats may interact with insects (predation) and pioneer fruit species (mutualism) that have been shown to increase at edges (Didham et al. 1998; Grindal 1996; Hein et al. 2009; Restrepo et al. 1999).

**Geometric edge effects**

The until recently ignored ‘geometric edge effects’ (Prevedello et al. 2012) provides an explanation for abundance- and species decreases at edges. The theory states that areas in the centre of a habitat patch will automatically receive more individuals than areas near the edge simply because the centre receives individuals from all directions whereas edges do not receive individuals from outside the patch. Although demonstrated for birds (Fletcher & Koford 2003; King et al. 1997), the role of geometric edge effects has not yet received attention in the bat literature. Many bat species are highly mobile and can pass through different habitat types during a night (Fleming 1982; Fenton et al. 1992). Therefore, it seems unlikely that edges have lower richness or abundance because they do not receive individuals from outside of the patch.

**2.3 Species composition**

Edges strongly influence assemblage structure in a variety of taxa, including tropical birds (Dale et al. 2000; Restrepo & Gomez 1998) and bats (Faria 2006). To improve our understanding of these compositional shifts, it can be useful to discern responses at the individual guild level.

**Guilds**

Guild classifications group species according to diet, foraging mode and habitat type (Kalko et al. 1996). Main food types ingested by bats include animals (tetrapods, arthropods and fish), fruits, nectar and blood. Foraging mode of the animalivores can be categorized as ‘gleaning’ for bats that glean prey from the vegetation or the ground or ‘aerial’ for hunters in open areas. Vertical stratification is more pronounced in frugivorous bats than in the other guilds: aerial insectivores are predominantly found in or above the canopy, whereas gleaning animalivores, nectarivores and hematophagous species are more restricted to the understory (Bernard 2001; Pereira et al. 2010). Therefore, I used the following guild classification: shrub-, canopy- and opportunistic frugivores, gleaning animalivores, aerial insectivores, nectarivores, and sanguivores.
**Nectarivores and shrub Frugivores**

Shrub frugivores and nectarivores show a dietary preference for understory pioneer plant genera, such as *Cecropia, Vismia, Solanum* and *Piper* (Muscarella & Fleming, 2007; Thies & Kalko 2004) which increase in disturbed areas such as edge- and matrix habitats. Therefore, abundance of shrub frugivores is often higher at the edge- and matrix compared to forest interiors (Cortés-Delgado & Pérez-Torres 2011; Klingbeil & Willig 2009; Sampaio 2000). Furthermore, many nectarivorous species are generalists, often including insects, pollen and fruit in their diets, which may benefit in disturbed habitats with potential new food sources (Brosset et al. 1996).

**Canopy frugivores**

Canopy specialists feed mainly on canopy fruits such as *Ficus* (Estrada-Villegas et al. 2010) that occur in low density, fruit asynchronously and for a short amount of time (Cosson et al. 1999). Canopy specialists thus need to be highly mobile in order to visit different feeding patches. Fig-eaters like *Artibeus jamaicensis* can travel up to 10km per night (Fleming 1982; Fenton et al. 1992), which minimizes the influence of habitat type on their abundance (Klingbeil & Willig 2009; Schulze et al. 2000). Small canopy frugivores may be more limited in their dispersal abilities and can respond negatively to edge- and matrix habitat due to a lack of roosts and canopy fruits (Sampaio 2000).

**Opportunistic frugivores**

Opportunistic frugivores use upper- and lower strata equally and have a high level of flexibility in habitat use, allowing them to persist in structurally different edge- and matrix habitat, while taking advantage of new food sources (i.e. *Cecropia, Vismia, Piper* fruits) (Bernard 2001; Estrada & Coates-Estrada 2002).

**Gleaning animalivores**

Despite the fact that prey species such as katydids (*Tettigoniidae*) and true bugs (*Hemiptera*) often accumulate at edges (Naskrecki 2008; Morris et al. 2010), gleaning animalivores are considered ‘edge-sensitive’ (Clarke et al. 2005; Kalko & Handley 2001; Morris et al. 2010; Meyer et al. 2008). Their foraging strategy and wing morphology constrain the gleaners to a life in structurally complex habitats and make them adverse to crossing open areas (Belwood 1988; Norberg & Rayner 1987). The fact that many gleaning animalivores have a small home range and specific roosting requirements provides an additional explanation to their sensitivity (Kalko et al. 2006).
**Aerial insectivores**

Aerial insectivores have a wing morphology and foraging strategy that is well suited for open areas along ‘high-contrast edges’, where they often occur in high densities to take advantage of elevated prey abundance (Cadenasso & Pickett 2000; Morris et al. 2010; Patriquin & Barclay 2003). Despite this, some aerial insectivores such as *Pteronotus parnellii* avoid open areas (Neuweiler 1990) but have been shown to use secondary forests frequently (Sampaio 2000).

**Sanguivores**

Sanguivores are usually not caught in sufficient numbers to make inferences about their response to habitat type (Faria 2006; Sampaio 2000; Schulze et al. 2000). *Desmodus* species feed on large mammals and can increase in matrix habitats where cattle is present (Delpietro et al. 1992). *Diaemus* species prey on large birds in the canopy and their abundance might map on to the habitat response of the prey (Bernard 2001).

**Edge-sensitive species**

Even closely related taxa within the same guild may exhibit varied responses to edge formation (Didham et al. 1998; Ewers & Didham 2006). Species that avoid matrix habitat and decline or disappear after fragmentation are often the same species that are sensitive to edges (Cosson et al. 1999; Meyer & Kalko 2008). Sensitivity to fragmentation/edges in bats has been associated with traits such as poor dispersal ability and maneuverability, higher trophic level, specialized habitat-/food requirements and naturally low in abundance (Cosson et al. 1999; Kalko et al. 1999; Klingbeil & Willig 2009; Meyer et al. 2008; Sampaio 2000).

2.4 **The impact of patch size and the interaction between patch size and edge effects**

Species declines with decreasing patch size have been well documented for several animal groups including butterflies (Holt et al. 1995), beetles (Laurance & Bierregaard 1996), gastropods (Baur & Erhardt 1995), understory birds (Ferraz et al. 2007), and primates (Boyle & Smith 2010).

For bats this pattern is again not consistent, with reports of positive (Estrada & Coates-Estrada 2002; Struebig et al. 2008), negative (Gorresen & Willig 2004; Klingbeil & Willig 2009) and neutral (Faria 2006; Schulze et al. 2000) relationships between richness and patch size. The direction of response has been shown to depend on several factors, such as guild- and species characteristics.
as well as spatial- (Meyer & Kalko 2008; Pinto & Keitt 2008) and temporal scale (Cosson et al. 1999).

To the best of my knowledge only one bat-study partially addressed the effect of patch size on edge effects. Faria (2006) found that capture rate and richness did not differ significantly between interiors of different sized patches and between edges of different sized patches. However, no comparison was made on the difference between edge and interior habitat for different patch sizes. Delaval and Charles-Dominique (2006) showed that some edge-related changes in the bat assemblage extended up to 3km into the forest. This implies that interior-habitats of smaller fragments exhibit more similarities in their bat assemblage to edge-habitats than interior-habitats of larger fragments, which confirms the general finding that small fragments (<100ha) may consist entirely of edge-habitat (Laurance 2008; Malcolm 1994).

2.5 Vegetation

2.5.1 The matrix

The faunal composition in fragment interiors and edges has to be viewed in context with the matrix habitat. For example, small shrub frugivores such as *Rhinophylla pumilio*, *Carollia castanea* and *Carollia perspicillata* decline in fragments surrounded by water (Cosson et al. 1999; Meyer and Kalko 2008) but increase in fragments surrounded by secondary forest or coffee/cacao plantations (Faria 2006; Numa et al. 2005; Schulze et al. 2000; Willig et al. 2007).

In the Neotropics deforestation is usually followed by the development of secondary forest which may attenuate edge effects (Fearnside 1996; Antongiovanni & Metzger 2005). However, forest interior habitat still differs profoundly from secondary forest vegetation and even different types or successional stages of secondary forests differ in vegetation characteristics (Ricketts 2012). For example, in the Amazon, sites that have been clear-cut without subsequent use develop in *Cecropia* dominated regrowth and sites that are clear-cut and burned and/or used as pastures develop in *Vismia* dominated vegetation (Mesquita et al. 2001). *Cecropia* regrowth is more divers (twice the number of plant species) than *Vismia*-dominated regrowth and has a faster return of primary forest species and vegetation characteristics that are common to the primary forest (e.g. high DBH), with consequent buffering impacts on edge effects (Mesquita et al. 2001). Bat species composition has been shown to differ between these two types of secondary regrowth (Brobowiec & Gribel 2010) which may influence potential edge effects on bats.
2.5.2 Vegetation characteristics

Several studies have explicitly related vegetation characteristics to bat assemblage attributes. Important determinants were vegetation density, structural complexity, height, and basal area (Cortés-Delgado & Pérez-Torres 2011; Fenton et al. 1998; Hein et al. 2009; Law & Chidel 2002; Pereira et al. 2010; Peters et al. 2006).

Understory vegetation is usually denser in edge- and matrix habitats than in forest interiors (Kalko & Schnitzler 1993; Patriquin & Barclay 2003) which has been shown to negatively impact animalivorous bats even despite higher prey availability (Law & Chidel 2002; Peters et al. 2006). Vegetation clutter may function as a movement barrier that requires energetically costly maneuverable flight (Kusch et al. 2004; Meyer et al. 2008) and interferes with acoustics echoes returning from prey (Fenton 1990; Schnitzler & Kalko 2001). Frugivores and nectarivores rely less on echolocation and have been shown to thrive well in dense understory vegetation (Peters et al. 2006; Schnitzler & Kalko 2001).

Structural habitat complexity (i.e. many vertical layers) has been related to bat diversity (Pereira et al. 2010) because it allows the co-existence of more species in the same area due to niche segregation (Delaval et al. 2005).

Finally, tree height and basal area have been positively related to bat abundance and richness (Cortés-Delgado & Pérez-Torres 2011; Erickson & West 2003; Fenton et al. 1998; Hein et al. 2009) which is probably related to higher roost availability in old large trees (Crampton & Barclay 1996; Estrada & Coates-Estrada 2001; Kalko et al. 1996). Edges also tend to have lower variance in tree height which may be preferred by fast-flying less maneuverable bats (Cortés-Delgado & Pérez-Torres 2011).

2.6 Expectations

Considering the background information, I expect to find the following results for the stated objectives:

1. Species richness, diversity and evenness may decrease at the edges and in the matrix due to a loss of sensitive species and an explosion in abundance of disturbance preferring species. I expect abundance levels to increase in edge- and matrix habitat driven by increases in frugivorous and nectarivorous species. Gleaning animalivores are expected to be edge-sensitive and have decreased abundances in edge- and matrix habitat compared
to interiors, while aerial insectivores, canopy frugivores and opportunistic frugivores may respond less sensitive. Considering these differences in guild representation, I expect species composition to differ between interior- edge- and matrix habitat with the latter two potentially being a subset of the first.

2. I expect area and edge effects to act synergistically such that differences between large and small patches are similar to differences between interior habitat compared to edge- and matrix habitat and I expect differences between interior habitat compared to edge- and matrix habitat to increase with patch size.

3. I expect to find clear differences in vegetation structure between interior habitat and edge- and matrix habitat, with interiors having taller stratified vegetation with more roosting opportunities (i.e. large trees, palms) which may explain part of the edge effects on bats that I expect to find.
3. Methods

3.1 Study site
I conducted the fieldwork in the experimental area of the Biological Dynamics of Forest Fragmentation Project (BDFFP). The BDFFP is the world’s longest running and largest scale ‘natural experiment’ of habitat fragmentation, covering a period of 33 years and an area of >1000 km² (Laurance et al. 2011).

The BDFFP is located 80 km north of Manaus, in the Brazilian Amazon (2°25’S, 59°50’W). The area is covered by low elevation (80-160m) ‘terra-firme’ forest on heavily weathered nutrient-poor acidic latosols, typical for the majority of the Amazon basin (Lovejoy & Bierregaard 1990). The area receives 1900 to 3500mm rainfall annually, with a rainy season from January to June and a dry season from June to October. Mean annual temperature is 26.7 ºC (Lovejoy and Bierregaard 1990).

The BDFFP-area was fragmented for research purposes in 1979 by clearing and burning (fig3.1). It comprises 11 forest fragments of different sizes (five of 1ha, four of 10 ha and two of 100ha) and is surrounded by vast expanses (~500.000ha) of continuous primary rainforest (fig 3.2) (Bierregaard et al. 2001). The matrix habitat consists of secondary forest in various successional stages (Mesquita 2001). For a complete description of the project design and history, please refer to Laurance & Bierregaard (1997) and Bierregaard et al. (2001).
3.2 Methodological framework

The methodology for this study included the sampling of the bat assemblage with mist nets and the sampling of the vegetation characteristics. The focus was on the family Phyllostomidae and the mustached bat (*Pteronotus parnelli*, family: Mormoopidae) because only these species can be sampled adequately and most effectively with mist nets (Fenton 1997; Kunz & Parsons 2009; Kunz & Kurta 1988). Species from other families, especially aerial insectivores which have better echolocation and/or forage over the canopy, remain underrepresented or completely undetected in mist nets (Kalko et al. 1996; Kunz & Parsons 2009).

In order to study edge effects on bats, an experimental design was developed that included 33 sampling sites scattered over six locations: Cabo Brío (CF), Florestal (FL), KM-41 (K41), Colosso (CO), Dimona (DI) and Porto Alegre (PA) (table 3.1, fig 3.2). Most of these sites had been sampled for bats in the period between January 1996 and June 1999 by E. Sampaio (2000), although she did not sampled the 100ha fragments nor systematically sampled the edge- and matrix habitat.

Sites were categorized by patch size and by habitat type (interior, -edge- or matrix) (table 3.1). There were three fragments of 1ha; three fragments of 10ha; two fragments of 100ha and three control plots in the continuous forest. Each fragment/control plot contained three paired sampling sites: one for each habitat type (interior-, edge- or matrix). The only exception was the control plot in KM-41. This plot is located in the middle of the continuous forest and does not have borders. Instead an edge- and matrix site was established at the border of the continuous forest in Dimona (table 3.1).
<table>
<thead>
<tr>
<th>Size</th>
<th>Replicates</th>
<th>Habitat type</th>
<th>mnh per treatment</th>
<th>Locations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 hectare</td>
<td>3</td>
<td>Interior</td>
<td>588</td>
<td>CO, DI, PA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Edge</td>
<td>378</td>
<td>CO, DI, PA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Matrix</td>
<td>378</td>
<td>CO, DI, PA</td>
</tr>
<tr>
<td>10 hectare</td>
<td>3</td>
<td>Interior</td>
<td>504</td>
<td>CO, DI, PA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Edge</td>
<td>378</td>
<td>CO, DI, PA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Matrix</td>
<td>378</td>
<td>CO, DI, PA</td>
</tr>
<tr>
<td>100 hectare</td>
<td>2</td>
<td>Interior</td>
<td>504</td>
<td>DI, PA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Edge</td>
<td>252</td>
<td>DI, PA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Matrix</td>
<td>252</td>
<td>DI, PA</td>
</tr>
<tr>
<td>Control (Continuous forest)</td>
<td>3</td>
<td>Interior</td>
<td>504</td>
<td>CF, FL, K41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Edge</td>
<td>378</td>
<td>CF, DI, FL</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Matrix</td>
<td>378</td>
<td>CF, DI, FL</td>
</tr>
<tr>
<td>Total</td>
<td>11</td>
<td>33</td>
<td>4872</td>
<td>6</td>
</tr>
</tbody>
</table>

The interior sites were situated in the centre of a fragment or in a continuous forest site. Here, two transects of seven mist nets each were established in a straight line. The edge sites contained one transect of seven mist nets that were positioned in a straight line right at the border between forest- and matrix habitat. The matrix sites also contained one transect of seven mist nets and these were established parallel to the edge at a distance of ~100m (figure 3.3).

![Diagram of sampling design](image)

**Figure 3.3:** Schematic overview of the sampling design, red line = mist net transect with 7 mist nets (~84m), grey rectangle = vegetation plot (5x20m).

Vegetation was sampled for a wide variety of characteristics (see below). Three 100m² vegetation plots were established at each side of the mist net transects (fig. 3.3). The plots were placed at a distance of ~5m from the mist net transect to avoid effects of the cleared area (trails) around the nets on the vegetation. Vegetation plots were spaced at a minimum distance of 5m from each
other to avoid an overlap in measurements. Together the vegetation plots covered approximately the total length of the mist net transect (~84m). From the two mist net transects at interior-sites, one was randomly selected for vegetation sampling. All areas adjacent to matrix- and edge transects were sampled. In total 198 plots (19,800m²) were sampled.

3.3 Field methods
Data was collected in the period between 22nd of March and 12th of July 2012. I personally contributed to the sampling from between 16th of April and 12th of July.

3.3.1 Bat sampling
Bats were captured using ground-level mist nets (12 m long, 2.5 m high, five shelves, mesh dimensions: 1.5x 1.5 cm). Each night, mist nets were left open between ~18:00 (sunset) and ~00:00 (with a variation of <10min).

Sites were never sampled at two consecutive nights to prevent potential capture bias due to net shyness and learning behaviour (Kunz & Brock 1975; Larsen et al. 2007; Sampaio 2000). The average period in between sampling was 28 days with only five occasions of less than 20 nights.

A possible capture bias may arise because we used forest trails t place the mist net transects. Human modifications are frequently used by phyllostomid bats as flyways but may favor certain species (specifically frugivores and nectarivores) more than others (O’Farrell and Gannon 1999; Palmeirim & Etheridge 1985). However, this bias should be equal for all treatments and replicates.

Nets were checked every ~15 minutes. Net- and shelf number and time of capture was noted. Species were identified with the help of identification keys by Aguirre, Vargas & Solari (2009); Lim & Engstrom 2001; Medellín et al. (1997) and Sampaio & Kalko (unpublished). I followed the taxonomic nomenclature of Gardner (2007). Captured bats were identified, weighed (Pesola spring balances of 30, 60, 100 and 300g; 0.5, 0.5, 1, and 2g accuracy respectively), length of forearm and tibia was measured and their sex, age class (juvenile, sub adult or adult) and reproductive status (females: non-reproductive, pregnant or lactating; males: testicle size) was determined.

Adult bats were marked to avoid double-counting and for potential future re-capture studies. Frugivores were marked with a stainless-steel ball-chain necklace with a unique number (Handley et al. 1991). Species with a small body size (i.e. all Glossophaginae and Mesophylla macconelli)
were not marked for health and safety reasons. Gleaning animalivorous bats were marked with a subcutaneous sterilized trovan® electronic identification system transponder of size: 2.6x0.15x40mm with a unique number and bar-code. Recaptures were identified with a trovan® LID-560 pocket transponder reader. All bats were released after handling.

### 3.3.2 Vegetation sampling

In each plot we counted the total number of stems that were at breast height or taller. All stems with a diameter >10cm, the DBH (Diameter at Breast Height) was measured. At 5m-intervals (5 points per plot) tree height of the five closest trees was estimated (i.e. 25 trees per plot).

At the same 5m interval points vegetation stratification was estimated. Vegetation density was classified (0= no vegetation, 1= very sparse vegetation 0-20%, 2= sparse vegetation 20-40%, 3= medium vegetation 40-60%, 4= dense vegetation 60-80%, 5= very dense vegetation 80-100%) for seven height intervals (0-1m, 1-2m, 2-4m, 4-8m, 8-16m, 16-24m, 24-32m). At each plot, canopy cover was measured as the average of four spherical densiometer (Model-C, Robert E. Lemmon forest densiometer, Forestry Suppliers Inc., Bartlesville, OK, USA) readings, taken at a minimum distance interval of 35m. Stem count, DBH, stratification and canopy cover are common variables for vegetation characterisation and have been shown to be related to species diversity and composition (Banks-leite & Cintra 2008; Banks-Leite et al. 2010; Meyer & Kalko 2008; Raman & Sukumar 2002; Schemske & Brokaw 2004; Schmiegelow et al. 1997; Watson et al. 2004).

The number of palms (dominant genera: Astrocaryum, Attalea and Bactris) within each plot was counted. Palms can make up a considerable proportion of understory vegetation in tropical forests and are used by a variety of bat species as roost sites (Kunz & Lumsden 2003; Scariot 1999). Liana density was classified at each 5m-interval to categories 0-5: from no lianas to very high liana density. Liana abundance has been shown to increase at edges and in disturbed forests, forming an important vegetation component which in turn can influence flora and fauna (Laurance et al. 2001; Schnitzer & Bongers 2011). Finally, the number of potential roost sites per plot was counted. Roost availability is often higher in primary forests compared to secondary forests and may have an important impact on bat presence (Morris et al. 2010; Bobrowiec & Gribel 2010; Schulze et al. 2000). Potential roost sites included: hollow (fallen) trunks and dead trees, trees with abundant/large crevices, large buttress roots, large abandoned termite piles etc. (Morris et al. 2010). At edge- and matrix sites, we identified what the most abundant plant genera in the plot was (mainly: Vismia and Cecropia).
To reduce bias caused by the subjectivity of some of the vegetation variables, the same observer was used for each task everywhere.

### 3.4 Analytical methods

**Completeness of the bat inventory**

To assess the completeness of the bat inventory, I calculated a sample-based (100 permutations) species accumulation curve for the entire landscape and for each habitat type individually (Gotelli & Colwell 2001). Additionally, I consulted an estimator choice-framework that accounts for movement heterogeneity of mobile animals, developed by Brose & Martinez (2004). In accordance with the framework, I chose the first-order Jackknife (Jack1) estimator to assess expected species richness in the edge-, interior- and matrix habitats.

**Species richness, diversity, evenness and abundance**

To enable comparative analysis between sites, I first had to correct for differences in sampling effort among sites (table 3.1). This was done by rarefying species richness by sampling effort (Gotelli & Graves 1996). Due to uncertainties over the correct identification of *Carollia benkeithi* and *Carollia brevicauda*, these species were grouped together as *Carollia sp.* and treated as one species in further analysis. Capture rate (number of individuals per mnh) was used as a standardized index of relative abundance, which is the mean number of bats for every hour of one open mist net. Recaptures of the same night were excluded from analysis.

As a measure of alpha diversity I used the ‘effective number of species’ based on a bias-controlled Shannon’s entropy. This is the exponential form of the Shannon’s index and is considered the most suitable measure when undersampling is suspected and completeness is higher than 50% (Beck & Schwanghart, 2010; Jost, 2006). As an evenness measure I used the Pielou’s index, which is a commonly used derivative of the Shannon-index (Pielou 1975).

I performed a Kolmogoroff-Smirnov test to test for differences in rank-abundance distributions of the different habitat types.

I compared differences in rarefied richness, diversity- and evenness indices and capture rates (at the assemblage- and guild level and for the four most abundant species) between habitat types with a repeated measures analysis of variance (RM-ANOVA) using the R-package ‘lme4’ (Bates et
al. 2011). Because data were not counts and were reasonably normal distributed, they were modeled using Gaussian errors (Deriche, 1993). I used the following three models:

\[
Y \sim \text{“habitat type”} + \{\text{“fragment”}\} \\
Y \sim \text{“habitat type”} + \text{“size”} + \{\text{“fragment”}\} \\
Y \sim \text{“habitat type”} + \text{“size”} + \{\text{“fragment”}\}
\]

In which ‘habitat type’ represents the interior-, edge- and matrix habitat, and ‘size’ represents the value of 1,10,100ha, and control sites. Pseudo replication was controlled statistically by including ‘{fragment}’ as a random effect.

The first model used ‘habitat type’ as only fixed effect and was used to assess the exclusive impact of the interior-, edge- and matrix habitat on the estimates of the bat community. The other two models were used to evaluate whether the size of forest patches influenced the response to habitat type. Model 2 was used to assess whether the mean value of the measures for a particular habitat type changed with size. Model 3 was used to assess whether the pattern of differences between habitat types changed with patch size. For example, this model could discern whether capture rate was lower in the interior compared to the edge habitat in small patches but higher in large patches.

The RM-ANOVA is a powerful method to assess differences between interior-, edge- and matrix habitat, as it controls for additional random variation by comparing the three habitat types within each fragment (e.g. 1 hectare in Colosso). If habitat types were not sampled in a paired design and instead located randomly, the statistical power would be much lower, due to unaccounted random variation, and more replicates would be needed.

The models were tested for significance by using a ‘deletion test’ starting with the most complex models (3 and 2) and ending with a comparison between model 1 and a null model that assumes no differences in the data (Crawley 2007).

**Species composition**

To estimate compositional differences of the bat assemblages between habitat types, I used a Principle Coordinate Analysis (PCoA) on a Bray-Curtis dissimilarity matrix based on species capture rates. The Bray-Curtis index assigns a higher weight to the presence of a species than to its absence and is considered robust for biological data (Magurran 2004). PCoA is a technique that
allows the positioning of the Bray-Curtis dissimilarity coefficients in a space of reduced dimensionality while largely preserving their distance relationships (Legendre & Legendre 1998).

Species abundance was corrected for differential sampling effort through the use of capture rates (see above). However, the number of species is still higher at sites with a larger sampling effort. To correct for this issue, I used the number of rarefied species (rounded to nearest integer) to draw from the assemblage which species were more likely to be sampled, using their capture rate as sampling probability. This allowed me to obtain a matrix of species by sites that contained information on species identity and yet was corrected for differences in sampling effort. The first two PCOA vectors were plotted against each other to find out how much of the differences in assemblage composition were explained by each axis. A ‘horseshoe’ or horizontal pattern would indicate high explanatory power of the first PCOA axis.

The first PCOA vector was analyzed with the same models as described above. The variance of the PCOA vector within each habitat type was compared to assess if beta-diversity was larger at a given habitat type.

**Differences in vegetation structure and composition between habitat types**

The means and standard deviations of the vegetation measures were scaled to a mean of 0 and standard deviation of 1, and then submitted to a Principle Component Analysis (PCA) (Tabachnick & Fidell 2007). The dominant plant genera were converted into a code (1=Vismia, 2=Cecropia, 3=interior habitat: no dominant genera) to enable inclusion into the ordination-matrix. The coefficients of the first PCA vector were compared between habitat types with the models described above. The relative importance of different vegetation characteristics was assessed by correlating these variables with the first PCA-vector.

**The influence of vegetation characteristics on bats**

The first vegetation PCA vector was used as an explanatory variable in a generalized linear model (GLM) with species richness, species composition (expressed as the first PCOA vector from the Bray-Curtis dissimilarity index), and capture rates (per 1000mnh and rounded to 0 decimals) as response variables. Because data showed a non-normal distribution with Poisson errors a model from the Poisson family was used.
All statistical analysis were performed using the R statistical package (version 2.13.2, R Development Core Team 2011), specifically: the ‘vegan package’ (Oksanen et al. 2011) and the ‘lme4 package’ (Bates et al. 2011).
4. Results

With a total effort of 4872 mnh, we captured 1272 bats (including 45 recaptures) from 23 genera and 37 species, representing all of the seven guilds. Appendix 1 provides a complete overview of the inventory and the respective capture rates in interior-, edge – and matrix habitats.

4.1 Completeness of the bat inventory

The species accumulation curve of the complete inventory (fig. 4.1) approaches, but does not fully reach, an asymptote. None of the species accumulation curves for the interior-, edge- and matrix habitats are close to reaching the asymptote (fig. 4.2), which demonstrates that the set of species captured is not complete.

Figure 4.1: Species accumulation curve for the complete inventory after a sampling effort of 4872 mist net hours, error bars indicate the 95% confidence interval.

Figure 4.2: Species accumulation curves for interior-, edge- and matrix habitat after sampling effort of 2100, 1386 and 1386 mnh respectively.

The Jackknife richness estimator indicates an overall completeness of 84.2% of the species at the landscape level. The completeness for each treatment individually was: 74.7% (interior); 64.8% (edge) and 77.0% (matrix).
4.2 *Species richness, diversity, evenness and abundance at the assemblage level*

Table 4.1 shows the mean values of rarefied richness, the diversity- and evenness index and capture rate. None of the RM-ANOVA’s demonstrated a significant difference in richness, diversity or evenness between interior-, edge-, and matrix habitats.

Table 4.1: Mean values of richness; evenness; capture rate (total; for each guild and for the three most abundant species) and first PC(O)A vectors for interior-, edge- and matrix habitats and the p-value of the RM-ANOVA model 1, 2 and 3. ** indicates a significant result (p<0.05), * indicates a near significant result (0.05<p<0.1).

<table>
<thead>
<tr>
<th>Assemblage</th>
<th>Mean value per habitat type</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Interior</td>
<td>Edge</td>
</tr>
<tr>
<td>Rarefied species richness</td>
<td>7.33(0.87)</td>
<td>6.55(0.73)</td>
</tr>
<tr>
<td>Shannon’s exponential diversity index</td>
<td>3.77(0.12)</td>
<td>4.74(0.13)</td>
</tr>
<tr>
<td>Pielou’s evenness index</td>
<td>0.75(0.04)</td>
<td>0.71(0.05)</td>
</tr>
<tr>
<td>Capture rate</td>
<td>0.15(0.03)</td>
<td>0.38(0.08)</td>
</tr>
</tbody>
</table>

Species composition

| PCOA-1 | -0.15(0.09) | 0.04(0.08) | 0.11(0.08) | 0.03** | 0.20 | 0.93 |

Guilds: capture rates

| Frugivores | 0.13(0.03) | 0.26(0.06) | 0.29(0.06) | 0.04** | 0.85 | 0.82 |
| Shrub frugivores | 0.11(0.02) | 0.22(0.04) | 0.23(0.03) | 0.03** | 1.00 | 0.38 |
| Canopy frugivores | 0.02(0.001) | 0.07(0.006) | 0.09(0.01) | 0.054* | 0.21 | 0.41 |
| Opportunistic frugivores | 0.04(0.003) | 0.07(0.02) | 0.10(0.03) | 0.54 | 0.45 | 0.81 |
| Gleaning animalivores | 0.04(0.01) | 0.09(0.01) | 0.09(0.005) | 0.43 | 0.03** | 0.62 |
| Nectivores | 0.01(0.002) | 0.002(0.002) | 0.003(0.002) | NA | NA | NA |
| Sanguivores | 0.001(NA) | 0.00 | 0.00 | NA | NA | NA |

Species: capture rates

| Carollia perspicillata | 0.08(0.02) | 0.17(0.04) | 0.18(0.04) | 0.04** | 0.84 | 0.63 |
| Rhinophylla pumilio | 0.02(0.005) | 0.03(0.01) | 0.04(0.01) | 0.33 | 0.06* | 0.60 |
| Artibeus obscurus | 0.01(0.002) | 0.02(0.02) | 0.03(0.02) | 0.49 | 0.46 | 0.81 |
| Pteronotus parnellii | 0.01(0.003) | 0.02(0.01) | 0.02(0.004) | 0.32 | 0.09* | 0.65 |

Vegetation

| PCA-1 | 3.68(0.35) | -0.90(0.5) | -1.89(0.49) | 2.26e^-10** | 0.08* | 0.83 |

Pielou's evenness was highly similar amongst the different habitat-types (mean: 0.72±0.02 and see table 4.2). This is confirmed by the fact that the rank abundance curves for each habitat type (fig. 4.3) are not statistically different as shown by the Kolmogoroff-Smirnov test outcomes (distribution interior vs. edge p=0.08; interior vs. matrix, p=0.08; edge vs. matrix p=0.6138). The abundance distribution followed the skewed pattern typical for Neotropical bat assemblages: few species with a high capture frequency and many species with a very low capture rate (Fleming 1986; Kalko & Handley 2001; Simmons & Vos 1998). At the assemblage level, the ten most frequently captured species accounted for 91.1% of captures, while 24 species had less than 10 captures, of which seven were singletons and six were doubletons.
Significant differences were found for capture rates at the assemblage level across the three habitat types, with lower capture rates in the interior- versus the edge- and matrix habitats in fragments (fig 4.4). This trend appears to apply only to fragments larger than 1ha. However, the models that included fragments size, either as an interactive or additive factor were all non-significantly different from model 1: habitat type as only explanatory variable.

### 4.3 Species composition

The differences in assemblage are almost completely explained by the first PCOA axis (fig. 4.5). Indeed, model 1 demonstrated significant differences in the first PCOA vector between interior, edge- and matrix habitats ($p=0.03$) (table 4.1).

The values of the first PCOA vector were more similar between edge- and matrix habitats than between edge-/matrix- and interior habitat (fig. 4.6). This result points to a different species composition in the interior- compared to the edge- and matrix habitats. The variance in PCOA-1 coefficients was not significantly different between habitat-types. This indicates that beta-diversity was similar for all habitat types.
Abundance patterns at the guild level

The frugivores guild was represented by the greatest number of individuals (all frugivores, 82.3%; shrub frugivores, 69.2%; opportunistic frugivores, 7.8%; canopy frugivores, 5.3%), followed by the gleaning animalivores (10.7%). The nectarivores and sanguivores had too few captures (7 and 1 resp.) to be further analyzed.

Habitat-type significantly influenced capture rate at the guild level (table 4.1). The frugivores guild (p=0.035) and the shrub frugivores (p=0.030) mirrored the abundance pattern of the entire assemblage (table 4.1 and fig. 4.2, 4.7A, B). For the gleaning animalivores model 2 was significant (p=0.03, table 4.1) which indicates that patch size influenced capture rate of the gleaners. Capture rates are especially different between the interior of the 1ha fragments and the interior of larger fragments, while capture rates at the edge seem to increase gradually with patch size (fig 4.7E). None of the models were significant for the other guilds, although the canopy frugivores showed a trend towards higher capture rate in the edge- and matrix habitat compared to the interior habitat (p=0.054).

Abundance patterns at the species level

The most frequently captured bat was Seba’s short-tailed bat (*Carollia perspicillata*, 51.5%), followed by the dwarf little fruit bat (*Rhinophylla pumilio*, 11.9%); the dark fruit-eating bat...
(Artibeus obscurus, 7.2%) and the Parnell’s mustashed bat (Pteronotus parrnellii, 5.3%). Only for C. perspicillata could we demonstrate a significant difference between habitat types (p=0.04, table 4.1), with capture rates closely resembling those of the (shrub)frugivores (fig. 4.7B,F). The two

models that included patch size were not significant for any of the species. However, the relation between patch size and capture rates was near significant for R. pumilio and P. parrnellii (table 4.1). R. pumilio is a shrub frugivore but showed a different trend to the capture rate of that guild (fig 4.7B,G). Capture rates in the interior were higher in the 10ha and 100ha fragment than the 1ha fragment and continuous forest and capture rates in the edge- and matrix habitat were lower in the 1ha fragment than the larger fragments (fig. 4.7G). Capture rate of P. parrnellii appears to increase with patch size (p=0.09, table 4.1, fig.4.7I) and both P.parrnellii and A. obscurus seem to
have peak capture rates in the 10ha edge- and/or matrix habitat (fig. 4.7I,H). The capture rate of *A. obscurus* closely mirrors the capture rate of the opportunistic frugivores (fig. 4.7D,H).

### 4.4 Differences in vegetation structure and composition between habitat types

Most of the variation in vegetation data is explained by the first PCA vector (fig. 4.8). This is confirmed by the results of model 1 that was significant for the first PCA vector (p=2.257e^-10, table 4.1). Patch size was nearly significantly related to the first PCA vector (p=0.08, table 4.1).

![Figure 4.8](image-url)  
*Figure 4.8: Vectors 1 and 2 of the principle component analysis of vegetation characteristics in interior-, edge side 1- (towards interior), edge side 2- (towards matrix), and matrix habitat, sizes of squares indicate fragment size (from small to large: 1ha; 10ha; 100ha; continuous forest).*

Figure 4.8 also demonstrates that interior sites cluster together, indicating similarity in vegetation characteristics. To a somewhat lesser extent, the same clustering can be observed for matrix sites. Edge sites are scattered around the graph, but it is interesting to see that the vegetation plots taken at the interior-side of the edge (side1) are grouped towards the interior sites on the right side of the graph. Vegetation plots taken at the matrix-side of the edge (edge 2) are grouped around the matrix sites on the left side of the graph. Interior sites of the small fragments (1ha) appear to be grouped more towards the matrix- and edge sites compared to interior sites of the larger fragments.
The vegetation characteristics with the most influence on the first PCA vector were vegetation density at the 16-24m level (85%); standard deviation in height (84%), density at the 8-16m level (78%), and DBH (65%) (table 4.2).

**Table 4.2:** Mean and standard error of the four vegetation characteristic with the most influence on the first vegetation PCA-1.

<table>
<thead>
<tr>
<th></th>
<th>Interior</th>
<th>Edge</th>
<th>Matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation density at 16-24m</td>
<td>2.86 ± 0.29</td>
<td>1.06 ± 0.22</td>
<td>0.61 ± 0.27</td>
</tr>
<tr>
<td>Standard deviation height</td>
<td>8.25 ± 0.47</td>
<td>4.89 ± 0.36</td>
<td>4.39 ± 0.54</td>
</tr>
<tr>
<td>Vegetation density at 8-16m</td>
<td>3.58 ± 0.16</td>
<td>2.46 ± 0.32</td>
<td>1.74 ± 0.37</td>
</tr>
<tr>
<td>DBH</td>
<td>23.56 ± 0.61</td>
<td>17.36 ± 1.28</td>
<td>16.41 ± 0.61</td>
</tr>
</tbody>
</table>

### 4.5 The influence of vegetation characteristics on bats

The capture rate of the entire assemblage is inversely related to the first vegetation PCA ($p=0.02$, fig 4.9). Interior sites cluster at the bottom right of the graph, indicating similarity in vegetation characteristics and capture rates of bats that is different from edge- and matrix habitats. When analyzing the interior-, edge- and matrix habitat separately no significant relation between PCA1 and capture rate was found. This points to similarity in vegetation characteristics (and related capture rates) within each habitat type. However, the relationship was near significant for the matrix habitat ($p=0.058$) and there appears to be a wide distribution of points for the matrix habitat (fig 4.9). There was no significant relation between the first PCA vector of vegetation characteristics and the first PCOA vector of bat species composition ($p=0.08$), species richness ($p=0.65$), diversity ($p=0.39$) or evenness ($p=0.82$).

![Figure 4.9: Capture rate of bats (individuals per 1000mnh) in relation to the first PCA vector of vegetation characteristics.](image)
5. Discussion

5.1. Edge effects

The results provide some support for the existence of an edge effect on bats, as overall capture rate was lower in the interior habitat compared to edge- and matrix habitats. Capture rate at the assemblage level was dominated by the most abundant guild (shrub-frugivores) and more specifically by the most abundant species \( C. \text{perspicillata} \).

These results are consistent with those of Delaval and Charles-Dominique (2006) and Cortés-Delgado and Pérez-Torres (2011). For example, in French Guyana, the edge-habitat harboured seven times more individuals as the forest interior which was caused by an increased abundance of a few frugivorous species such as \( C. \text{perspicillata} \). Elevated capture rates in matrix habitat compared to forest-/fragment interiors of bat assemblages that are driven by an increase in shrub-frugivores such as \( C. \text{perspicillata} \) have also been demonstrated for a variety of matrix habitats including: secondary forests (Castro-Luna et al. 2007; Sampaio 2000), shade cacao- or coffee plantations (Faria 2006; Faria et al. 2006), crop fields (Willig et al. 2007) and logged forests (Peters et al. 2006) and this group and species have even been suggested as an indicator of habitat disruption in the Neotropics (Medellín et al. 2000; Wilson et al. 1996).

Increased abundances of shrub-frugivores can be related to their preferred pioneer fruit trees (e.g. \( \text{Piper} \), \( \text{Cecropia} \) and \( \text{Vismia} \)) which are highly abundant in edge- and matrix habitats (Muscarella & Fleming 2007). Specifically at the edges, abundance may increase because shrub frugivores such as \( C. \text{perspicillata} \) and \( R. \text{pumilio} \) frequently enter and exit the fragments to reach complementary resources (i.e. roosts and fruits) (Cortés-Delgado and Pérez-Torres 2011; Sampaio 2000). Finally, capture rates of shrub frugivores and \( C. \text{perspicillata} \) have been negatively correlated to similar vegetation characteristics that are typical for forest interior, as in our study, i.e. high canopy foliage density (Castro-Luna et al. 2007; Peters et al. 2006; Rex et al. 2011), large tree basal area and high variability in tree trunk height (Cortés-Delgado & Pérez-Torres 2011).

Other studies (i.e. Faria 2006, Meyer & Kalko 2008) did not demonstrate pronounced differences in capture rates between edge- and interior habitats at the assemblage level and/or for shrub-frugivores. However, Faria (2006) sampled ‘edges’ 20m from the border inside the forest fragment, where shrub-frugivores may fly through but don’t spend time foraging since the availability of pioneer fruit species is higher outside the fragment. Meyer & Kalko (2008) found no
differences in vegetation structure variables between their edge- and interior sites. In contrast, the study by Cortés-Delgado and Pérez-Torres (2011) as well as the present study, found significant differences in vegetation structure between edge- and interior habitat which was significantly related to capture rate at the assemblage level.

Canopy frugivores showed a near significant trend of higher capture rates in edge- and or matrix habitats when compared to forest interior. However, when looking at the data more closely, the canopy frugivores appear to show a clumped distribution. For instance, the relatively high capture rates in the matrix surrounding 10-, and 100ha fragments were based mostly on two locations: Porto Alegre and Dimona. In the matrix of the 10ha fragment in Porto Alegre only large canopy species were caught (*Artibeus concolor* and *Artibeus literatus*), whereas in the matrix of the 10- and 100ha fragments in Dimona only small canopy frugivores were caught (*Artibeus cinereus* and *Artibeus gnomus*).

These inconsistencies may be caused by the mapping of these species onto their preferred fruiting trees, which indicates that factors other than habitat type, such as fruiting phenology, might be more important in determining the abundance of canopy species (Brosset & Charles-Dominique 1990). Trees that are commonly used as food resource by canopy frugivores (e.g. figs) are relatively low in abundance near Manaus (Nee 1995), which provides further support for this hypothesis. In contrast, another study in which fig tree density was very high showed an overall high canopy frugivore abundance, with three canopy species accounting for almost 90% of the captures (Meyer & Kalko 2008).

Future studies in this area could be improved by locating important fruiting trees for canopy species and recording their fruiting events. Furthermore, a combined sampling design with ground-level and canopy-level mist nets may give a more complete picture of the response of the canopy frugivores (Bernard 2001; Kalko & Handley 2001; Sampaio et al. 2003).

None of the other guilds showed significant differences in capture rates between the different habitat types. The general low abundance of nectarivorous guild may seem surprising because most previous studies have shown distinct increases in nectarivorous species such as *Glossophaga soricina* and *Lonchophylla thomasi* in disturbed areas such as forest edges (Delaval and Charles-Dominique 2006; Meyer & Kalko 2008) and in matrix habitat (Estrada & Coates-Estrada 2002; Sampaio 2000) compared to interiors. Meyer (2007) even found a more than thousand fold increase in *G. soricina* on land-bridge islands compared to mainland in Panamá. Previous studies at the BDFFP in both continuous forest and matrix habitat in an earlier successional stage (Bernard 2001; Sampaio 2000) also found low capture rates for the nectarivores, which suggest
they are naturally low in abundance in both the undisturbed and altered habitats of our study area (Estrada & Coates-Estrada 2001; Faria 2006; Willig et al. 2007).

Gleaning animalivorous species are known to be ‘edge-sensitive’ (Meyer et al. 2008) and previous studies have shown decreased capture rates at forest edges (Meyer & Kalko 2008) and disturbed habitats (Medellín et al. 2000; Peters et al. 2006) compared to forest interior habitat and have negatively associated the gleaners to edge-density at the landscape level (Klingbeil & Willig 2009). In contrast to expectations, an edge effect on the abundance of gleaning animalivores was not apparent and all but one of the species of this guild was found in edge- and/or matrix habitat. Possibly, the old secondary forest at our study site is relatively hospitable for the animalivores, providing a buffering impact on the strength of the edge effect (Didham & Lawton 1999; Kupfer et al. 2006. For example, the abundance of gleaning animalivores declines markedly in fragments surrounded by a water-matrix with some species (e.g. Lophostoma silvicolum, Trachops cirrhosus) even completely disappearing (Meyer & Kalko 2008), whereas the same species persist in fragments embedded in a secondary forest and may even increase in the matrix habitat (Sampaio 2000). Similar results have been found for birds, for example, Bierregaard & Stouffer (1997) found that disturbance-sensitive insectivorous birds disappeared quickly after fragmentation of the BDFFP, but were also amongst the first to return when secondary forest started to develop in the matrix.

The secondary growth in our matrix habitat was relatively mature, reaching a mean tree height of 7.35(±0.15m) at edges and 7.30(±0.24m) in the matrix compared to 9.26(±0.24m) in the forest interior. This successional stage of the secondary forest might provide sufficient vegetation clutter to enable gleaning bats to forage or at least traverse the matrix as to combine resources from several fragments (Ewers & Didham 2006; Tscharntke et al. 2002). Indeed, studies by Castro-Luna et al. (2007) and Brobowiec and Gribel (2010) demonstrated that gleaning animalivores of the sub-family Phyllostominae were lacking in young secondary forest or pasture but persisted in secondary forest.

Despite the relatively ‘soft’ conditions of the matrix in our study area, I was still able to find an edge effect on species composition. There did not appear to be a distinct ‘edge-species community’. Rather species composition was similar in edge- and matrix habitat, but distinct from interior habitat. Again, this result is probably related to the relative high abundance of frugivorous species in the edge- and matrix compared to interior habitat. These results somewhat contrast the findings of Faria (2006) where the edge assemblage was a mere subset of the interior.
assemblage. This does not seem to be the case in our study area since only five species were captured exclusively in the interior-habitat, compared to one and four in the edge- and matrix habitat respectively, with 76% of the species captured in at least two of the habitat-types.

5.2 Area effects

I did not find a significant difference in richness, diversity, evenness or capture rate at the assemblage level for any of the three habitat types with patch size, nor did patch size influence the strength of any of the edge effects that were found (i.e. the difference between interior-compare to edge- or matrix habitat for any of the bat assemblage attributes). This is in contrast to prior findings in the same research area. Sampaio (2000) found species richness and diversity to increase with patch size for interior habitats and found lower capture rates in the interiors of 1ha fragments compared to the interiors of 10ha fragments (100ha fragments were not sampled). Struebig et al. (2008) and Cosson et al. (1999) also found significant impacts of patch size on bat species richness, abundance, and/or species composition in the interiors of fragments embedded in an agriculture/secondary forest matrix and water matrix respectively and Gorresen & Willig (2004) found these measures to change with patch size at the landscape level in a system dominated by pasture and water. Again, these contrasting findings might be related to the more hostile conditions of the matrix in these other studies compared to mine.

However, at the guild level, gleaning animalivores had higher capture rates in all habitat types in larger patches compared to smaller patches. Capture rate of the gleaners differed most pronouncedly with size in the interior habitat, with especially low abundances in the 1ha fragment. Higher capture rates in the edge- and matrix habitat with increasing patch size may be explained by ‘spill over’ from interior habitats that hold source populations (Didham 1997; Holt et al. 1997).

For the capture rate of the gleaners, no edge effect could be discerned, nor could I find the difference between habitat types to change with patch size. These results suggest that the area effect is stronger than the edge effect for gleaning animalivores. Edge-sensitivity may be less pronounced in study systems with a low contrast matrix like ours compared to systems embedded in water- or pasture (Meyer et al. 2008). In contrast, area sensitivity may remain because small fragments may not hold sufficient resources (e.g. roosts) and/or may hold vulnerable small populations that are subject to demographic and genetic stochasticity (Gaggiotti & Hanski 2004). Vegetation characteristics varied nearly significantly with patch size at this study area, which may be part of the explanation for the observed pattern because the gleaners have
been shown to be negatively impacted by low canopy foliage density, small DBH and low variation in tree height (Castro-Luna et al. 2007; Cortés-Delgado & Pérez-Torres 2011; Peters et al. 2006). For example, some gleaners (i.e. *Tonatia saurophila*) require trees with a minimum DBH of 40cm for roosting (Kalko et al. 1999).

However, edge effects cannot be completely excluded as mechanism behind the observed pattern. Edge effects increase disproportionately with size (Laurance & Yensen 1991) and unlike the larger fragments, the 1ha fragment interiors may have been subject to the effects of multiple edges (Malcolm 1994). Edge and area effects may thus have played a synergistic role in the 1ha fragments, which is a common finding in studies that explicitly address the two mechanisms (e.g. Banks-Leite et al. 2010; Didham 1997; Ewers et al. 2007)

At the species level, *R. pumilio* seemed to have peak interior-abundances in medium-sized fragments (10 and 100ha), while edge-, and matrix abundance was consistently higher around fragments larger than 1ha and in continuous forest (trends were however, not significant). A distinct response to fragmentation of *R. pumilio* relative to other shrub frugivores have been reported before (Faria et al. 2006; Presley et al. 2009). For example, Faria et al. (2006) found that *R. pumilio* was more abundant in patches of shade-cacao plantations than forest fragments in a landscape dominated by primary forest, but represented just 2% of total captures in shade-cacao plantations set in a more disturbed landscape where their abundance in forest remnants increased. The abundance of *R. pumilio* may thus be determined by a complex combination of patch size and relative abundance of complementary resources from primary forest (e.g. roosts in palm- and *Heleconia* leaves) and disturbed matrix (e.g. *Piper* fruits) (Cosson et al. 1999; Faria 2006).

5.3 Caveats

Edge-related changes in species richness, diversity and evenness have been demonstrated for organisms such as invertebrates (Didham 1997), butterflies (Brown & Hutchings 1997), small mammals (Malcolm 1997), birds and bats (Delaval & Charles-Dominique 2006; Meyer & Kalko 2008). However, we did not find species richness, diversity and evenness -to be affected either by habitat type or by patch size. There is a general inconsistency in the bat literature regarding these measures (Cunto & Bernard 2012) which is due in part to the fact that they reflect the composite of numerous variable species responses (Ewers & Didham 2006) but also to the wide variety of experimental designs and research systems used in the study of bats (Cunto & Bernard 2012). This
raises the question whether these measures were truly unrelated to habitat, or if this was just an artifact of our study limitations, as discussed in the following.

This study was conducted over a short time frame. Despite the fact that we captured a considerable number of individuals and species (as a comparison Sampaio et al. (2003) captured 90% of the expected species number after 29,950mnh, while we capture 84,2% with less than 1/6th of that capture effort), stochastic events may become more important over a small timeframe. For example, although not statistically significant, A. obscurus seemed to have highly elevated capture rates at the edge and in the matrix of the 10ha fragments. However, looking at the data more closely, 70% of all A.obscurus captures were obtained during merely one night of sampling at the 10ha edge- and matrix habitat of Porto Alegre. This was a night with unusually high capture rates (141 captures compared to a mean of 23, edge- and matrix combined) and also an unusually high proportion of A. obscurus (45% of total captures compared to a mean of 2%). The underlying cause of this exceptional nights I unknown bur might be related to a fruiting event of a preferred food tree by this species (e.g. Ficus) (Kalko & Handley 2001). Stochasticities like this may have a disproportional impact in smaller datasets, which could obscure results or lead to the detection of spurious patterns (Banks-Leite et al. 2012). Sampling over a long timeframe would also control for seasonal variation (Banks-Leite et al. 2012), although seasonal impacts are not apparent for most bat species in this area (Sampaio 2000).

Another possible caveat of this study might be related to the conditions under which fragmentation has occurred here. It is likely that the low contrast between matrix and forest and the proximity of vast expanses of primary forest had a mitigating impact on possible edge effects on bats (Bernard & Fenton 2003; Klingbeil & Willig 2009; Sampaio 2000). Studies that were set in more hostile matrices of pasture (e.g. Bobrowiec & Gribel 2010; Cortés-Delgado & Pérez-Torres, 2011) or water (Cosson et al. 1999; Meyer & Kalko 2008) have shown different and stronger responses to disturbance. On the other hand, our results might be more realistic and applicable to the ‘real world’, considering that 47% of deforested land in the Brazilian Amazon was covered by secondary regrowth in 1990 (Fearnside 1996) and this proportion has increased ever since (Wright 2010).

Bearing in mind these limitations, the results that we found are based on a strong experimental and analytical design using standardized methods that are observer-independent and thus suitable for replication and possibly extrapolation to other study areas.
5.4 Conservation Implications

Species composition differed between the edge- and matrix habitat compared to the interior habitat. Furthermore, the capture rate of one guild (shrub frugivores) and one species (C. perspicillata) increased at the edges and in the matrix compared to forest interior, which may have positive impacts on forest regeneration through the seed dispersal of successional plants provided by this group (Muscarella & Fleming 2007). However, the proliferation of one guild or species at the expense of another may lead to ecological distortion that ends in less diverse and simplified ecosystems (Terborgh et al. 1997). Also, the frugivorous guild clearly masked the negative impact of decreasing patch size on the capture rate of the animalivorous guild. It is important that fragmentation studies on bats consider guilds and species individually to avoid displaying ‘false’ positive results.

From the perspective of the gleaning animalivorous bats, which reacted sensitively to patch size, conservation efforts should focus on the maintenance of sufficiently large forest remnants, which are generally considered superior to small reserves for the long-term persistence of area-sensitive species (Ferraz et al., 2003) because they can retain larger populations (Connor et al. 2000) and are less encroached by edge effects that may degrade the interior habitat (Laurance et al. 2002). For example, in Amazonian forest fragments, edge effects such as elevated tree mortality, reduced canopy height and canopy density may extend several hundreds of meters into the fragment interior (Laurance 2008; Laurence et al. 2002). This may in turn have detrimental impacts on roost-site availability for the gleaners that is associated with large trees. Retaining large forest remnants with a low perimeter: area ratio could also mitigate the amount of area exposed to edge effects on bats such as the altered species composition and change in relative abundance that was observed in this study.

Nonetheless, edge and area effects on the bats in our study area can be considered relatively moderate compared to high-contrast study systems embedded in a water- (Kalko & Meyer 2008) or pasture matrix (Brobowiec & Gribel 2010). Even in the same study system, the negative impacts of patch size on species richness, diversity and abundance that were observed 15 years ago when forest stands were younger and shorter (Sampaio 2000) seem to have faded (although this should be interpreted with caution because of the larger sampling effort in the previous study).
These findings are most likely related to the mitigating impacts of the relatively mature secondary forest in the matrix of our study area, which confirms the important role of matrix management in conservation (Koh & Gazoul 2010; Santos-Barrera & Urbina-Cardona 2011; Watling et al. 2011). This also sheds a positive light on bat conservation with an eye on current reforestation rates, for example Wright (2010) reports 21,500km$^2$ yr$^{-1}$ of regenerating forest on abandoned land (~34% of global deforestation rate) in just 29% of the entire moist tropical forest biome and Brazil is the country with the highest woody vegetation gain of Latin America (Aide et al. 2012). The ambitious target of the Brazilian government to reduce deforestation rates with 20% relative to the 1996-2005 rate by 2020 (Government of Brazil, Presidential decree 2007) has led to an expanded protected area network (e.g. Amazon Region Protected Areas Program) (Montiel 2004), increased enforcement of the environmental law and pressure on the cattle- and soy industry which have contributed to a decline in deforestation rate by 36% in 2009 compared to the 1996-2005 baseline (Nepstad 2009).

However, a recent revision of Brazil’s most important legal framework for conservation ‘the Forest Code’ (Sparovek et al. 2012) will reduce prior legal requirements for private land owners to restore native vegetation and may promote extensive deforestation of tropical forests on a regional scale (Metzger et al. 2010; Sparovek et al. 2011). Such developments would cause habitat loss and fragmentation to such a degree that bats, as well as many other organisms, may become severely imperiled (Michalski et al. 2010; Soares-Filho et al. 2006; Wearn et al. 2012).
References


Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K. & Syme,


Grindal, S., & Brigham, R. (1999) Impacts of forest harvesting on habitat use by foraging
insectivorous bats at different spatial scales. *Ecoscience*, 6, 25–34.


Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.V., Voll, E,


edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. *Biological Conservation*, 120(3), 311-327.


## Appendix 1  Bat Inventory

<table>
<thead>
<tr>
<th>Phyllostomidae</th>
<th>Guild*</th>
<th>Individuals captured</th>
<th>Interior</th>
<th>Edge</th>
<th>Matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Carollinae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carollia perspicillata</td>
<td>FR SH</td>
<td>655</td>
<td>6.57</td>
<td>16.52</td>
<td>17.60</td>
</tr>
<tr>
<td>Carollia sp. (benkeithi/brevicauda)</td>
<td>FR SH</td>
<td>69</td>
<td>0.61</td>
<td>1.66</td>
<td>2.09</td>
</tr>
<tr>
<td>Rhinophylla fischerae</td>
<td>FR SH</td>
<td>1</td>
<td>0.00</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Rhinophylla pumilio</td>
<td>FR SH</td>
<td>151</td>
<td>1.91</td>
<td>3.39</td>
<td>3.68</td>
</tr>
<tr>
<td><strong>Desmodontinae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Desmodus rotundus</td>
<td>SAN</td>
<td>1</td>
<td>0.04</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Glossophaginae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anoura caudifera</td>
<td>NEC</td>
<td>2</td>
<td>0.04</td>
<td>0.07</td>
<td>0.00</td>
</tr>
<tr>
<td>Choeroniscus minor</td>
<td>NEC</td>
<td>3</td>
<td>0.11</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Glossophaga soricina</td>
<td>NEC</td>
<td>2</td>
<td>0.07</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Lonchophylla thomasi</td>
<td>ANI</td>
<td>4</td>
<td>0.11</td>
<td>0.07</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>Phyllostominae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glyphonycteris daviesi</td>
<td>ANI</td>
<td>2</td>
<td>0.04</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Lophostoma schulzi</td>
<td>ANI</td>
<td>4</td>
<td>0.04</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>Lophostoma silvicolum</td>
<td>ANI</td>
<td>25</td>
<td>0.29</td>
<td>0.72</td>
<td>0.51</td>
</tr>
<tr>
<td>Lampronycteris brachyotis</td>
<td>ANI</td>
<td>1</td>
<td>0.04</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Micronycteris nicefori</td>
<td>ANI</td>
<td>1</td>
<td>0.04</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Mimon crenulatum</td>
<td>ANI</td>
<td>26</td>
<td>0.22</td>
<td>0.87</td>
<td>0.58</td>
</tr>
<tr>
<td>Phyloderma stenops</td>
<td>FR -</td>
<td>3</td>
<td>0.00</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>Phyllostomus discolor</td>
<td>ANI</td>
<td>4</td>
<td>0.04</td>
<td>0.14</td>
<td>0.07</td>
</tr>
<tr>
<td>Phyllostomus elongatus</td>
<td>ANI</td>
<td>7</td>
<td>0.18</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>Phyllostomus hastatus</td>
<td>ANI</td>
<td>2</td>
<td>0.04</td>
<td>0.07</td>
<td>0.00</td>
</tr>
<tr>
<td>Tonatia saurophila</td>
<td>ANI</td>
<td>18</td>
<td>0.58</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>Trachops cirrhosus</td>
<td>ANI</td>
<td>31</td>
<td>0.72</td>
<td>0.14</td>
<td>0.65</td>
</tr>
<tr>
<td>Trinysteris nicefori</td>
<td>ANI</td>
<td>5</td>
<td>0.08</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td><strong>Stenodermatinae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Artibes cinereus</td>
<td>FR CN</td>
<td>9</td>
<td>0.00</td>
<td>0.29</td>
<td>0.36</td>
</tr>
<tr>
<td>Artibes concolor</td>
<td>FR CN</td>
<td>23</td>
<td>0.07</td>
<td>0.79</td>
<td>0.72</td>
</tr>
<tr>
<td>Artibes gnomus</td>
<td>FR CN</td>
<td>14</td>
<td>0.07</td>
<td>0.43</td>
<td>0.43</td>
</tr>
<tr>
<td>Artibes lituratus</td>
<td>FR CN</td>
<td>16</td>
<td>0.18</td>
<td>0.07</td>
<td>0.72</td>
</tr>
<tr>
<td>Artibes obscurus</td>
<td>FR OPP</td>
<td>92</td>
<td>0.54</td>
<td>2.31</td>
<td>3.25</td>
</tr>
<tr>
<td>Artibes planirostris</td>
<td>FR OPP</td>
<td>6</td>
<td>0.18</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Mesophylla macconnelli</td>
<td>FR SH</td>
<td>4</td>
<td>0.14</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Platyminus helleri</td>
<td>FR OPP</td>
<td>1</td>
<td>0.00</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Stumira tildae</td>
<td>FR -</td>
<td>11</td>
<td>0.00</td>
<td>0.07</td>
<td>0.72</td>
</tr>
<tr>
<td>Urodema bilobatum</td>
<td>FR CN</td>
<td>1</td>
<td>0.00</td>
<td>0.00</td>
<td>0.07</td>
</tr>
<tr>
<td>Vampyressa bidens</td>
<td>FR CN</td>
<td>2</td>
<td>0.00</td>
<td>0.00</td>
<td>0.14</td>
</tr>
<tr>
<td>Vampyressa brocki</td>
<td>FR CN</td>
<td>2</td>
<td>0.04</td>
<td>0.07</td>
<td>0.00</td>
</tr>
<tr>
<td>Vampyressa pussilia</td>
<td>FR -</td>
<td>1</td>
<td>0.00</td>
<td>0.07</td>
<td>0.00</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mormoopidae</th>
<th>Guild*</th>
<th>Individuals captured</th>
<th>Interior</th>
<th>Edge</th>
<th>Matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pteronotus parnellii</td>
<td>INS</td>
<td>67</td>
<td>0.87</td>
<td>1.52</td>
<td>1.59</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>1266</td>
<td>13.82</td>
<td>29.65</td>
<td>34.05</td>
</tr>
</tbody>
</table>

* Guilds: ANI, gleaning animalivores; FR CN, canopy frugivores; FR OPP, opportunistic frugivores; FR SH, shrub-frugivores; INS, aereal insectivores, NEC, nectarivores, SAN:sanguivores.