Universidade de Lisboa
Faculdade de Ciências
Departamento de Biologia Animal

BAT SPECIES VULNERABILITY TO FOREST FRAGMENTATION IN THE CENTRAL AMAZON

Fábio Zanella Farneda

Dissertação
MESTRADO EM BIOLOGIA DA CONSERVAÇÃO

2013

Universidade de Lisboa
Faculdade de Ciências
Departamento de Biologia Animal

BAT SPECIES VULNERABILITY TO FOREST FRAGMENTATION IN THE CENTRAL AMAZON

Fábio Zanella Farneda

Orientadores
Dr. Christoph Friedrich Johannes Meyer
Dr. Paulo Estefano Dineli Bobrowiec

2013

“Nossas preciosas matas desaparecem, vítimas do fogo e do machado, da ignorância e do egoísmo...

...Virá então o dia em que a ultrajada natureza se enche vingada de tantos crimes”

UM SOPRO DE DESTRUIÇÃO: PENSAMENTO POLÍTICO E CRÍTICA AMBIENTAL
NO BRASIL ESCRAVISTA, ***José Bonifácio, 1825.***

Agradecimentos

Esta pesquisa foi financiada pela Fundação para a Ciência e a Tecnologia (FCT) através do projeto "Temporal dynamics of the impacts of forest fragmentation on Neotropical bat assemblages".

Sou imensamente grato ao meu orientador Christoph Meyer pela oportunidade de trabalhar no projeto. Obrigado pela enorme paciência, confiança, ajuda com a estatística, pelo inestimável apoio, pelas revisões e sugestões da tese e por todo o tempo despendido em me atender.

Ao Jorge Palmeirim, a quem muito admiro profissionalmente, sou extremamente grato pela indicação ao projeto, confiança e pelo apoio.

Ao Paulo Bobrowiec pelo apoio, pelas revisões e sugestões da tese. E por permitir o uso de sua sala particular de trabalho como meu espaço de estudo e dormitório.

Agradeço ao Instituto Nacional de Pesquisas da Amazônia (INPA) e à coordenação do Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF): José Camargo pela atenção e ajuda com muitos tipos de entrave, Ary Ferreira por tratar dos mais diversos contratempos em campo, Rosely Hipólito pela atenção e favores sempre atendidos, Mirtes Bernardes pelas conversas e o café de todo dia, Luiz de Queiroz e Josimar Menezes por serem nossos motoristas.

Aos amigos e colegas Rodrigo Marciente, Adrià López-Baucells, Alaércio dos Reis, Roberta da Silva, Ricardo Rocha, Douglas Pinheiro, Madalena Boto e Gilberto Fernandez pelo auxílio nas atividades de campo e/ou discussões que contribuíram para o melhoramento deste trabalho. Novamente um obrigado ao Rodrigo pela ajuda com o ImageJ, ao Adrià pelas conversas e ajuda com a matemática das fórmulas, ao Ricardo pelas sugestões, ao Gilberto e à Madalena pelos momentos de filosofia e descontração que fizeram passar mais agradavelmente as horas na mata.

Aos amigos de meus momentos difíceis: Reinaldo von Mühlen e Luci Stempkosky. Obrigado pelo incentivo, por socorrer minhas indecisões e por todos os conselhos cheios de sabedoria que muito me ajudaram a superar os obstáculos (que não foram poucos nem fáceis!).

Agradeço ao Marlon Zortéa, por ter-me apresentado o curso de mestrado em Biologia da Conservação da Universidade de Lisboa.

À Karla Gomes pela ajuda com meu visto de estudos. E à Sónia e à Rosa Pina por terem sido meu “guia de sobrevivência em Lisboa” logo que aqui cheguei. Sei que estou em débitos!

À minha praticamente segunda mãe, Maria Helena Gamito, por ter-me “adotado” em Portugal, pelas conversas, pela atenção e preocupação que teve comigo.

Ao Pedro Rufino e à Paula Carvalho, e à Patrícia Lopes e ao Pedro Gamito por me hospedarem em suas casas durante alguns dias que tive que passar por Lisboa nesta segunda etapa em terras lusitanas.

Um enorme obrigado ao Manuel Eduardo dos Santos por igualmente permitir minha estadia em sua casa nestes últimos (e decisivos!) meses. Obrigado pelo convívio e ambiente que muito ajudou a terminar este trabalho.

À minha família por tudo. Maristela, Celso Luiz, Denise, Lica. A presença de vocês ao meu lado foi fundamental para eu estar agora escrevendo os agradecimentos. Agradeço à minha nonna Libera Farneda pelas orações e a todos os demais parentes, amigos e conhecidos que me enviaram pensamentos positivos.

Agradeço, muito especialmente, à Zulmira Helena Gamito, minha companheira de todos os momentos. Obrigado por tornar minha vida mais suave e alegre, pela paciência, atenção, amizade, pelo incentivo, carinho e amor incondicional! Sou sempre grato por ter ao meu lado uma conservacionista cheia de planos!

E à “natureza”.

Table of contents

List of figures

List of tables

Abstract

1. To understand the ecological trait interspecific variation on the capacity of bat species to persist in fragments and recolonize new patches in the fragmented landscape is fundamental for the creation of conservation effective plans. In this context, the study assesses 26 bat species vulnerability in a forest fragmentation local scale with low fragment-matrix contrast.

2. The study was carried out in Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazon, Brazil. Bats were captured over a 2-year period in 8 forest fragments and 3 control plots of continuous forest, considering the interior, the edge and the matrix at the each local. The ecological traits values were obtained from our capture data and/or literature: (1) abundance in continuous forest, (2) body mass, (3) edge-sensibility, (4) matrix tolerance, (5) trophic level, (6) dietary specialization, (7) vertical stratification, (8) mobility, (9) wing morphology, (10) ecological scaled landscape indices (*ESLIs*). After phylogenetic correction, these variables were used separately and in combination to assess their association with two indices of fragmentation sensitivity: species prevalence (proportion of fragments occupied) and change in abundance. The correlation between the different traits and the environmental gradients were assessed using the RLQ and fourth-corner analysis.

3. Model selection based on Akaike's information criterion identified abundance in continuous forest as the best correlate of vulnerability to fragmentation. The main positive relationships found for the RLQ analysis was between abundance in continuous forest and forest fragmentation, and animalivorous bats and continuous forests. Abundance in continuous forest and trophic level also showed positive correlations with the fragmentation according to fourth-corner analysis, as well as edge-sense and matrix tolerance.

4. *Synthesis and applications*. Our results support that environmental filters and ecological traits consistently shape the bat assemblages in BDFFP fragmented landscape. The fragmented landscape will selectively benefit the most abundant, more matrix tolerant, less edge-sensitive and frugivorous species. The structural and functional connectivity among remnant patches is a main factor allowing persistence and dispersal of the species, mainly of those with low ability to use the matrix and the small fragments (≤ 10 ha). As a practical suggestion to minimize local extinctions, investment in the creation, restoration and maintenance of natural corridors is recommended, as well as the management of the matrix by improving its quality.

Key-words: Chiroptera, ecological traits, habitat fragmentation, tropical rainforest, environmental filters, Brazil, sensitivity, extinction risk, RLQ and fourth-corner analysis

Resumo

1. Entender a variação interespecífica das características ecológicas sobre a capacidade das espécies de morcegos de persistir em fragmentos e recolonizar novas áreas na paisagem fragmentada é fundamental para a criação de planos efetivos de conservação. Neste contexto, o estudo avalia a vulnerabilidade de 26 espécies de morcegos em uma escala local de fragmentação florestal com baixo contraste entre fragmentos-matriz.

2. O estudo foi conduzido nas áreas do Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF), Amazônia Central, Brasil. Os morcegos foram capturados ao longo de 2 anos em 8 fragmentos florestais e 3 áreas controle de floresta contínua, considerando o interior, a borda e a matriz de cada local. Os valores das variáveis ecológicas foram obtidos de nossos dados de captura e/ou de literatura: (1) abundância em floresta contínua, (2) tamanho corporal, (3) sensibilidade ao efeito de borda, (4) tolerância à matriz, (5) nível trófico, (6) especialização da dieta, (7) estratificação vertical, (8) mobilidade, (9) morfologia de asa, (10) índices de conectividade funcional (*ESLIs*). Após uma correção filogenética, as variáveis foram usadas separadamente e em combinação para avaliar sua associação com dois índices de sensibilidade à fragmentação: prevalência das espécies (proporção de fragmentos ocupados) e variação na abundância. As correlações entre diferentes características e gradientes ambientais foram avaliadas utilizando as análises RLQ e fourth-corner.

3. O critério de informação de Akaike identificou abundância em floresta contínua como o melhor modelo para explicar a vulnerabilidade à fragmentação. As principais relações positivas encontradas pela análise RLQ foram entre abundância em floresta contínua e fragmentação florestal, e morcegos animalívoros e florestas contínuas. Abundância em floresta contínua e nível trófico também apresentaram correlações positivas com a fragmentação pela análise fourth-corner, bem como sensibilidade ao efeito de borda e tolerância à matriz.

4. *Síntese e predições*. Nossos resultados confirmam que os filtros ambientais e as variáveis ecológicas moldam as comunidades de morcegos na paisagem fragmentada do PDBFF. A paisagem fragmentada vem seletivamente beneficiar as espécies mais abundantes, mais tolerantes à matriz, menos sensíveis aos efeitos de borda e frugívoras. A conectividade estrutural e funcional entre fragmentos remanescentes é o principal fator para a persistência e dispersão das espécies, principalmente daquelas com baixa capacidade de usar a matriz e os pequenos fragmentos (≤ 10 ha). Como sugestão prática para minimizar as extinções locais, é recomendando o investimento na criação, restauração e manutenção de corredores naturais, bem como uma gestão da matriz que melhore sua qualidade.

Palavras-chave: Chiroptera, características ecológicas, fragmentação de habitat, floresta tropical, filtros ambientais, Brasil, sensibilidade, risco de extinção, análises RLQ e fourth-corner

Introduction

The rainforests of the world are in decline due to various and increasing anthropogenic pressures (Corlett & Primack 2008, Hansen et al. 2008, Bradshaw et al. 2009). Concerning the Amazon rainforest, such scenario is due to the gradual loss of vast forest areas to livestock and agricultural activities, urban expansion, illegal logging, mining and dam construction (Gascon et al. 2001, Fearnside 2003, Kirby et al. 2006, DeFries et al. 2010, Macedo et al. 2012). The Brazilian Amazon lost about 33 million ha of forest in the last 20 years (Instituto Nacional de Pesquisas Espaciais 2013). Forest loss and fragmentation pose serious risks to the conservation of biodiversity (Laurance 2007, Morris 2010), and one of the biggest and urgent current challenges of conservation biology is to understand how these anthropogenic drivers of environmental change contribute to local species extinction risk, which allows the establishment of effective management and conservation plans.

A recent study predicts an increase of more than 80% in vertebrate species extinction rates associated with habitat loss in the Brazilian Amazon by 2050, and suggests that locally will lose an average of nine vertebrate species and have a further 16 committed to extinction (Wearn et al. 2012). This can potentially be catastrophic for ecosystem stability due the loss of functional groups that, by providing a specific ecosystem service or function, may have a cascading effect of species extinctions (Grelle 2005).

In the Amazon, bats are a good model group to assess how forest fragmentation influences the structure of their ecologically diverse communities (e.g. Sampaio 2000, Bernard & Fenton 2003, Bobrowiec & Gribel 2010). Besides their high species richness, bats are important seed dispersers, pollinators, prey, and regulators of animal populations (Kunz & Fenton 2003, Kunz et al. 2011), and their reduction or local extinction may significantly influence the dynamics of tropical ecosystems. For this reason, they have also been considered good bioindicators of habitat alteration (Fenton et al. 1992, Jones et al. 2009).

Species adaptation to fragmented landscapes depends on their biological traits (physiological requirements, morphological adaptations, life histories), ecological traits (environmental preferences and associated behaviors) and strategies of resource use (Davies et al. 2000, Cardillo et al. 2008). Traits such as wing morphology, mobility, diet, body size and geographic range have usually been used to assess the vulnerability of bat species to extinction at a global scale (e.g. Jones et al. 2003, Safi & Kerth 2004, Boyle & Storn 2007). However, different taxa vary in their responses to environmental changes (Meyer et al. 2008), and the vulnerability pathways are also defined by independent combinations of multiple traits (Purvis et al. 2000, Davidson et al. 2009). Henle et al. (2004) suggest that small population size, large population fluctuations and a high degree of habitat specialization are good predictors of species sensitivity at the local scale.

Although bats have great dispersal potential due to their flight capacity compared with other mammals (Estrada et al. 2004, Medina et al. 2007), certain species may be sensitive to forest loss and fragmentation because the fragmented landscape may act as an environmental filter that constrains their persistence via functional species traits (Medellín et al. 2000, Estrada-Villegas et al. 2010). A number of studies have compared bat species diversity and habitat use in fragmented landscapes (e.g. Brosset et al. 1996, Cosson et al. 1999, Sampaio 2000, Estrada & Coates-Estrada 2001, Bernard & Fenton 2007, Meyer & Kalko 2008, Presley et al. 2009, Estrada-Villegas et al. 2010), but at a small spatial scale few have evaluated whether species responses are associated with particular ecological traits (Duchamp & Swihart 2008, Meyer et al. 2008, Threlfall et al. 2011, Hanspach et al. 2012). In the Neotropics, the only work that details the vulnerability of bats to habitat fragmentation comes from a landbridge island system in Panama (Meyer et al. 2008), characterized by a high structural contrast between fragments and the surrounding matrix. The results by Meyer et al. (2008) indicated edge-sensitivity as the most important correlate of bat vulnerability to small-scale fragmentation and the authors recommended comparative studies in landscapes of different fragment-matrix contrast for a more efficient management of conservation plans.

The primary objective of this study therefore was to gain insights into which bat species ecological traits are correlated with their fragmentation sensitivity in a fragmented landscape with low fragment-matrix contrast. Specifically, we wanted to (a) define which ecological traits contribute most to species’ vulnerability, (b) identify which bat species are most vulnerable to fragmentation, (c) understand how specific environmental traits set pathways to local extinction risk. We tested the hypothesis that there is a significant relationship between species ecological traits, patterns of species distribution and environmental gradients (fragments and continuous forest interiors, forest edges and matrix). We expected that most gleaning animalivorous bats that are more habitat specialized, rare, heavier, top predators, and less mobile are more vulnerable to forest fragmentation. We compare our findings with the results found by Meyer et al. (2008) through the use of ten ecological traits as predictors of species responses to habitat fragmentation.

Material and Methods

Study area and experimental design

The study was carried out at the Biological Dynamics of Forest Fragments Project (BDFFP) located ca. 80 km north of Manaus, Central Amazon, Brazil (Fig. 1), an area which spans ~1000 km^2 (2°25´S-59°50’W) (Lovejoy & Bierregaard 1990). The area is characterized by a mosaic of unflooded (*terra firme*) Amazonian rainforest, secondary forest and primary forest fragments. The climate is monsoon – *Am* (Köppen) (Peel et al. 2007). Mean annual temperature is 26 ºC (range 19-39 ºC) (Oliveira & Mori 1999) and mean annual rainfall ranges from 1.900-3.500 mm. The rainy season lasts from October-May (Laurance 2001). The topography is relatively flat (80-160 m elevation), intersected by small streams (Laurance et al. 2011). The dominant soil type is yellow latosols, which are well-drained and nutrient-poor (Laurance et al. 1999). The primary forest canopy is 30-37 m tall, with emergent trees to 55 m (Laurance et al. 2011). Fruiting usually occurs during the rainy season (Rankin-de Merona et al. 1992). In the early 1980s, 11 fragments were isolated from continuous forest by distances of 80-650 m by clearing and burning the surrounding forest. Since then, each fragment was re-isolated on 3-4 occasions, most recently between 1999 and 2001 (Laurance et al. 2011). The matrix is characterized by secondary growth in various successional stages and is dominated mainly by *Vismia* spp. (areas that were cleared and burned) and *Cecropia* spp. (areas that were cleared without fire) (Mesquita et al. 1999).

The study included eight forest fragments (three of 1 ha, three of 10 ha, two of 100 ha – distributed in Dimona, Porto Alegre and Colosso camps) and nine control plots in three areas of continuous forest (Cabo Frio, Florestal and Km 41 camps) (Fig. 1). Sampling was conducted in the interiors and at the edges of all 8 fragments as well as at 8 sites located 100 m from the fragment border into the adjacent matrix. The same sampling scheme was applied for the continuous forest sites using 9 sampling points in the interior, 3 at the edge and 3 in the matrix.

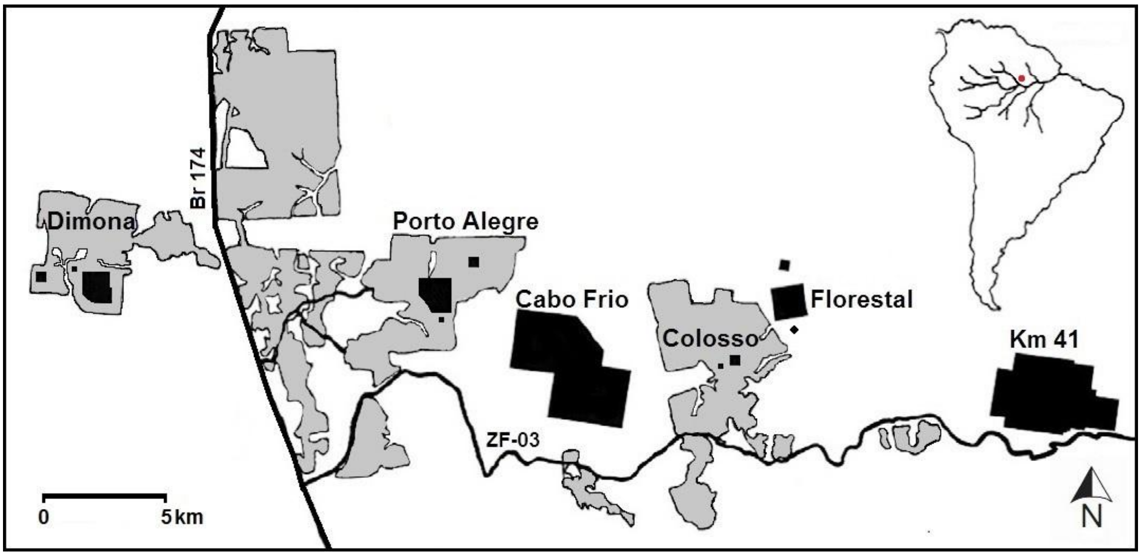


Fig. 1. Experimental area of the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazon, Brazil. Black areas represent Dimona, Porto Alegre and Colosso fragments, and areas of continuous forest in Cabo Frio, Florestal and Km 41. Grey areas represent the surrounding matrix.

Bat sampling

We used 31 mist-nets (2.5 x 12 m) for sampling each replica both in continuous forest and fragments: 14 ground-level nets in the interiors, 7 at the edges, 7 in the matrix, and (up to) 3 canopy nets in the interiors. The nets were revised at intervals of 10-30 minutes. Canopy net height in continuous forest and fragments averaged 18 m and 17 m, respectively. Each site was sampled for eight nights (from dusk until six hours after exposure) over a 2-year period (August 2011 to June 2013) by a shifting team with which I collaborated during the last sampling year. There were never two consecutive nights at the same sampling point. The bats were individually marked with numbered metal necklaces (frugivorous phyllostomid bats and *Pternotus parnellii*) or transponders – pit-tags (gleaning animalivorous bats), and released at the capture site. Species identification followed Simmons & Voss (1998), Lim & Engstrom (2001), Charles-Dominique et al. (2001), Gardner (2008) and Sampaio & Kalko (unpublished data). Taxonomy follows Simmons (2005). In total, we obtained 4,845 bat captures (4,207 at ground level and 638 at canopy level) representing six families and 59 species (unpublished data). For the purpose of this study we considered only species of the Phyllostomidae and *Pteronotus parnellii* (Mormoopidae) because they are sampled adequately with mist-nets (Kalko 1998), as well as all species with more than three captures in continuous forest. This resulted in 26 study species for analysis (Tab. 1).

Species traits

We examined the relationships between measures of species sensitivity to fragmentation and the following traits (compare Meyer et al. 2008): abundance in continuous forest, body mass, edge-sensitivity, matrix tolerance, trophic level, dietary specialization, vertical stratification, mobility, wing morphology and ecologically scaled landscape indices (*ESLIs*) (see Table S1 in Supplementary material).

Abundance in continuous forest. Recaptures (177) were excluded of the analyses and abundance calculations were standardized by capture effort (1 mist-net hour, mnh = one 12-m net open for 1 h). Total capture effort at ground level at continuous forest interiors was 6,034 mnh.

Body mass. Body size was calculated based on the average body mass of each species recorded in our study.

Edge-sensitivity and matrix tolerance. Edge-sensitivity and matrix tolerance were measured separately using the same index (IN), which uses the capture frequency of each species in the two habitat types relative to continuous forest sites: $IN = (N_{edge, matrix} – N_{interior})/(N_{edge, matrix} + N_{interior})$ (Harper et al. 2005), where negative values (-1) indicate captures only in continuous forest, while positive values (+1) refer to captures only at the edge or in the matrix.

Trophic level. Based on the trophic structure that best reflects the assemblage of phyllostomid bats in our study area (Bernard 2002), species were assigned to broad trophic categories, animalivorous or phytophagous (see Table S1 in Supplementary material). We considered animalivorous and frugivorous those species for which one prey order or one plant genus, respectively, contributed more than three-quarters of the food records, based on published accounts (see Table S1 for references).

Dietary specialization. We divided the food items into six categories: (a) fruit, (b) nectar or pollen, (c) leaves (d) arthropods (e) blood and (f) vertebrates. We calculated the percentage of the contribution of each food item to the total dietary records for each bat species (e.g. Heithaus et al. 1975, Bernard 2002, Thies & Kalko 2004, Giannini & Kalko 2005; see Table S1 for complete list of references). Three categories describing the degree of dietary specialization were established: (1) two or more food items contributed > 10% to all food records, (2) one single food item contributed > 90% to all food records, and (3) restricted food category of one particular item of food.

Vertical stratification. The use of the vertical forest niche of each species was measured through the proportion of captures in ground nets *vs*. canopy nets. The canopy net captures were counted from *c*. 6 m upwards (sub-canopy level). The calculations were based on abundance/capture effort (mnh). The species were assigned to three categories of vertical stratification: (U) understory species, < 33% of all captures in canopy nets; (N) opportunistic species without preference, 33-66% of all captures in canopy nets, (C) species with canopy preference, > 66% of all captures in canopy nets.

Mobility. Mobility patterns were determined through mark-recapture data obtained during our study (by calculating the distance between marking and recapture site) and/or based on the literature – where preference was given to radio-tracking studies for best representing species' home ranges (e.g. Bernard & Fenton 2003, Albrecht et al. 2007, Henry & Kalko 2007; see Table S1 for complete list of references). For 9 species for which no information on mobility was available, mean and maximum distances were predicted by linear regression on body mass ($F_{1,15} = 5.38$, $P = 0.034$, $r^2 = 0.26$; $F_{1,15} = 5.06$, $P = 0.039$, $r^2 = 0.25$, respectively). The species were then grouped into three categories of mobility according to mean and maximum recapture distances: low, intermediate and high (see Supplementary material, Figure S1).

Wing morphology. Different measures describing wing morphology, aspect ratio (wing span^2/wing area), wing loading (total body mass*gravitational acceleration/wing area) and relative wing loading (wing loading/body mass*$9.81^{0.33}$) (Norberg & Rayner 1987, Norberg 1998) were calculated by averaging measurement values of up to five individuals of each bat species recorded in our study. Measurements were made based on digital photographs and analyzed with the program ImageJ 1.47. As recommended by Norberg & Rayner (1987), the head was excluded from calculations of wing area.

ESLIs. We calculated two *ESLIs*, average carrying capacity (*ESLIk*) and patch connectivity (*ESLIc*; Vos et al. 2001, Swihart & Verboom 2004). *ESLIk* is defined as:

$$ESLIk = \sum_{i=1}^{n} \left(\frac{A_i}{IAR_i} \right) \Big/ n,$$

where A_i is the area of patch i and IAR_i is the individual area requirement of one reproductive unit of a particular species in patch i. In the same landscape, this index is higher for species with small individual area requirements. The patch connectivity index combines the degree of isolation of a specific patch with the mobility of the species:

$$ESLIc = \sum_{i=1}^{n} \left(A_j e^{-\alpha d_{ij}} \right) \Big/ n,$$

where d_{ij} is the distance between patches i and j, and α is a species-specific dispersal parameter. Species with good dispersal abilities, i.e. small α, therefore exhibit larger connectivity values. For *ESLIc*, the dispersal parameter was calculated based on maximum dispersal distances obtained from mark-recapture data from our study, the literature, or by linear regression as above. α was calculated as $\alpha = -\ln(0.001)/d_{\max}$ (Vos et al. 2001, Swihart et al. 2003). To quantify the *ESLIc* circular buffers of 1.5 km radius were delimited around the center of each forest fragment. Buffer scale was chosen so as to encompass the home ranges of different-sized bat species (Meyer et al. 2008). For the calculation of *ESLIk* maximum individual area requirements were obtained directly from the literature or by linear regression between maximum recapture distances and maximum home range sizes ($F_{1,9} = 38.08$, $P = 0.0001$, $r^2 = 0.81$).

Four models were included using a combination of traits:

1. *Dispersal*: mobility, body mass, relative wing loading, aspect ratio, edge-sensitivity and matrix tolerance.
2. *Population size*: abundance in continuous forest, body mass and trophic level.
3. *Specialization*: dietary specialization, vertical stratification, edge-sensitivity and matrix tolerance.
4. *ESLIs*: *ESLIc* and *ESLIk*.

Data analysis

Trait correlates of fragmentation sensitivity

To avoid statistical problems related to phylogeny in this multi-species study phylogenetically independent contrasts were applied to control for the non-independence of the data (Felsenstein 1985, Garland et al. 1992). Phylogenetic correction was performed using the R package ape (Paradis et al. 2004). Taxonomic relationships between species were based on the phylogeny proposed by Jones et al. (2002). Results with and without phylogenetic correction are presented in the Supplementary material, Table S2 and S3, respectively.

To ensure comparability with the results of Meyer et al. (2008), we compared two measures of sensitivity to fragmentation: (1) proportion of fragments in which a particular species was present (arcsine-transformed), (2) index of change in abundance adapted from Davies et al. (2000) – relative species abundance (RA; bats/mnh) in fragments and in continuous forest sites. A small number (0.0001) was added to the relative abundance of each species as *Glyphonycteris daviesi* was not captured in fragments: $y = \log_e (\mathrm{RA}_{\mathrm{fragments}} + 0.0001/\mathrm{RA}_{\mathrm{continuous\ forest}} + 0.0001)$.

Logarithmic transformations were performed on body mass, abundance in continuous forest and *ESLIs*. Both response variables followed a normal probability distribution (Shapiro–Wilk test, $P > 0.05$) after phylogenetic correction, and were modeled using generalized linear models (GLMs) assuming a Gaussian distribution. Regressions for all models were forced through the origin (Garland et al. 1992). For each response variable, goodness-of-fit was examined based on the global model as percentage of explained deviance (Crawley 2005). The selection of the best model was made using the Akaike information criterion (AIC) corrected for small-sample size ($\mathrm{AIC_c}$). Delta values $\Delta_i < 2$ and high values of Akaike weights (w_i) (i.e. closest to one) identified the models that received the strongest support. Model selection frequencies (π_i), which based on bootstrapping (10,000 resamples) of the original data give the proportion of times each model was the one best supported from the candidate set, were further calculated to assess model selection uncertainty (Burnham & Anderson 2002). We also computed weighted estimates of regression coefficients and unconditional standard errors for the best-supported model in the confidence set:

$$\theta_j = \sum_{i=1}^{R} w_i \theta^{+}_{j,i},$$

where w_i is the Akaike weight of model i, and $\theta^{+}_{j,i}$ is the estimator of the regression coefficient if ecological trait j is included in model i (Burnham & Anderson 2002). The analyses were performed using the R package AICcmodavg (Mazerolle 2013).

Trait-environment relationships

The relationships between species ecological traits (only individual traits were considered) and environmental variables were tested by RLQ (Dolédec et al. 1996) and fourth-corner analysis (Legendre et al. 1997, Dray & Legendre 2008). These are two complementary multivariate analyses linking data from three tables: R, L and Q. The R table comprises the environmental variables (39 sites x 3 variables) and here considered forest size (1, 10, 100 ha fragments and continuous forest), habitat category 1 (fragments or continuous forest) and habitat category 2 (interior, edge or matrix). The L table comprised species abundances (39 sites x 26 species) and the Q table all ecological traits (26 species x 13 traits). RLQ analysis maximizes the covariance between sites and species based on environmental variables and ecological traits (Dolédec et al. 1996). The L species table was analyzed by correspondence analysis (CA) and the R and Q tables by Hill-Smith principal components analysis (PCA) for mixed quantitative and qualitative data (Hill & Smith 1976), using the CA site and species scores, respectively, as row weights, thus allowing R and Q to be linked to the L table. We compared the variance explained (%) by the first two RLQ axes with those of the separate ordinations. Significance was tested using 999 permutations. We then applied fourth-corner analysis, which quantifies and tests the relationships between environmental variables and species ecological traits. The result is a matrix of correlation between ecological and environmental variables with community composition. We used a combination of model 2 – which links the matrices L and Q and tests the null hypothesis that communities of species are not dependent on the environmental variables of the sites where they are found, with model 4 – which links matrices L and R and tests the null hypothesis that the distribution of species between sites with favorable conditions does not depend on the species' ecological traits (Legendre et al. 1997, Dray & Legendre 2008). Significance of the relationship between species ecological traits and environmental variables was assessed based on 999 permutations through the fourthcorner2 function, which offers a multivariate statistic (equal to the sum of eigenvalues of RLQ analysis) and measures the link between two variables by a square correlation coefficient (two quantitative variables), a Chi^2/sum (L) (two qualitative variables) and a correlation ratio (one quantitative and one qualitative variable). RLQ and fourth-corner analysis were performed with the package ade4 (Dray & Dufour 2007) in R v.3.0.1 (R Development Core Team 2013).

Results

Trait correlates of fragmentation sensitivity

Abundance in continuous forest received overriding support as the best model explaining species' sensitivity to forest fragmentation for both response variables: species prevalence (w_i 0.93) and index of change in abundance (w_i 0.89) (Tab. 2). The composite "population size" model was ranked second ($\Delta \mathrm{AIC_c}$ 5.14, w_i 0.07 – species prevalence; $\Delta \mathrm{AIC_c}$ 4.25, w_i 0.11 – index of change in abundance), but based on Akaike weights was more than eight times less likely than the best ranking model. No other models in the candidate set were supported ($\Delta \mathrm{AIC_c} \geq 23$) (Tab. 2; Supplementary material, Table S2). Bootstrap selection frequencies confirmed the strong evidence for a correlation between fragmentation sensitivity and abundance in continuous forest:

55.9% of all cases (π_i = 0.559) species prevalence and 62.6% (π_i = 0.626) change in abundance (Tab. 2). The regression coefficient indicated a positive association between species prevalence (θ = 0.16) and change in abundance (θ = 0.95) with abundance in continuous forest.

Trait-environment relationships

The RLQ analysis included all 26 bat species and showed a significant relationship between species traits and environmental variables ($P = 0.001$). RLQ axis 1 accounted for 83.6% of the total co-inertia (i.e. link between the traits and environmental variables) compared with 8.6% for the second axis (Tab. 3). This represented 71.7% of the correlation expressed in the CA of species composition (table L), and 81.6% and 93.3% of the variance expressed in the Hill-Smith PCA of the environmental variables (table R) and ecological traits (table Q), respectively (Tab. 3). The PCA plot of environmental variables and of the RLQ axis 1 shows opposite trends between intact forest sites and fragmented habitats (Fig. 2a and 3). Continuous forest interior sites and 100 ha fragment interiors showed greater species richness, indicating that species richness increases with habitat integrity (Fig. 2a). Animalivores, canopy foragers and large species were associated with continuous forest and 100 ha fragment interiors. In comparison, high abundance in continuous forest, high matrix tolerance, low edge-sensitivity, high relative wing loading and a plant diet were associated positively with smaller fragments, edge and matrix habitats (Fig. 2 and 3). Aspect ratio, dietary specialization, *ESLIs*, mobility, and an understory or opportunistic foraging habit were traits not strongly correlated with the environmental variables (Fig. 3). Based on the fourth-corner analysis, we found a significant relationship ($P < 0.05$) between abundance in continuous forest and trophic level with the three environmental variables size (1, 10, 100 ha fragments and continuous forest), habitat category 1 (fragments or continuous forest), and habitat category 2 (interior, edge or matrix). Edge-sensitivity and matrix tolerance were positively correlated with habitat category 2 (Fig. 4).

Table 1. Responses to forest fragmentation recorded for 26 bat species in the fragmented landscape of the BDFFP, Brazil. Fragmentation sensitivity was assessed as species prevalence (fraction of fragments occupied) and through an index of change in abundance (decline/increase in species relative abundance relative to continuous forest interior sites).

Species	*Acronym*	*Fraction of fragments occupied*	*Change in abundance*
Artibeus cinereus	Acin	0.63	-2.022
Artibeus concolor	Acon	0.50	-1.883
Artibeus gnomus	Agno	0.38	-2.356
Artibeus lituratus	Alit	0.38	-2.360
Artibeus obscurus	Aobs	0.75	-0.753
Artibeus planirostris	Apla	0.50	-1.889
Carollia brevicauda	Cbre	0.88	-0.538
Carollia perspicillata	Cper	1.00	2.450
Chrotopterus auritus	Caur	0.25	-3.225
Desmodus rotundus	Drot	0.25	-3.255
Glyphonycteris daviesi	Gdav	0.00	-6.160
Lonchophylla thomasi	Ltho	0.63	-1.198
Lophostoma schulzi	Lsch	0.25	-3.238
Lophostoma silviculum	Lsil	0.63	-1.487
Mesophylla macconnelli	Mmac	0.50	-2.358
Micronycteris microtis	Mmic	0.38	-2.851
Mimon crenulatum	Mcre	0.50	-1.264
Phylloderma stenops	Pste	0.25	-2.857
Phyllostomus discolor	Pdis	0.25	-2.838
Phyllostomus elongatus	Pelo	0.50	-2.023
Pteronotus parnellii	Ppar	1.00	0.016
Rhinophylla pumilio	Rpum	1.00	1.175
Tonatia saurophila	Tsau	0.50	-0.753
Trachops cirrhosus	Tcir	0.88	-0.677
Trinycteris nicefori	Tnic	0.25	-3.238
Vampyressa bidens	Vbid	0.25	-2.356

Table 2. The two best-supported models from the set of candidate GLMs for the two measures of fragmentation sensitivity. Sample-size adjusted AIC (AIC_c), Akaike differences (Δ_i), Akaike weights (w_i), and bootstrap selection frequencies (π_i), as well as model-averaged parameter estimates (θ) and unconditional standard errors (SE) are presented. Traits included in the population size model were: AC – abundance in continuous forest; BM – body mass; TL – trophic level. Percentage deviance explained (% dev.) is given for each response variable.

Response variable	*Model*	AIC_c	Δ_i	w_i	π_i	θ	*SE*
Species prevalence	Abundance in continuous forest (AC)	-34.12	0.00	0.93	0.626	0.16	0.02
(% dev. = 75.9)	Population size (AC + BM + TL)	-28.99	5.14	0.07	0.194		
	Other models		> 23	0.00			
Change in abundance	Abundance in continuous forest (AC)	50.71	0.00	0.89	0.559	0.95	0.14
(% dev. = 82.3)	Population size (AC + BM + TL)	54.96	4.25	0.11	0.215		
	Other models		> 25	0.00			

Table 3. Results from RLQ analysis using environmental variables and species traits. a) Eigenvalues (and % of total co-inertia) for the first two axes. Ordinations of tables R (principal components analysis – PCA Hill-Smith), L (correspondence analysis – CA) and Q (principal components analysis – PCA Hill-Smith). b) Summary of RLQ analysis: eigenvalues and percentage of total co-inertia accounted for by the first two RLQ axes, covariance and correlation (and % variance) with the correspondence analysis of the L matrix, and projected variance (and % variance) with the R and Q matrices.

	Axis 1 (%)	*Axis 2 (%)*
a)		
R table PCA (Hill-Smith)	3 (20.00)	2 (13.33)
L table CA	0.15 (25.53)	0.08 (13.52)
Q table PCA (Hill-Smith)	3.81 (29.34)	3.26 (25.09)
b)		
RLQ axis eigenvalues	0.69 (83.60)	0.07 (8.64)
Covariance	0.83	0.26
Correlation: L	0.28 (71.75)	0.13 (48.61)
Projected variance R	1.56 (81.60)	1.19 (4.16)
Projected variance Q	1.88 (93.35)	1.61 (6.20)

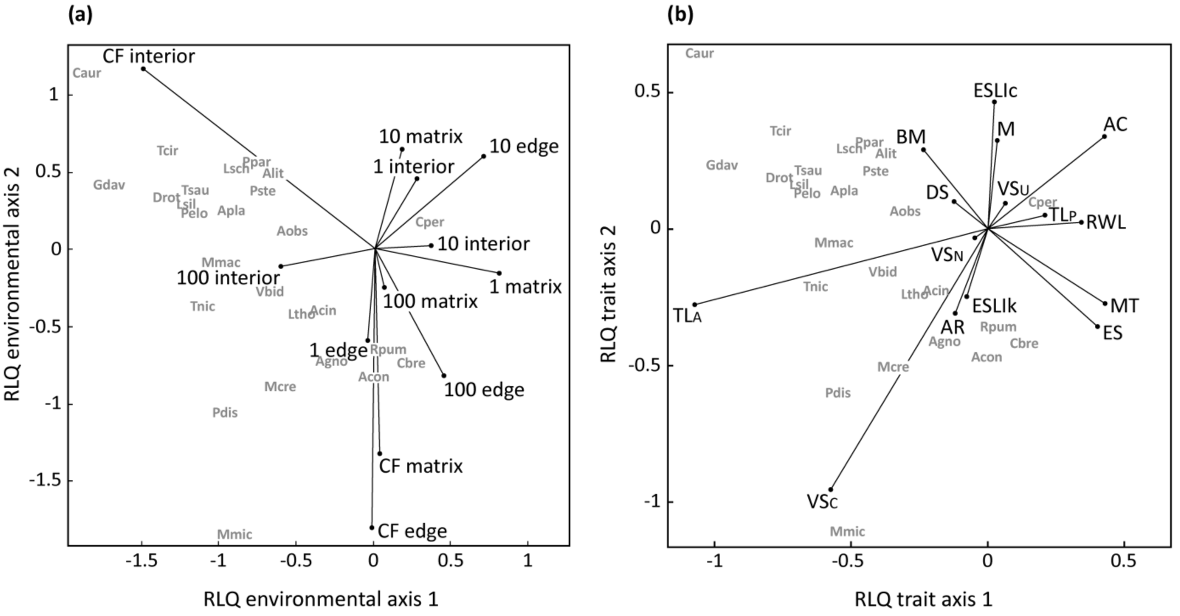


Fig. 2. Principal component analysis (PCA Hill-Smith) analyzing the covariation of environmental variables (a) and ecological traits (b) across all 26 bat species. Abbreviations: a) CF = continuous forest; b) AC = abundance in continuous forest, BM = body mass, ES = edge-sensitivity, MT = matrix tolerance, TL = trophic level, DB = dietary specialization, VS = vertical stratification, MO = mobility, AR = aspect ratio, RWL = relative wing loading, ESLIc – ESLIk = ecologically scaled landscape indices. See Table 1 for full species names.

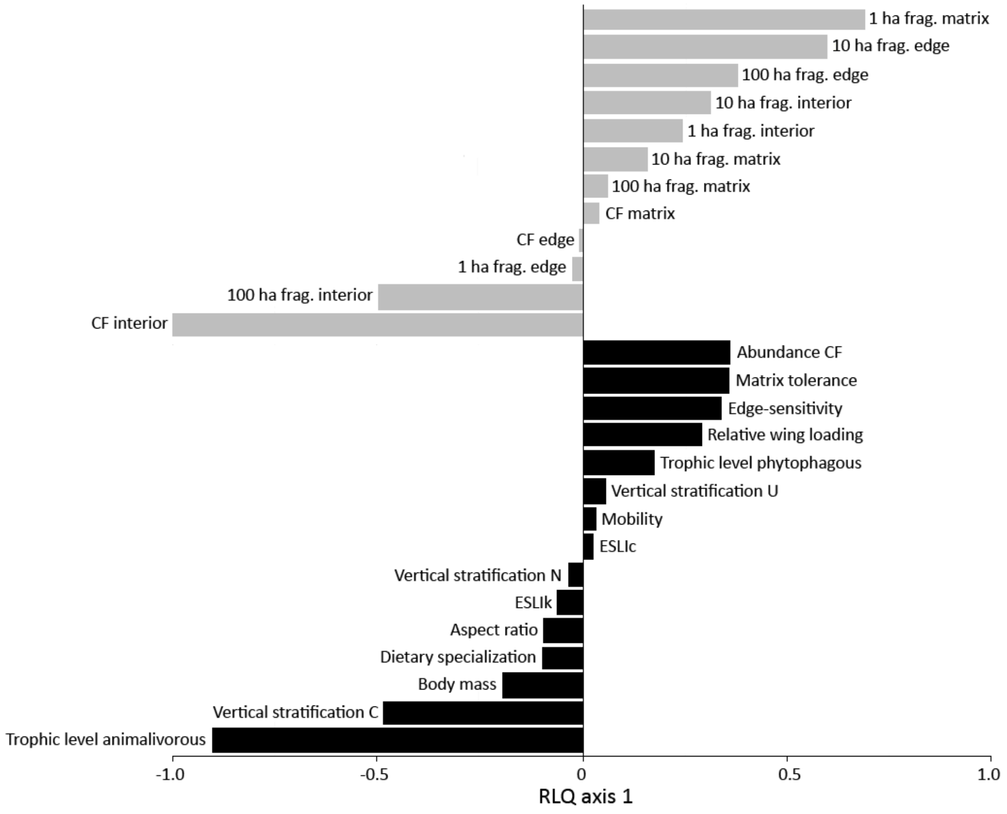
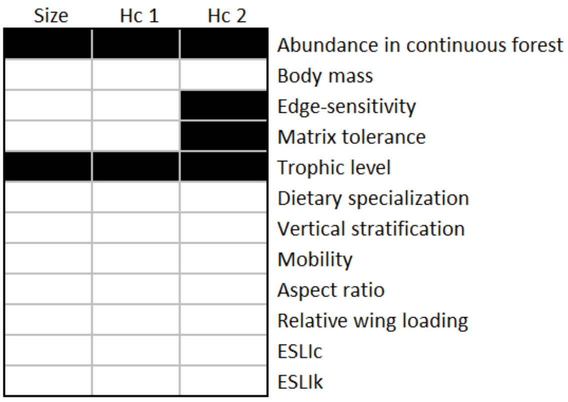


Fig. 3. Plot of RLQ analysis relating bat species traits (black bars) and environmental variables (grey bars) along RLQ axis 1. Abbreviations: CF = continuous forest, ESLIc – ESLIk = ecologically scaled landscape indices.



	Size	Hc 1	Hc 2
Abundance in continuous forest	■	■	■
Body mass			
Edge-sensitivity			■
Matrix tolerance			■
Trophic level	■	■	■
Dietary specialization			
Vertical stratification			
Mobility			
Aspect ratio			
Relative wing loading			
ESLIc			
ESLIk			

Fig. 4. Fourth-corner correlations between species traits (rows) and environmental variables (columns) using all 26 bat species. Black fields represent significant ($P < 0.05$) relationships based on 999 randomizations. Abbreviations: size (1, 10, 100 ha fragments and continuous forest), Hc 1 = Habitat category 1 (fragments or continuous forest), Hc 2 = Habitat category 2 (interior, edge or matrix).

Discussion

There has been a substantial impact of forest fragmentation on the bat assemblages studied at the BDFFP, as evidenced by the observed patterns of species prevalence and change in abundance in fragments relative to continuous forest controls. For certain functional groups, like gleaning animalivorous bats, species prevalence and change in abundance values were similar between this study and Meyer et al. (2008). Unlike the response variable species prevalence, the index of abundance change allows measuring the differences in species abundances between fragments and continuous forest (Meyer et al. 2008), presenting a more informative framework for analyzing the less abundant or rare species, which in turn should be more susceptible to local extinction (Henle et al. 2004). However, species prevalence and change in abundance showed no great differences in the choice of the best models, irrespective of whether the data were corrected for phylogeny or not (see Supplementary material, Table S2 and S3). Abundance in continuous forest was the ecological trait associated most strongly with species vulnerability to fragmentation based on AICc (Table 2). The "population size" model also received limited support and its ranking as the second best model is probably due to its inclusion of abundance in continuous forest as a variable in this composite model (Table 2). Ecological traits such as body mass, trophic level, dietary specialization, vertical stratification, wing morphology, mobility and *ESLIs* did not receive support as being good predictors (Table 2). The results of Meyer et al. (2008) indicate abundance in continuous forest as the second best model for species prevalence, but the regression coefficient values were low compared with the best model in their study: edge-sensitivity.

Abundance in continuous forest, high trophic level, edge-sensitivity and matrix tolerance received support as good predictors of species sensitivity based on the RLQ and fourth-corner analysis (Table 3 and 4). The most abundant species such as *Carollia perspicillata*, *Carollia brevicauda* and *Rhinophylla pumilio* apparently benefited from fragmentation since they were recorded in a greater number of habitats, and thus can be assumed to be less affected by demographic and environmental stochasticity (Lande et al. 2003). Such results refute the arguments of Tilman et al. (1994) that abundant species tend to be good competitors and poor dispersers, which would make them more susceptible to extinction in fragmented landscapes, and agree with McCarthy et al. (1997) in that poor competitors and rare species are more vulnerable to habitat loss. Species that occur at low population densities in continuous forest present greater difficulties in maintaining viable populations in small fragments (< 100 ha) and in the secondary forest matrix, being driven to extinction faster.

Abundance in continuous forest and animalivorous bats showed positive correlations with the structure and area of vegetation (Fig. 4), being the first positively related with the fragment interior-edge-matrix gradient, and the second with continuous forest interiors and 100 ha fragments, respectively (Fig. 2 and 3). Most species were strongly associated with continuous forest interior sites and 100 ha fragments (i.e., with greater forest integrity) (Fig. 2a), thus reflecting the fact that the intensity of fragmentation effects was correlated with abundance in continuous forest. Probably the lower prey abundances (e.g. small mammals, large arthropods) and roost availability at edges, as well as in the matrix and small fragment interiors (≤ 10 ha) in the BDFFP landscape (e.g. Gascon et al. 1999, Bobrowiec & Gribel 2010, Vasconcelos & Bruna 2012) make gleaning animalivorous bats highly dependent on continuous forest and more vulnerable to fragmentation (Medellín et al. 2000, Meyer et al. 2008). Environmental filters supposedly are less intense in continuous forest sites compared with edge and matrix habitats, where have more microhabitats due to vertical stratification (Jabot et al. 2008, Mayfield et al. 2009).

In spite of the low fragment-matrix contrast of the BDFFP landscape, edge-sensitivity and matrix tolerance were associated with forest fragmentation (Fig. 2 and 3) and with the fragment interior-edge-matrix-gradient (habitat category 2) (Fig. 4). Species with lower edge-sensitivity also have a higher matrix tolerance, since edge and matrix tolerance showed a significant, positive correlation (Pearson r = 0.44, *P* = 0.02). These results demonstrate that the low contrast matrix filtering apparently takes place for certain forest-interior species. Jantzen & Fenton (2013) found that the activity of some insectivorous bat species in mixed deciduous-coniferous forest in Canada increases after 40 m into the forest, and Delaval & Charles-Dominique (2006) concluded that edge effects on frugivorous and nectarivorous bat communities in a neotropical primary forest in French Guiana may occur up to 3 km into the forest. Meyer et al. (2008) suggested that the high contrast between fragments and the matrix in a landbridge island system explains the strong association between edge-sensitivity and bat species vulnerability. In another study, Bobrowiec & Gribel (2010) at the BDFFP observed that matrix tolerance for some phyllostomid bat species was directly related to food preferences – *Vismia* spp., *Cecropia* spp. and *Solanum* spp. fruit plants.

Although species at higher trophic levels tend to be larger, and larger species tend to be more vulnerable to fragmentation (e.g. Purvis et al. 2000, Henle et al. 2004), the importance of body mass as predictor has been found to differ between studies. Our study and Meyer et al. (2008), for example, found no strong association between body mass and vulnerability. By contrast, Threlfall et al. (2011) found an association of insectivorous bat species of greater body mass and open areas in an urban landscape, and Hanspach et al. (2012) found that sites with dense tree cover were associated with smaller species in a mosaic of forest and agriculture, both in Australia.

In the Neotropics many frugivorous and nectarivorous bat species adjust their diet according to seasonal or local availability (Fleming 1986, Kunz & Ingalls 1994, Ramos-Pereira et al. 2010a), and are often strongly associated with plants of disturbed habitats, as the BDFFP matrix (Muscarella & Fleming 2007, Bobrowiec & Gribel 2010). Our results corroborate the findings of Safi & Kerth (2004) and Meyer et al. (2008), who found no relationship between species most at risk of extinction and a narrow dietary niche. In contrast, Duchamp & Swihart (2008) found a positive relationship of forest cover with species characterized by a broad dietary niche in an agriculturally-dominated, fragmented landscape in the USA.

Specialization in terms of their vertical foraging niche may render some bat species vulnerable if a particular food item in a particular forest stratum declines as a consequence of fragmentation (Bernard 2001, Kalko & Handley 2001). However, based on our analysis, we cannot assert that the species occupying higher forest strata are more vulnerable to fragmentation (Fig. 3). The majority of gleaning animalivorous bats are generally associated with lower forest strata (Bernard 2001, Ramos-Pereira et al. 2010b, Rex et al. 2011). On the other hand, the height of capture may not reflect foraging height, since there is often no clear distinction between many canopy and understory species (Bernard 2001, Kalko & Handley 2001, Ramos-Pereira et al. 2010b, Rex et al. 2011, Silva 2012).

Mobility was not a strong correlate of fragmentation sensitivity based on the analyses (Fig. 3 and 4), which may be a result of: i) increased fragment connectivity in response to the forest regenerating around the fragments, ii) low rate of recaptures, iii) general lack of published studies on mobility patterns and home ranges. It is recommended that future bat studies in the Amazon use radio-telemetry, which allows assessing the movement, foraging patterns, roost use and minimum home ranges, once the local landscape matrix is represented by large areas that, hypothetically, can reduce the resources and interfere with species' movement and habitat use. Mobility or mobility-related traits received some support in Meyer et al. (2008), as *ESLIs* in the case of the index of abundance change were the second best model, receiving still reasonably high bootstrap frequencies. Due to a lack of data, the home range sizes (*ESLIk*) and maximum dispersal distances (*ESLIc*) for many species had to be predicted by regression. This may have resulted in a large variation in precision of the measures among species. The low fragment-matrix contrast of the BDFFP landscape did not prove the utility of the *ESLIs*.

In relation to wing morphology, aspect ratio was not an important predictor, and relative wing loading, which takes into account the relative size of the bat, was positively associated with forest fragmentation (Fig. 3), but both variables were not significant in the fourth-corner analysis (Fig. 4). Threlfall et al. (2011) found an association of insectivorous bat species with greater wing loading and open areas, and Duchamp & Swihart (2008) found a positive relationship of forest cover with species characterized by high wing-tip shape index in a fragmented landscape. In general, wing morphology appears to have greater predictive power of the risk of extinction for open-space aerial insectivorous bat species (Jones et al. 2003, Safi & Kerth 2004, Threlfall et al. 2011, Duchamp & Swihart, 2008), however, not for strongly forest-dependent bats, as was the case here and in Meyer et al. (2008).

Conclusions

Our study in a system of low structural contrast between fragments and the intervening matrix indicates four main species traits related to bat species vulnerability to fragmentation at the local scale: abundance in continuous forest, trophic level, edge-sensitivity and matrix tolerance. Our results support that environmental filters and ecological traits consistently shape the bat assemblages in the BDFFP fragmented landscape, suggesting that environmental variables particularly related to habitat-categories, will selectively benefit the most abundant, more matrix tolerant, less edge-sensitive and frugivorous species in this fragmented landscape. The degree of contrast between fragments and the matrix and temporal heterogeneity of secondary vegetation (i.e. quality and type of the matrix) are crucial for the maintenance of viable bat populations in small fragments (≤ 10 ha) (e.g. Cosson et al. 1999, Estrada & Coates-Estrada 2002, Bernard & Fenton 2003, Faria 2006, Meyer & Kalko 2008, Bobrowiec & Gribel 2010). Our results suggest that species with greater ability to use the matrix (i.e. most frugivorous phyllostomid bats) are also the ones that occupy the small fragments (≤ 10 ha). This insight provides an applied tool for landscape management where the structural and functional connectivity among remnant patches is a main factor for persistence and dispersal of the species, in particular for the moderately sensitive. As a practical suggestion to minimize local extinctions, investment in the creation, restoration and maintenance of natural corridors in fragmented landscapes is recommended, as well as the management of the matrix by improving its quality, since the matrix functions as a buffer zone to edge effects, increasing the effective interior area of fragments (Mesquita et al. 1999, Antongiovanni & Metzger 2005).

References

Albrecht, L., Meyer, C.F.J. & Kalko, E.K.V. (2007) Differential mobility in two small phyllostomid bats, *Artibeus watsoni* and *Micronycteris microtis*, in a fragmented Neotropical landscape. *Acta Theriologica*, **52**, 141-149.

Antongiovanni, M. & Metzger, J.P. (2005) Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation*, **122**, 441-451.

Bernard, E. (2001) Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. *Journal of Tropical Ecology*, **17**, 115-126.

Bernard, E. (2002) Diet, activity and reproduction of bat species (Mammalia, Chiroptera) in Central Amazonia, Brazil. *Zoologia*, **19**, 173-188.

Bernard, E. & Fenton, M.B. (2003) Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. *Biotropica*, **35**, 262-277.

Bernard, E. & Fenton, M.B. (2007) Bats in a fragmented landscape: species composition, diversity and habitat interactions in savannas of Santarém, Central Amazonia, Brazil. *Biological Conservation*, **134**, 332-343.

Bobrowiec, P.E.D. & Gribel, R. (2010) Effects of different secondary vegetation types on bat community composition in Central Amazonia, Brazil. *Animal Conservation*, **13**, 204-216.

Boyle, J.G. & Storn, J.J. (2007) The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *Plos One*, **2**, e672.

Bradshaw, C.J.A., Sodhi, N.S. & Brook, B.W. (2009) Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, **7**, 79-87.

Brosset, A., Charles-Dominique P., Cockle, A., Cosson, J.F. & Masson, D. (1996) Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology*, **74**, 1974-1982.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer, New York.

Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J. & Purvis, A. (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1441-1448.

Charles-Dominique, P., Brosset, A. & Jouard, S. (2001) Les chauves-souris de Guyane. *Patrimoines Naturels*, **49**, 1-150.

Corlett, R.T. & Primack, R.B. (2008) Tropical rainforest conservation: a global perspective. *Tropical Forest Community Ecology* (eds W.P. Carson & S.A. Schnitzer). Oxford, UK: Wiley-Blackwell.

Cosson, J., Pons, J. & Masson, D. (1999) Effects of forest fragmentation on frugivorous and nectarivorus bats in French Guiana. *Journal of Tropical Ecology*, **15**, 515-534.

Crawley, M.J. (2005) *Statistics: an Introduction Using* R. John Wiley, New York.

Davidson, A.D., Hamilton, M.J., Boyer, A.G., Brown, J.H. & Ceballos, G. (2009) Multiple ecological pathways to extinction. *PNAS*, **106**, 10702-10705,

Davies, K.F., Margules, C.R. & Lawrence, J.F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**, 1450-1461.

DeFries, R.S., Rudel, T., Uriarte, M. & Hansen, M. (2010) Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience*, **3**, 178-181.

Delaval, M. & Charles-Dominique, P. (2006) Edge effects on frugivorous and nectarivorous bat communities in a neotropical primary forest in French Guiana. *Revue d'Ecologie la Terre et la Vie*, **61**, 343-352.

Dolédec, S., Chessel, D., Ter Braak, C.J.F. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination methods. *Environmental and Ecological Statistics*, **3**, 143-166.

Dray, S. & Dufour, A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1-20.

Dray, E. & Legendre, P. (2008) Testing the species traits-environmental relationships: the fourth-corner problem revisited. *Ecology*, **89**, 3400-3412.

Duchamp, J.E. & Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology*, **23**, 849-860.

Estrada, A. & Coates-Estrada, R. (2001) Bats species richness in live and corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography*, **24**, 94-102.

Estrada, A., Jiménez, C., Rivera, A. & Fuentes, E. (2004) General bat activity measured with an ultrasound detector in a fragmented tropical landscape in Los Tuxtlas, Mexico. *Animal Biodiversity and Conservation*, **27**, 5-13.

Estrada-Villegas, S., Meyer, C.F.J. & Kalko, E.K.V. (2010) Effects of tropical forest fragmentation on aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, **143**, 597-608.

Faria, D. (2006) Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest. *Journal of Tropical Ecology*, **22**, 531-542

Fearnside, P.M. (2003) *A Floresta Amazônica nas Mudanças Globais*. Manaus: INPA.

Felsestein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1-15.

Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K. & Syme, D.M. (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the neotropics. *Biotropica*, **24**, 440-446.

Fleming, T.H. (1986) Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. *Frugivores and seed dispersal* (eds A. Estrada & T.H. Fleming), pp. 105-118. Dr. W. Junk Publishers, Dordrecht.

Gardner, A.L. (2008) Mammals of South America, Vol. 1: *Marsupials, Xenarthrans, Shrews and Bats*. The University of Chicago Press, Chicago and London.

Garland, T. Jr, Harvey, P.H. & Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*, **41**, 18-32.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, **91**, 223-229.

Gascon, C., Bierregaard, R.O., Laurance, W.F. & Rankin-de Merona, J. (2001) Deforestation and forest fragmentation in the Amazon. *Lessons from Amazonia: ecology and conservation of a fragmented forest* (eds R.O. Bierregaard, C. Gascon, T.E. Lovejoy & R. Mesquita), pp. 22-30. New Haven: Yale University Press.

Giannini, N.P. & Kalko, E.K.V. (2005) The guild structure of animalivorous leaf-nosed bats of Barro Colorado Island, Panama, revisited. *Acta Chiropterologica,* **7,** 131-146.

Grelle, C.E.V. (2005) Predicting extinction of mammals in the Brazilian Amazon. *Oryx*, **39**, 347-350.

Hansen, M.C., Stehman, S.V., Potapov, P.V., Loveland, T.R., Townshend, J.R., DeFries, R.S., Pittman, K.W., Arunarwati, B., Stolle, F., Steininger, M.K., Carroll, M. & DiMiceli, C. (2008) Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *PNAS*, **105**, 9439-9444.

Hanspach, J., Fischer, J., Ikin, K., Stott, J. & Law, B.S. (2012) Using trait-based filtering as a predictive framework for conservation: a case study of bats on farms in southeastern Australia. *Journal of Applied Ecology*, **49**, 842-850.

Harper, K.A., MacDonald, S.E., Burton, P.E., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Maiteh, M.S. & Esseen, P.-A. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, **19**, 768-782.

Heithaus, E.R., Fleming, T.H. & Opler, P.A. (1975) Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, **56,** 841-854.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207-251.

Henry, M. & Kalko, E.K.V. (2007) Foraging strategy and breeding constraints of *Rhinophylla pumilio* (Phyllostomidae) in the Amazon lowlands. *Journal of Mammalogy*, **88**, 81-93.

Hill, M.O. & Smith, A.J.E. (1976) Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon*, **25**, 249-255.

Instituto Nacional de Pesquisas Espaciais [INPE]. (2013) *Deforestation estimates for the brazilian Amazon*. São José dos Campos, Brazil.

Jabot, F., Etienne, R.S. & Chave, J. (2008) Reconciling neutral community models and environmental filtering: theory and an empirical test. *Oikos*, **117**, 1308-1320.

Jantzen, M.K. & Fenton, M.B. (2013) The depth of edge influence among insectivorous bats at forest-field interfaces. *Canadian Journal of Zoology*, **91**, 287-292.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93-115.

Jones, K.E., Purvis, A. & Gittleman, J.L. (2003) Biological correlates of extinction risk in bats. *The American Naturalist*, **161**, 601-614.

Jones, K.E., Purvis, A., MacLarnon, A., Bininda-Emonds, O.R.P. & Simmons, N.B. (2002) A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews of the Cambridge Philosophical Society*, **77**, 223-259.

Kalko, E.K.V. (1998) Organisation and diversity of tropical bat communities through space and time. *Zoology*, **101**, 281-297.

Kalko, E.K.V. & Handley, C.O. Jr (2001) Neotropical bats in the canopy: diversity, community structure, and implications for conservation. *Plant Ecology*, **153**, 319-333.

Kirby, K.R., Laurance, W.F., Albernaz, A.L.K.M., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M. & Costa, C.D. (2006) The future of deforestation in the Brazilian Amazon. *Futures*, **38**, 432-453.

Kunz, T.H. & Fenton, M.B. (2003) *Bat ecology*. Chicago: The University of Chicago Press.

Kunz, T.H. & Ingalls, K.A. (1994) Folivory in bats: an adaptation derived from frugivory. *Functional Ecology*, **8**, 665-668.

Kunz, T.H., Torrez, E.B., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*. 1-38p.

Lande, R., Engen, S. & Sæther, B-E. (2003) *Stochastic population dynamics in ecology and conservation*. Oxford University Press.

Laurance, W.F. (2001) The hyper-diverse flora of the central Amazon: an overview. *Lessons from Amazonia: ecology and conservation of a fragmented forest* (eds R.O. Bierregaard, C. Gascon, T.E. Lovejoy & R. Mesquita), pp. 47-53. New Haven: Yale University Press.

Laurance, W.F. (2007) Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, **22**, 65-70.

Laurance, W.F., Camargo, J., Luizão, R., Laurance, S., Pimm, S., Bruna, E., Stouffer, P., Williamson, G., Benitez-Malvido, J., Vasconcelos, H., Van Houtan, K., Zartman, C., Boyle, S., Didham, R., Andrade, A. & Lovejoy, T.E. (2011) The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation*, **144,** 56-67.

Laurance, W.F., Fearside, P.M., Laurance, S.G., Delamônica, P., Lovejoy, T.E., Rankin-de Merona, J.M., Chambers, J.Q. & Gascon, C. (1999) Relationship between soils and amazon forest biomass: a landscape-scale study. *Forest Ecology and Management*, **118**, 127-138.

Legendre, P., Galzin, R. & Harmelin-Vivien, M.L. (1997) Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology*, **78**, 547-562.

Lim, B.K. & Engstrom, M.D. (2001) Species diversity of bats (Mammalia: Chiroptera) in Iwokrama Forest, Guyana, and the Guianan subregion: implications for conservation. *Biodiversity and Conservation*, **10**, 613-657.

Lovejoy, T.E. & Bierregaard, R.O. (1990) Central amazonian forests and the minimum critical size of ecosystems project. *Four Neotropical Rainforests* (ed A.H. Gentry). Yale University Press, New Haven.

Macedo, M.N., DeFries, R.S., Morton, D.C., Stickler, C.M., Galford, G.L. & Shimabukuro, Y.E. (2012) Decoupling of deforestation and soy production in the southern Amazon during the late 2000s. *PNAS*, **109**, 1341–1346.

Mayfield, M.M., Boni, M.F. & Ackerly, D.D. (2009) Traits, habitats, and clades: identifying traits of potential importance to environmental filtering. *The American Naturalist*, **174**, 1-22.

Mazerolle, M.J. (2013) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 3.0.1.

McCarthy, M.A., Lindenmayer, D.B. & Drechsler, M. (1997) Extinction debts and risks faced by abundant species. *Conservation Biology*, **11**, 221-226.

Medellín, R.A., Equihua, M. & Amin, M.A. (2000) Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conservation Biology*, **14,** 1666-1675.

Medina, A., Harvey, C.A., Sanchez, D., Vilchez, S. & Hernandez, B. (2007) Bat diversity and movement in a Neotropical agricultural landscape. *Biotropica*, **39**, 120-128.

Mesquita, R.C.G., Delamônica, P. & Laurance, W.F. (1999) Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation*, **91**, 129-134.

Meyer, C.F.J., Fründ, J., Lizano, W.P. & Kalko, E.K.V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381-391.

Meyer, C.F.J. & Kalko, E.K.V. (2008) Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: land-bridge islands as a model system. *Journal of Biogeography*, **35**, 1711-1726.

Morris, R.J. (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society*, **365**, 3709-3718.

Muscarella, R. & Fleming, T. H. (2007) The role of frugivorous bats in forest sucession. *Biological Reviews*, **82**, 573-590.

Norberg, U.M. (1998) Morphological adaptations for flight in bats. *Bat Biology and Conservation* (eds T.H. Kunz & P.A. Racey), pp. 93-108. Smithsonian Institution Press, Washington, DC.

Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society London, Series B*, **316**, 335-427.

Oliveira, A.A. & Mori, S.A. (1999) A Central Amazonian terra firme forest. I. High tree species richness on poor soils. *Biodiversity and Conservation*, **8**, 1219-1244.

Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289-290.

Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, **11**, 1633-1644.

Presley, S.J., Willig, M.R., Castro-Arellano, I. & Weaver, S.C. (2009) Effects of habitat conversion on temporal activity patterns of phyllostomid bats in lowland Amazonian rainforest. *Journal of Mammalogy*, **90**, 210-221.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society London, Series B*, **267**, 1947-1952.

R Development Core Team (2013) *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org, accessed June 2013.

Ramos-Pereira, M.J., Marques J.T. & Palmeirim J.M. (2010a) Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forests. *Biotropica*, **42**, 680-687.

Ramos-Pereira, M.J., Marques, J.T. & Palmeirim, J.M. (2010b) Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests. *Current Zoology*, **56**, 469-478.

Rankin-de Merona, J.M., Prance, G.T., Hutchings, R.W., Silva, F.M., Rodrigues, W.A. & Uehling M.E. (1992) Preliminary results of large scale tree inventory of upland rain forest in the central Amazon. *Acta Amazonica,* **22**, 493-534.

Rex, K., Michener, R., Kunz, T.H. & Voigt, C.C. (2011) Vertical stratification of Neotropical leaf-nosed bats (Phyllostomidae: Chiroptera) revealed by stable carbon isotopes. *Journal of Tropical Ecology*, **27**, 211-222.

Safi, K. & Kerth, G. (2004) Acomparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology,* **18**, 1293-1303.

Sampaio, E.M. 2000. *Effects of forest fragmentation on the diversity and abundance patterns of Central Amazonian bats*. PhD thesis. Tübingen University, Germany.

Silva, I.M.S. (2012) *Estratificação vertical e efeito da fragmentação numa comunidade de morcegos (Chiroptera, Mammalia) na Amazónia Central*. Master thesis, Universidade de Lisboa, Portugal.

Simmons, N.B. (2005) Order Chiroptera. *Mammal Species of the World: a Taxonomic and Geographic Reference* (eds D.E. Wilson & D.M. Reeder), pp. 312-529. Johns Hopkins University Press, Baltimore, MD.

Simmons, N.B. & Voss, R.S. (1998) The mammals of Paracou, French Guiana: a neotropical lowdland rainforest fauna. part 1. Bats. *Bulletin of the American Museum of Natural History*, **237**, 1-219.

Swihart, R.K., Atwood, T.C., Goheen, J.E., Scheiman, D.M., Munroe, K.E. & Gehring, T.M. (2003) Patch occupancy of North American mammals: is patchiness in the eye of the beholder? *Journal of Biogeography*, **30**, 1259-1279.

Swihart, R.K. & Verboom, J. (2004) Using ecologically scaled landscape indices to assess biodiversity consequences of land-use decisions. *Conserving Biodiversity in Agricultural Landscapes: Model-Based Planning Tools* (eds R.K. Swihart & J.E. Moore), pp. 81–101. Purdue University Press, West Lafayette.

Thies, W. & Kalko, E.K.V. (2004) Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos,* **104,** 362-376.

Threlfall, C., Law, B., Penman, T. & Banks, P.B. (2011) Ecological processes in urban landscapes: mechanisms influencing the distribution and activity of insectivorous bats. *Ecography*, **34**, 814-826.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65-66.

Vasconcelos, H.L. & Bruna, E.M. (2012) Arthropod responses to the experimental isolation of Amazonian forest fragments. *Zoologia*, **29**, 515-530.

Vos, C.C., Verboom, J., Opdam, P.F.M. & ter Braak, C.J.F. (2001) Toward ecologically scaled landscape indices. *The American Naturalist*, **183**, 24-41.

Wearn, O.R., Reuman, D.C. & Ewers, R.M. (2012) Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science*, **337**, 228-232.

Supplementary material

Table S1 Explanatory variables used in modeling fragmentation sensitivity.

Table S2 AIC model selection results based on analyses with phylogenetic correction.

Table S3 AIC model selection results based on analyses without phylogenetic correction.

Figure S1 Plot used to group species into three mobility categories.

Table S1 Values of each explanatory variable used to assess bat species sensitivity to forest fragmentation at the BDFFP, Brazil. AC = abundance in continuous forest (bats/mnh), BM = body mass, ES = edge-sensitivity, MT = matrix tolerance, TL = trophic level, DB = dietary specialization, VS = vertical stratification, MO = mobility, AR = aspect ratio, RWL = relative wing loading, *ESLIc* – *ESLIk* = ecologically scaled landscape indices.

Species	*AC*	*BM*	*ES*	*MT*	*TL*	*DB*[1]	*VS*[2]	*MO*[3]	*AR*	*RWL*	*ESLIc*	*ESLIk*
Artibeus cinereus	0.1989	10.5	0.1984	-0.0007	Phytophagous	2	C	2	6.19	18.26	812.38	0.1091
Artibeus concolor	0.0663	20.8	0.8854	0.8619	Phytophagous	2	C	2	6.57	16.85	842.92	0.1330
Artibeus gnomus	0.1657	10.9	0.4988	0.0903	Phytophagous	2	C	1	6.10	17.41	737.69	0.1825
Artibeus lituratus	0.3977	67.5	-0.1445	0.3327	Phytophagous	2	C	3	6.25	18.14	1194.28	0.0435
Artibeus obscurus	0.3812	40.2	0.0196	0.1314	Phytophagous	2	N	2	6.59	16.71	1007.87	0.0817
Artibeus planirostris	0.1657	51.0	-0.2516	-1.0000	Phytophagous	2	N	2	6.33	19.25	568.29	0.3207
Carollia brevicauda	0.2983	12.9	0.7686	0.6997	Phytophagous	2	U	1	6.39	18.41	689.18	0.1374
Carollia perspicillata	4.9221	16.1	0.4280	0.4321	Phytophagous	2	U	2	5.86	18.16	943.58	0.1226
Chrotopterus auritus	0.0497	75.2	-1.0000	-1.0000	Animalivorous	2	U	3	4.67	12.46	1137.09	0.0537
Desmodus rotundus	0.1160	28.5	-0.0786	-1.0000	Animalivorous	3	U	3	7.28	18.63	1021.85	0.0783
Glyphonycteris daviesi	0.0497	21.1	-1.0000	-1.0000	Animalivorous	2	U	2	6.22	12.93	845.64	0.1321
Lonchophylla thomasi	0.2154	7.0	-0.3699	-0.3690	Phytophagous	1	U	1	6.48	17.01	687.81	0.2115
Lophostoma schulzi	0.0663	18.4	-1.0000	0.1994	Animalivorous	2	U	2	4.98	16.90	819.39	0.1421
Lophostoma silviculum	0.7458	36.7	-0.3058	-0.7650	Animalivorous	2	U	1	5.46	15.69	770.39	0.3641
Mesophylla macconnelli	0.2652	7.5	-1.0000	-1.0000	Phytophagous	2	C	1	6.05	19.50	694.29	0.2091
Micronycteris microtis	0.0829	5.9	0.0893	0.5648	Animalivorous	2	U	1	5.97	14.71	43.15	3.8833
Mimon crenulatum	0.3646	12.6	0.5838	0.5845	Animalivorous	2	U	1	6.18	12.91	530.78	0.4073
Phylloderma stenops	0.1160	47.0	-0.0786	-0.0776	Phytophagous	2	U	3	6.44	15.21	880.85	0.0642
Phyllostomus discolor	0.0497	35.6	0.7135	-1.0000	Animalivorous	1	C	1	7.06	18.90	549.84	0.3444
Phyllostomus elongatus	0.2652	37.4	-0.1445	-1.0000	Animalivorous	1	U	2	6.41	15.73	1032.52	0.0757
Pteronotus parnellii	1.9224	24.4	-0.0659	-0.1606	Animalivorous	2	U	3	6.04	15.52	1185.03	0.0451
Rhinophylla pumilio	1.8727	9.6	0.3583	0.2727	Phytophagous	2	N	1	6.25	19.13	521.01	0.3873
Tonatia saurophila	0.5303	26.8	-0.4559	-0.4551	Animalivorous	2	N	1	5.54	14.75	1062.05	0.0883
Trachops cirrhosus	1.1269	38.6	-0.3892	-0.3883	Animalivorous	3	U	2	6.07	14.75	1057.37	0.0639
Trinycteris nicefori	0.0663	9.0	-1.0000	0.1994	Animalivorous	2	C	1	5.94	17.18	713.45	0.1959
Vampyressa bidens	0.1657	12.6	-1.0000	0.2851	Phytophagous	2	C	1	6.07	18.14	757.27	0.1708

[1] Categories: 1 = low, 2 = intermediate, 3 = high; Sources: Sampaio (2000); Bernard & Fenton (2003); Weinbeer & Kalko (2004); Bonaccorso et al. (2006); Thies et al. (2006); Albrecht et al. (2007); Henry & Kalko (2007); Bianconi (2009).

[2] Categories: 1 = low, 2 = intermediate, 3 = high; Sources: Fleming et al. 1972; Heithaus et al. 1975; Willig et al. 1993; Zortéa & Mendes 1993; Kunz & Diaz 1995; Kalko et al. 1996; Bernard 2002; Herrera et al. 2001; 2002; Giannini & Kalko 2004; 2005; Thies & Kalko 2004; Kalka & Kalko 2006; Bredt et al. 2012.

[3] U = understory preference, N = no preference, C = canopy preference

References to Table S1

Albrecht, L., Meyer, C.F.J. & Kalko, E.K.V. (2007) Differential mobility in two small phyllostomid bats, *Artibeus watsoni* and *Micronycteris microtis*, in a fragmented Neotropical landscape. *Acta Theriologica,* **52**, 141-149.

Bernard, E. (2002) Diet, activity and reproduction of bat species (Mammalia, Chiroptera) in Central Amazonia, Brazil. *Zoologia,* **19**, 173-188.

Bernard, E. & Fenton, M.B. (2003) Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. *Biotropica,* **35,** 262-277.

Bianconi, G.V. (2009) *Morcegos frugívoros no uso do hábitat fragmentado e seu potencial para a recuperação de áreas degradadas: subsídios para uma nova ferramenta voltada à conservação*. PhD thesis. Universidade Estadual Paulista "Júlio de Mesquita Filho", Brazil.

Bonaccorso, F.J., Winkelmann, J.R., Shin, D., Agrawal, C.I., Aslami, N., Bonne, C., Hsu, A., Jekielek, P.E., Knox, A.K., Kopach, S.J., Jennings, T.D., Lasky, J.R., Menesale, S.A., Richards, J.H., Rutland, J.A., Sessa, A.K., Zhaurova, L. & Kunz, T.H. (2006) Evidence for exploitative competition: Comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). *Biotropica*, **39**, 249-256.

Bredt, A., Uieda W. & Pedro W.A. (2012) *Plantas e morcegos: na recuperação de áreas degradadas e na paisagem urbana*. Brasília: Rede de Sementes do Cerrado. 273p.

Fleming, T.H., Hooper, E.T. & Wilson, D.E. (1972) Three Central American bat communities: Structure, reproductive cycles, and movement patterns. *Ecology,* **53,** 555-569.

Giannini, N.P. & Kalko, E.K.V. (2004) Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos,* **105,** 209-220.

Giannini, N.P. & Kalko, E.K.V. (2005) The guild structure of animalivorous leaf-nosed bats of Barro Colorado Island, Panama, revisited. *Acta Chiropterologica,* **7,** 131-146.

Heithaus, E.R., Fleming, T.H. & Opler, P.A. (1975) Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology,* **56,** 841-854.

Henry, M. & Kalko, E.K.V. (2007) Foraging strategy and breeding constraints of *Rhinophylla pumilio* (Phyllostomidae) in the Amazon lowlands. *Journal of Mammalogy,* **88**, 81-93.

Herrera, L.G., Gutierrez, E., Hobson, K.A., Altube, B., Diaz, W.G. & Sanchez-Cordero, V. (2002) Sources of assimilated protein in five species of New World frugivorous bats. *Oecologia,* **133,** 280- 287.

Herrera, M.L.G., Hobson, K.A., Mirón, M.L., Ramírez, P.N., Méndez, C.G. & Sánchez-Cordero, V. (2001) Sources of protein in two species of phytophagous bats in a seasonal dry forest: Evidence from stable-isotope analysis. *Journal of Mammalogy,* **82,** 352-361.

Kalka, M. & Kalko, E.K.V. (2006) Gleaning bats as underestimated predators of herbivorous insects: diet of *Micronycteris microtis* (Phyllostomidae) in Panama. *Journal of Tropical Ecology,* **22,** 1-10.

Kalko, E.K.V., Handley, C.O. Jr. & Handley, D. (1996) Organization, diversity and long-term dynamics of a Neotropical bat community. *Long-Term Studies in Vertebrate Communities* (eds M.L. Cody & J. Smallwood), pp. 503-553. Academic Press, Los Angeles.

Kunz, T.H. & Diaz, C.A. (1995) Folivory in fruit-eating bats, with new evidence from *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica,* **27,** 106-120.

Sampaio E. M. (2000) *Effects of forest fragmentation on the diversity and abundance patterns of Central Amazonian bats*. PhD thesis. Tübingen University, Germany.

Thies, W. & Kalko, E.K.V. (2004) Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos,* **104,** 362-376.

Thies, W., Kalko, E.K.V. & Schnitzler, H.U. (2006) Influence of environment and resource availability on activity patterns of *Carollia castanea* (Phyllostomidae) in Panama. *Journal of Mammalogy*, **87**, 331-338

Weinbeer, M. & E.K.V. Kalko. (2004) Morphological characteristics predict alternate foraging strategy and microhabitat selection in the Orange-bellied Bat, *Lampronycteris brachyotis*. *Journal of Mammalogy,* **85**, 1116-1123.

Willig, M.R., Camilo, G.R. & Noble, S.J. (1993) Dietary overlap in frugivorous and insectivorous bats from edaphic Cerrado habitats of Brazil. *Journal of Mammalogy,* **74,** 117-128.

Zortéa, M. & Mendes, S.L. (1993) Folivory in the big fruit-eating bat, *Artibeus lituratus* (Chiroptera: Phyllostomidae) in eastern Brazil. *Journal of Tropical Ecology,* **9,** 117-120.

Table S2 Full results of AIC-based model selection assessing the association between two measures of fragmentation sensitivity and a set of candidate GLMs, following phylogenetic correction. For each model, the log-likelihood (Log-*L*), number of estimable parameters (*K*), sample-size adjusted Akaike Information Criterion (*AICc*), Akaike differences (Δ_i), Akaike weights (w_i), and bootstrap selection frequencies (π_i) are presented. Model fit as evaluated based on the global model is given for each response variable as percentage deviance explained (% dev.).

Response variable	*Model description*	*Log (L)*	*K*	*AICc*	Δ_i	w_i	π_i
Species prevalence	*Abundance in continuous forest* (AC)	19.33	2	-34.12	0.00	0.93	0.6264
(% dev. = 75.9)	*Population size* (AC + BM + TL)	21.07	4	-28.99	5.14	0.07	0.1949
	Mobility (M)	7.54	2	-10.53	23.60	0.00	0.0005
	Edge-sensitivity (ES)	7.47	2	-10.40	23.72	0.00	0.0000
	Body mass (BM)	7.28	2	-10.01	24.11	0.00	0.0001
	Matrix tolerance (MT)	7.01	2	-9.48	24.64	0.00	0.0000
	Vertical stratification (VS)	6.94	2	-9.34	24.79	0.00	0.0003
	Aspect ratio (AS)	6.80	2	-9.05	25.07	0.00	0.0001
	Relative wing loading (RWL)	6.79	2	-9.03	25.09	0.00	0.0002
	Dietary specialization (DS)	6.79	2	-9.03	25.09	0.00	0.0000
	Trophic level (TL)	6.77	2	-8.99	25.13	0.00	0.0000
	ESLIc + ESLIk	7.40	3	-4.80	29.32	0.00	0.0001
	Specialization (DS + VS + ES + MT)	8.07	5	0.52	34.65	0.00	0.0004
	Dispersal (M + RWL + AR + BM + ES + MT)	8.27	7	8.46	42.58	0.00	0.0001
Change in abundance	*Abundance in continuous forest* (AC)	-23.08	2	50.71	0.00	0.89	0.5592
(% dev. = 82.3)	*Population size* (AC + BM + TL)	-20.90	4	54.96	4.25	0.11	0.2154
	Mobility (M)	-35.99	2	76.52	25.81	0.00	0.0012
	Matrix tolerance (MT)	-36.00	2	76.54	25.83	0.00	0.0008
	Edge-sensitivity (ES)	-36.20	2	76.94	26.23	0.00	0.0000
	Body mass (BM)	-36.40	2	77.34	26.63	0.00	0.0003
	Vertical stratification (VS)	-36.82	2	78.19	27.48	0.00	0.0002
	Aspect ratio (AS)	-36.95	2	78.45	27.75	0.00	0.0000
	Trophic level (TL)	-36.96	2	78.46	27.75	0.00	0.0000
	Dietary specialization (DS)	-36.96	2	78.47	27.76	0.00	0.0000
	Relative wing loading (RWL)	-36.96	2	78.47	27.76	0.00	0.0002
	ESLIc + ESLIk	-36.66	3	83.32	32.62	0.00	0.0000
	Specialization (DS + VS + ES + MT)	-35.61	5	87.89	37.18	0.00	0.0001
	Dispersal (M + RWL + AR + BM + ES + MT)	-34.71	7	94.43	43.72	0.00	0.0007

Table S3 Model selection results of species-level analyses conducted on data not corrected for the effects of phylogeny. For each model, the log-likelihood (Log-*L*), number of estimable parameters (*K*), sample-size adjusted Akaike Information Criterion (*AICc*), Akaike differences (Δ_i) and Akaike weights (w_i) are presented. Species prevalence was modeled using generalized linear models (GLMs) with a binomial distribution, whereas for the index of change in abundance GLMs assumed a Gaussian error distribution. Model fit as evaluated based on the global model is given for each response variable as percentage deviance explained (% dev.).

Response variable	*Model description*	*Log (L)*	*K*	*AICc*	Δ_i	w_i
Species prevalence	*Abundance in continuous forest* (AC)	-38.45	2	81.42	0.00	0.82
(% dev. = 86.1)	*Population size* (AC + BM + TL)	-37.27	4	84.44	3.01	0.18
	Specialization (DS, VS, ES, MT)	-53.41	5	123.23	41.81	0.00
	Edge-sensitivity (ES)	-59.72	2	123.96	42.53	0.00
	Vertical stratification (VS)	-59.04	2	125.18	43.76	0.00
	Matrix tolerance (MT)	-60.89	2	126.30	44.88	0.00
	Trophic level (TL)	-61.20	2	126.93	45.51	0.00
	Relative wing loading (RWL)	-62.19	2	128.89	47.47	0.00
	Body mass (BM)	-63.16	2	130.84	49.42	0.00
	Dietary specialization (DS)	-63.46	2	131.44	50.02	0.00
	Mobility (M)	-63.48	2	131.48	50.06	0.00
	Aspect ratio (AR)	-63.65	2	131.81	50.39	0.00
	Dispersal (M + RWL + AR + BM + ES + MT)	-56.18	7	132.58	51.16	0.00
	ESLIc + ESLIk	-63.35	3	133.79	52.37	0.00
Change in abundance	*Abundance in continuous forest* (AC)	-30.72	2	68.54	0.00	0.73
(% dev. = 90.9)	*Population size* (AC + BM + TL)	-28.76	4	70.53	1.99	0.27
	Edge-sensitivity (ES)	-47.21	2	101.52	32.98	0.00
	Matrix tolerance (MT)	-47.38	2	101.85	33.31	0.00
	Trophic level (TL)	-47.83	2	102.76	34.22	0.00
	Relative wing loading (RWL)	-48.36	2	103.80	35.26	0.00
	Mobility (M)	-49.11	2	105.31	36.78	0.00
	Body mass (BM)	-49.21	2	105.50	36.97	0.00
	Dietary specialization (DS)	-49.37	2	105.83	37.29	0.00
	Aspect ratio (AR)	-49.37	2	105.84	37.30	0.00
	Vertical stratification (VS)	-47.97	2	105.85	37.31	0.00
	ESLIc + ESLIk	-49.05	3	108.00	39.47	0.00
	Specialization (DS + VS + ES + MT)	-44.28	5	108.78	40.24	0.00
	Dispersal (M + RWL + AR + BM + ES + MT)	-43.96	7	112.40	43.86	0.00

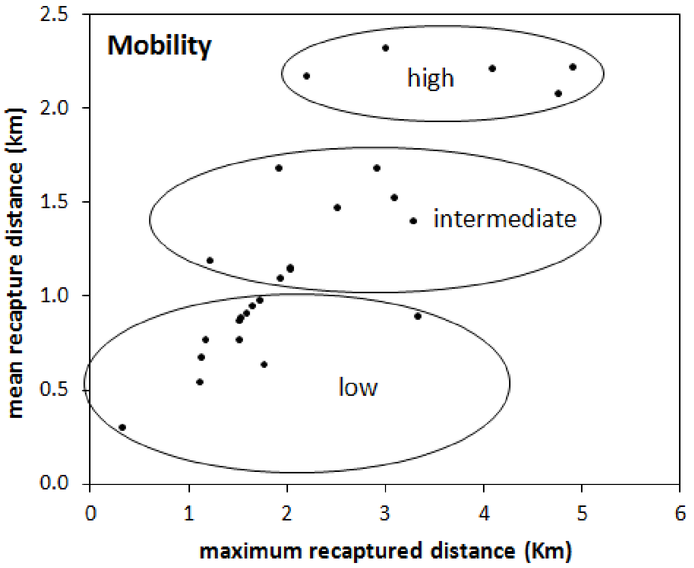


Figure S1 Plot used to group species into three mobility categories: low, intermediate and high.