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**INFLUÊNCIAS MULTI-ESCALA DA PAISAGEM E LIMIAR DA  
FRAGMENTAÇÃO EM MORCEGOS NO CERRADO**

**RENATA DE LARA MUYLAERT**

Dissertação apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista Júlio de Mesquita Filho, como parte dos requisitos para obtenção do título de Mestre em Ciências Biológicas (Zoologia).

Orientador: Milton Cezar Ribeiro

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*Dedico este trabalho ao meu pai,  
e ao universo em expansão*

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*“How many parameters  
does it take to fit an elephant?”*

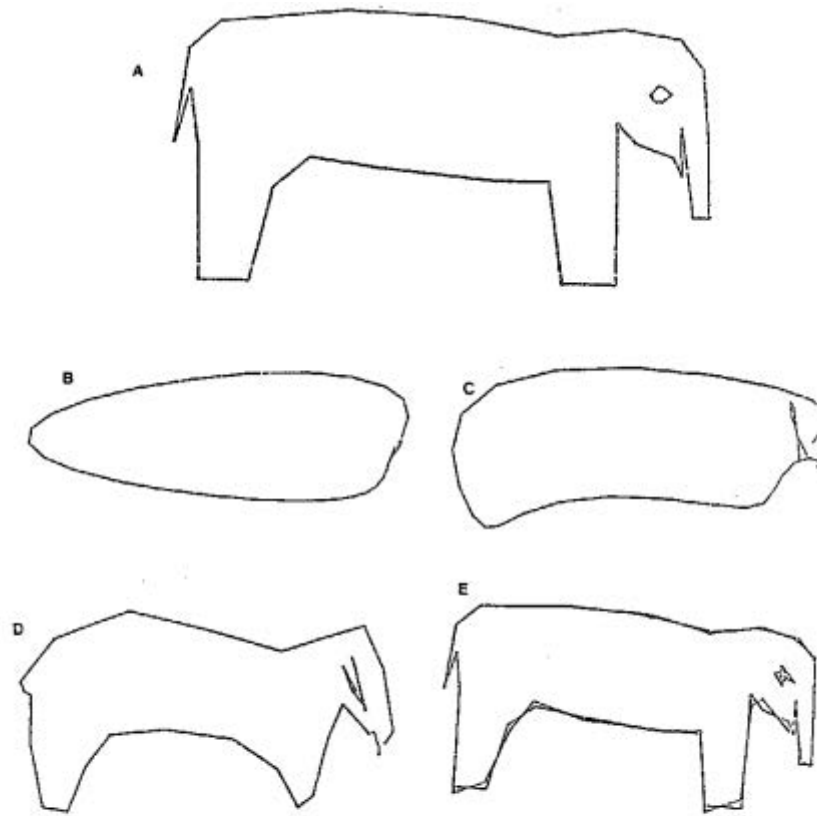


FIGURE 1.2. “How many parameters does it take to fit an elephant?” was answered by Wei (1975). He started with an idealized drawing (A) defined by 36 points and used least squares Fourier sine series fits of the form  $x(t) = \alpha_0 + \sum \alpha_i \sin(it\pi/36)$  and  $y(t) = \beta_0 + \sum \beta_i \sin(it\pi/36)$  for  $i = 1, \dots, N$ . He examined fits for  $K = 5, 10, 20$ , and 30 (shown in B–E) and stopped with the fit of a 30 term model. He concluded that the 30-term model “may not satisfy the third-grade art teacher, but would carry most chemical engineers into preliminary design.”

## **Resumo**

O conhecimento a respeito de quais fatores determinam a biodiversidade nas atuais condições de perda de habitat e fragmentação é essencial para o desenvolvimento de estratégias para a conservação das espécies. A biodiversidade pode apresentar respostas em limiar em relação à variação na estrutura da paisagem (limiares da fragmentação), particularmente em relação à quantidade de habitat. A detecção destes limiares pode nortear programas de conservação, restauração e manejo de paisagens. Este estudo avaliou respostas de morcegos às variáveis de configuração e composição da paisagem em uma abordagem exploratória, e também testamos se existe um limiar de resposta da riqueza de morcegos em função quantidade de habitat na paisagem. Utilizamos riqueza como variável operacional para biodiversidade, número de capturas para abundância de morcegos, e cobertura florestal para quantidade de habitat adequado. Avaliamos as respostas da ocorrência das seguintes guildas a variáveis locais e estrutura da paisagem em uma abordagem multi-escala (0,5 a 5,0 km): frugívoros, nectarívoros, hematófagos e animalívoros. O estudo foi conduzido em 15 paisagens distribuídas em um gradiente de quantidade de habitat (9 a 100%) no sudeste do Brasil em formações de cerrado florestal. A amostragem foi realizada por meio de redes-de-neblina com esforço padronizado, em quatro pontos amostrais e cinco noites de captura por paisagem. As análises foram realizadas por seleção de modelos com múltiplas hipóteses concorrentes, baseada na Teoria da Informação de Akaike e estimativas de máxima verossimilhança restrita. As guildas de morcegos apresentaram relações não lineares em função de borda, forma média de fragmento, conectividade, quantidade e diversidade de habitat e variáveis locais (quantidade de frutos e altura de dossel). Identificamos um limiar em torno de 47% de habitat para riqueza, com uma queda abrupta no número de espécies em paisagens com quantidades de habitat menores do este valor. Sugerimos que estratégias de restauração busquem aumentar a conectividade das paisagens, já que a região de estudo encontra-se em um contexto de resiliência de paisagem baixa ou moderada. Este estudo é inovador, pois corrobora a hipótese de limiar da biodiversidade utilizando como modelo um grupo de animais abundantes e bastante diversificados, o que é alarmante considerando as atuais taxas de extinção de mamíferos.

**Palavras-chave:** perda de habitat, Chiroptera, paisagem, conservação, fragmentação, escala espacial, gradiente

## Abstract

The knowledge about which factors determine biodiversity on the present conditions of habitat loss and fragmentation is essential to develop strategies for species conservation. The biodiversity can present threshold responses to landscape structure variation (fragmentation threshold), particularly to habitat amount. Detecting these thresholds might support conservation, restoration and management programs. This study explored bat responses to landscape composition and configuration variables (exploratory approach), and we tested if there is a threshold response in bat richness as a function of habitat amount on landscape. We used richness as an operational variable for biodiversity, capture number for abundance and forest cover for adequate habitat amount to the group. We evaluated abundance responses of bat guilds to local and landscape structure variables on a multi-scale approach (0.5 to 5 km): frugivores, nectarivores, animalivores and sanguivores. The study was conducted on 15 landscapes spread on a gradient of habitat amount (9 to 100%) on southeastern Brazil, in forest cerrados. We sampled bats with mist nets with the same effort in four sampling points for five nights per landscape. The analysis was made by model selection by multiple hypotheses based on Akaike Information criterion and restricted maximum likelihood estimates. Bat guilds presented nonlinear responses to habitat amount, edge, mean fragment shape, connectivity, habitat diversity and local variables (fruit availability and canopy height). We identified a threshold around 45% of habitat amount to bat biodiversity, with a accentuate drop on landscapes below this threshold point. We suggest that restoration strategies look for increasing the connectivity of these landscapes, since the region is on a context of moderate to low landscape resilience. This study is novel because supports the fragmentation threshold hypothesis using such an ecologically diverse and abundant animal group, what is alarming considering present conditions of extinction rates for mammals.

**Key-words:** habitat loss, Chiroptera, landscape, conservation, fragmentation, spatial scale, gradient

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## INTRODUÇÃO

A presente dissertação tem como objetivo entender quais características locais e da paisagem influenciam na variação de assembleias de morcegos Neotropicais em um gradiente de cobertura florestal e em múltiplas escalas. Ela está estruturada em dois capítulos. O primeiro, intitulado “LOCAL AND MULTISCALE LANDSCAPE EFFECTS ON PHYLLOSTOMIDAE BATS IN HIGHLY FRAGMENTED SAVANNAS”, está formatado para submissão à revista *Ecological Applications*. O segundo tem como título "THRESHOLD EFFECT OF HABITAT LOSS ON BAT RICHNESS IN SAVANNA-FOREST LANDSCAPES", está formatado para submissão à *Landscape Ecology*.

O primeiro capítulo busca avaliar a contribuição relativa de variáveis de composição, configuração da paisagem e locais para explicar a ocorrência de morcegos. Utilizamos seleção de modelos para verificar quais variáveis locais e de paisagem são plausíveis para explicar a abundância de morcegos frugívoros, nectarívoros, animalívoros e hematófagos.

Dentre as propriedades da paisagem, a quantidade de habitat remanescente está entre os fatores que melhor explicam as respostas ecológicas relacionadas às mudanças nas funções ecossistêmicas (PARDINI *et al.*, 2010). Mudanças na cobertura e configuração dos remanescentes de vegetação nativa podem alterar a composição de espécies e de processos ecológicos (FAHRIG, 2003). Comparando paisagens caracterizadas por níveis decrescentes de quantidade de vegetação nativa, podemos esperar que: (1) efeitos positivos da área do fragmento na abundância local e na diversidade deverão ser evidentes apenas a partir de níveis intermediários de cobertura de vegetação remanescente e (2) uma queda abrupta na diversidade de espécies mais especialistas deve ser observada em baixos níveis de cobertura vegetal remanescente, principalmente entre 10-30%. Isto é o que prevê a teoria do **limiar da fragmentação** (ANDREN, 1994; FAHRIG, 2003) ou **limiar da biodiversidade** (PARDINI *et al.*, 2010; ESTAVILLO; PARDINI; DA ROCHA, 2013). Além disso, estes conceitos estão relacionados a uma proposta de que o fator mais importante determinando a persistência e ocorrência de espécies seria a quantidade de habitat na paisagem ou *Habitat amount hypothesis* (FAHRIG, 2013). Esta hipótese justifica desconsiderar variáveis como tamanho de fragmento focal e isolamento (típicas da abordagem de Biogeografia de ilhas de (ROBERT MCARTHUR; WILSON, 1963), e substituí-los pela quantidade de habitat na paisagem, na qual riqueza é avaliada considerando uma amostragem padronizada.

Sendo assim, no segundo capítulo testamos a hipótese de que uma distribuição em forma de limiar explica melhor a variação na riqueza de morcegos ao longo de um gradiente de cobertura florestal (quantidade de habitat) do que uma distribuição linear, nula ou neutra. No caso, a distribuição neutra seria aquela em que a riqueza aumenta proporcionalmente com o aumento de indivíduos capturados no gradiente de habitat. Nossa hipótese principal é de que existe um limiar de reposta da diversidade de morcegos e que o ponto limiar se encontraria próximo a 30% de quantidade de habitat. Sendo assim a proporção de cobertura florestal influencia na composição de espécies, havendo diminuição mais acentuada da riqueza em paisagens com menores proporções de vegetação.

Escolhemos os morcegos para este estudo, pois muitos trabalhos que consideram gradientes de cobertura florestal focam em mamíferos não voadores (ANDREN, 1994; PARDINI *et al.*, 2010) e aves (ANDREN, 1994; BETTS; FORBES; DIAMOND, 2007; MARTENSEN *et al.*, 2012; RADFORD; BENNETT; CHEERS, 2005), porém as respostas de morcegos a variáveis de paisagem até então idiossincráticas (CUNTO; BERNARD, 2012), e não trazem um consenso. Para responder às nossas perguntas, foram amostradas 15 paisagens de 5 km de raio localizadas em paisagens fragmentadas do estado de São Paulo, sudeste do Brasil. Para acessar a variabilidade nas assembleias, realizamos levantamentos de morcegos por meio de redes de neblina.

## **JUSTIFICATIVA**

Já foi observada grande variação na composição de espécies de quirópteros em gradientes de habitat florestais e adjacências não florestais, como cultura de frutos, bordas de mata e cidades (MEDELLÍN; EQUIHUA; AMIN, 2000; DUCHAMP; SWIHART, 2008). Também foi observado que a variação entre paisagens deve contribuir para diferenças de padrões de ocupação por morcegos (MEDELLÍN; EQUIHUA; AMIN, 2000). Portanto, é provável que haja variação entre paisagens com diferentes proporções de cobertura vegetal. Além disso, morcegos podem utilizar diferentes elementos da paisagem como meios para obter recursos (ETHIER; FAHRIG, 2011), porém habitam nas florestas com maior frequência (ESTRADA; COATES-ESTRADA; JR, 1993), o que reforça a hipótese de que haja um limiar relacionando maiores níveis de diversidade para maiores proporções de cobertura vegetal.

## A VEGETAÇÃO NA REGIÃO DE ESTUDO

A região de estudo caracteriza-se por áreas em um contexto de grandes monoculturas de cana de açúcar (PIRES, 1995; DURIGAN *et al.*, 2007), às quais no texto nos referimos como matrizes ou não-habitat. Essas são consideradas como inadequadas para serem utilizadas como refúgio por morcegos. A região comporta poucos fragmentos de cerrado típico bem preservados (EITEN, 1972). O cerrado se mantém e se renova pela dinâmica de fogo, o que ainda ocorre em algumas áreas (DODONOV *et al.*, 2014). Porém muitas áreas nas quais o fogo não passa há tempos (BATALHA; MANTOVANI; DE MESQUITA JÚNIOR, 2001) estão alternado de um contexto de cerrado *stricto sensu* para uma transição entre cerrado denso ou florestal (cerradão) e mata semidecidual, com o progressivo crescimento de espécies florestais (Reinaldo Monteiro, pers. com; (PINHEIRO; AZEVEDO; MONTEIRO, 2010). Desta forma, os fragmentos amostrados apresentam estrutura de cerrado florestal, na maioria dos quais não passa fogo há mais de 20 anos (REYS *et al.*, 2013; Monteiro, pers. Com). Na área UFSCAR, o último fogo ocorreu há sete anos (pers. Obs). Estas áreas são de alta relevância ecológica, já que há menos de 0.81% (KRONKA, F.J.N. *et al.*, 2005) remanescente de cerrado no estado de São Paulo, uma motivação forte para estudos voltados para limiares ecológicos e alterações na paisagem.

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**CHAPTER 1: LOCAL AND MULTISCALE LANDSCAPE EFFECTS ON  
PHYLLOSTOMIDAE BATS IN HIGHLY FRAGMENTED SAVANNAS**

Running title: Local and landscape effects on phyllostomids

## **Local and multiscale landscape effects on phyllostomid bats in highly fragmented savannas**

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*Abstract:* Many studies relate bat diversity with patch size or forest succession, but rarely to other landscape aspects such as scale, matrix or local variables combined with landscape attributes. The aims of this study were: (1) to understand the relationship between phyllostomid guild abundances and the landscape structure at six different scales (0.5 to 5 km) in an 9 to 100% gradient of suitable habitat amount within 15 highly fragmented forest-savanna landscapes; (2) estimate the relative contributions of local variables and landscape structure to explain frugivore and animalivore abundance. We performed model selection based on restricted maximum likelihood and Akaike's information criterion to select the adequate scales of guild responses to landscape characteristics. Our results indicate that phyllostomid bats vary in response to scale, but respond mostly at smaller and intermediate scales. In highly fragmented landscapes different guilds vary in responses to habitat loss and fragmentation. An important and new finding was the prevalence of edge amount over the habitat amount to predict frugivore abundance, but not nectarivore abundance. Nectarivorous and animalivorous bats seem to be the most affected by habitat and connectivity loss, an important information for management of protected areas and planning for restoration. We highlight the importance of considering composition and configuration in conservation and restoration planning.

**Key words:** Cerrado, spatial scale, Chiroptera, landscape structure, frugivores, local filters, additive mixed models.

## Introduction

Understanding how species traits and landscape attributes interact to determine animal dispersal is one of the 100 fundamental questions in Ecology (Sutherland *et al.* 2013). Many studies relate bat diversity to patch size or forest succession (Cunto and Bernard 2012), but rarely to other landscape aspects such as scale (Pinto and Keitt 2008, Henry *et al.* 2010), matrix or local variables confronting landscape metrics (Meyer *et al.* 2009, Avila-Cabadilla *et al.* 2012).

It may be misleading to model variation in community processes' in terms of single causes (Quinn and Dunham 1983). Thus, to better understand complex responses of biodiversity in a more realistic approach may include local and landscape variables as filters that potentially determine habitat use and persistence of species. For bats, in particular, single scale approaches do not seem to be adequate for understanding biotic responses to habitat modifications (Gorrensens and Willig 2004, Klingbeil and Willig 2009). However, among different regions and landscape contexts we expect these responses to vary, and responses from a certain biome may not necessarily be extrapolated to others even for the same species or similar community species composition.

Recent studies indicate that many bat species are able to colonize and forage in habitats at different stages of succession with success (Trevelin *et al.* 2013, Saldaña-Vásquez 2014). Therefore, maybe the determinant for bat prevalence is not succession stage alone, but also landscape attributes that facilitate their use of space, such as edge and habitat amount, that are important factors affecting animal dispersal in changing world (see Fahrig 2013). Ethier and Fahrig (2011) found positive effects of fragmentation that were independent of forest amount on bats, suggesting that landscape complementation might be leading to those responses, since increased fragmentation also increases access to both foraging and roosting sites for insectivorous bats. We might expect a similar response for other animal groups that are highly mobile and forage in different landscape elements.

The aims of this study are twofold: (1) understand the relationship between phyllostomid occurrence and landscape structure at different scales (0.5 to 5 km, smaller to coarser) in a context of highly fragmented forest-savanna landscapes; (2) estimate the relative contributions of local variables and landscape structure to explain the occurrence of two phyllostomid groups: frugivores and animalivores.

Although this is an exploratory study, we pose some hypotheses based on our knowledge about animal responses to landscape characteristics (Fig. 1). In relation to scale, we expected the highest contributions of landscape characteristics at intermediate or smaller spatial scales (0.5-2.5 km), since bat daily movements frequently cover ranges smaller than 2.5 km in fragmented landscapes (Bernard and Fenton 2003), and extent of each study area should be at least twice the largest process under study (Fortin and Dale 2005). Broadly we expected that overall abundances would increase in response to amount of habitat in the landscape (Fahrig 2013) and to edge amount. Positive responses to habitat amount are known for many groups, such as birds (Martensen *et al.* 2012, Betts *et al.* 2007), rodents (Estavillo *et al.* 2013), and plants (Drinnan 2005).

We posed two guild hypotheses combining local and landscape variables, based on our knowledge of frugivores and animalivores. (I) Frugivores in the edge: As frugivorous bats can be highly mobile and usually rely on fruits common in secondary stage of succession (Lobova *et al.* 2009, Saldaña-Vásquez 2014), a food resource highly available at the edges, we expected that edge would be an important variable affecting their abundance, mainly combined with abundance of fruit; (II) Forest for animalivores: since animalivorous bats are considered more affected to fragmentation (Medellín *et al.* 2000), we expected to find them in forests with higher canopy height and also high adequate habitat amount and connectivity.

| Hypotheses               | Description                                                                                                                            | Visual representation |
|--------------------------|----------------------------------------------------------------------------------------------------------------------------------------|-----------------------|
| Edge and habitat         | Edge and habitat amount as facilitating forces to the use of space by bats                                                             |                       |
| Frugivores in edge       | Edge and fruit as determinants for frugivore occupancy, since they benefit from living in the forests, but near the fruits in the edge |                       |
| Forest for animalivorous | Habitat amount, conectivity and canopy should be good predictors for animalivorous, since they are more affected by loss of Habitat    |                       |
| Null                     | None of response variables are affected by landscape metrics or local variables                                                        |                       |

**Fig. 1.** Working hypotheses for bat guild abundances as a function of local and landscape variables.

## Methods

### *Ethics statement*

Fieldwork was carried out under research permits granted by the Chico Mendes Institute for Conservation and Biodiversity (SISBIO #31163-1, #35901-1), São Paulo Forest Institute (IF/COTEC #260108 - 007.043 for sampling in protected areas), São Paulo State University (Ethics Committee and sampling in area 4) and campus Administration of Federal University of São Carlos (#022/07 DISG/PU for sampling in area 12). In the capture and handling of bats we followed the guidelines for the care and use of mammals in research suggested by the American Society of Mammalogists (Sikes *et al.* 2011).

Bats were identified to the species level in the field using a combination of taxonomic keys (Vizotto and Taddei 1973, Gardner 2007). Vouchers will be deposited at the Museum of Zoology (UFRRJ).

### *Study areas*

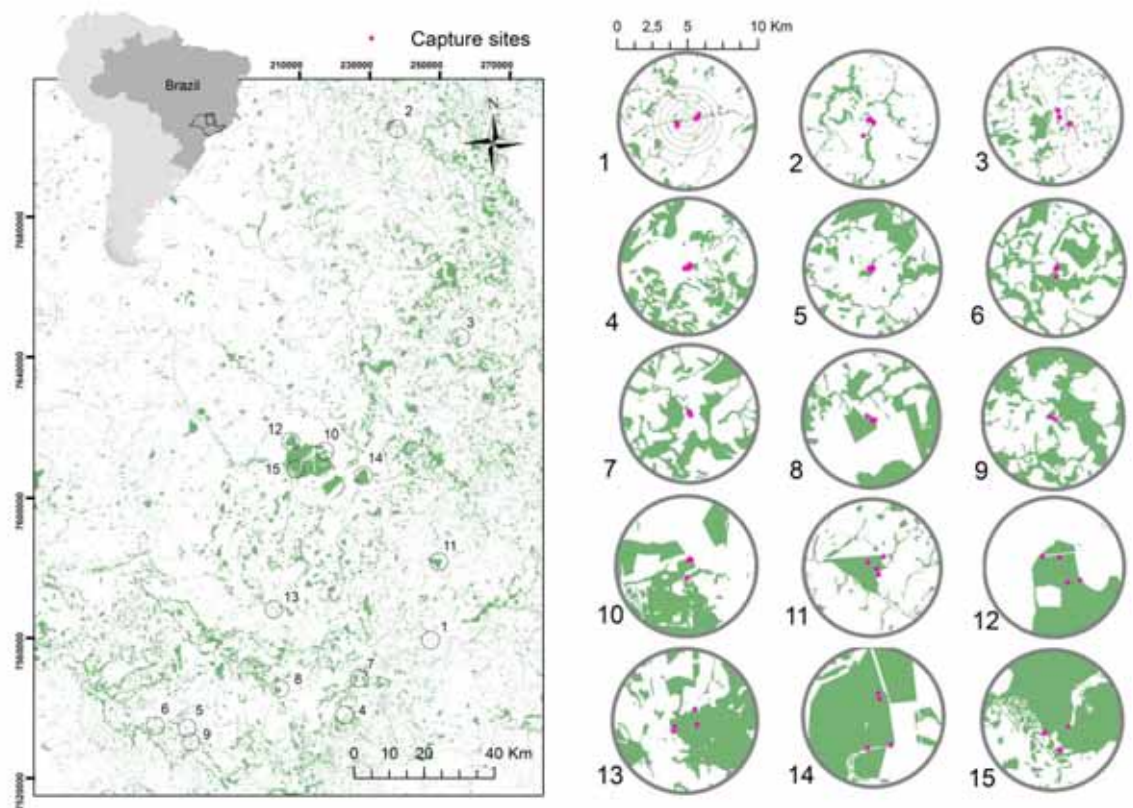
This study was conducted in landscapes selected within an area (33,850 km<sup>2</sup>) in the northeast of São Paulo State, southeastern Brazil (Fig. 2). The region is located at the boundaries of Interior Atlantic Forest and Cerrado biomes (Oliveira-Filho and Fontes 2000). Native vegetation in the region is composed of a mosaic of interior Atlantic Forest (semideciduous) and Brazilian Savanna physiognomies (cerrado *sensu* Shida 2005), in which the predominant vegetation is composed of savanna formations surrounding riparian forests. With respect to savanna physiognomies, most of this region is dominated by cerradão, a sclerophyllous woodland, and cerrado *sensu stricto*, a typical savanna (Coutinho 1978; Oliveira and Marquis 2002). The matrix is composed mainly of monocultures especially of sugarcane, *Eucalyptus* sp. and *Citrus* sp. (Brannstrom 2001; Shida 2005; Durigan *et al.* 2007). The sampled areas were composed mainly by cerradão (Oliveira and Marquis 2002). The climate of the region is Cwa (tropical of altitude) according to the Köppen system (Center of weather research CEPAGRI – UNICAMP).

### *Landscape selection*

We sampled 15 landscapes (Fig. 2), selected using moving windows with spatial dimensions of 5 x 5 km. We generated a surface model of habitat proportion within the the study region in order to identify potential landscapes in a gradient of habitat amount. Then, study landscapes were chosen based on the following criteria: (1) together, landscapes must span the entire gradient of habitat amount of native vegetation in *a priori* fixed scale of 2.5 km radii in a circular buffer; (2) centroids of landscapes must be separated by a distance of at least 5 km; (3) areas that did not vary in terms of relief, so only flat areas were selected; (4) areas with cerradão forests; (5) areas with prior approval from landowners. All chosen landscapes are covered with similar vegetation types, surrounded by monocultures.

A landcover map was derived from a georeferenced Landsat satellite image (acquired in 2010, spatial resolution of 30 m, cloud free). The classification procedure for the landcover map followed three stages: (1) identification of the vegetation types according to the map of remaining

vegetation of São Paulo state (resolution of 30 m, Kronka *et al.* 2005); (2) map editing and (3) field validation. The map-editing was based on the authors' knowledge and on high resolution images available at Google Earth throughout the Open Layer plug-in in QGIS 2.0.1 (cartographic data from 2013, Nanni *et al.* 2013), where different textures of vegetation types can be discriminated. The working scale using open layer was set up to 1:8,000. The vegetation classes are described on *Multiscaled landscape metrics* section. This region is highly fragmented compared with more coastal forest areas (Klink and Machado 2005) and only 7.1% of the original forest cover remains in interior forest, with 86% of patches smaller than 50 ha in size (Ribeiro *et al.* 2009).



**Fig. 2.** Spatial distribution of 15 landscapes in southeastern Brazil in order of percent of habitat amount at 5 km scale. Each landscape is centered on the centroid among the four sampling points. The gray circles around 1 represent the six scales of analysis. Green areas are vegetation patches. In pink are capture sites where bats were sampled with mist nets.

### *Sampling design*

We captured bats at four sampling points in each landscape. We set a total of 12 nets (model 716/7P, 12 x 3 m; denier 70/2, mesh 16 × 16 mm; Ecotone Inc., Gdynia, Poland) at each sampling

site. We captured bats for five days in each landscape, with effort for the entire study of 162,000 m<sup>2</sup>h. Sampling points were at least 50 m distant from each other (mean=287 m±107 m). Nets were opened at sunset and remained open for 6 h, since many Neotropical bats are more active during the first hours of the night (Aguilar and Marinho-Filho 2004). Each sampling site had two sampling points, one on the edge (six mist nets, referred now as *edge*) and one in the patch's interior (six mist nets, referred now as *forest*). The edge sampling points were always set in the exact limit between forest end and matrix beginning, parallel to the edge. The nets were set *in tandem* as a transect. We did five nights of capture per landscape, three conducted in summer (2012-2013) and two in winter (2013). Each sampling site was georeferenced with a GPS (error up to 8 m in forest, model Garmin 60CSX). We did not sample on full moons because of net shyness (Mello *et al.* 2013), and we avoided heavy rains, since bats frequently stop their activity on rainy nights (Thies *et al.* 2006). Nets were checked every 40 min and captured bats were identified, marked with plastic collars and then released.

### *Response variables*

We used observed number of captures as a measure of abundance. We used all bat observations per sampling point to assess responses to landscape (all guilds) and local factors (frugivores and animalivores). We analyzed abundance within feeding guilds using the definition adapted from other works on neotropical bat trophic guilds (Gardner 1977). The guilds are: animalivore (subfamily Phyllostominae), sanguivore (*Desmodus rotundus*), omnivore (*Phyllostomus discolor*, *Phyllostomus hastatus*), frugivore (subfamilies Carrollinae and Stenodermatinae) and nectarivore (Glossophaginae). We also considered frugivore abundance and small and large frugivores separately (similarly to Henry *et al.* 2010): small frugivores, with body mass <25 g, and large frugivores with >25 g. As we had low captures of omnivorous bats, what can impede modeling, we grouped them on animalivores group, making this group a group for phyllostomine bats.

We performed a Procrustes analysis of matrix association (Legendre and Legendre 2012) in order to verify if using guild responses reflected well the patterns of community structure. Due to the high positive and significant association between the community structure matrix and the guild matrix (Correlation in a symmetric Procrustes rotation  $r= 0.66$ , procrustes  $m^2= 0.55$ ,  $p<0.001$ , 10,000 permutations), we decided to include in models only guilds as response variables, since we wanted to minimize the number of dependent variables, which is more parsimonious.

We performed models with capture numbers as response variable (Table 1), as a surrogate of bat abundance or occurrence. To assess differences between captures in summer and winter, we performed a t-test (Zar 1996). To assess influences of temperature and relative humidity among samples, we used Spearman correlations between these variables and abundance of bats (we considered low correlations those with Pearson's  $r$  lower than 0.7 following Zuur *et al.* 2009). As these correlations were low, we did not include these variables in models. We calculated sample completeness by dividing the sampled richness by the mean of sums of jackknife estimates of first and second orders for the data following Magurran (2004).

**Table 1.** List of response and predictor variables that were components of the generalized additive models.

| Type             | Variables               | Description and unity                                                               |
|------------------|-------------------------|-------------------------------------------------------------------------------------|
| <b>Response</b>  |                         | Frugivore abundance                                                                 |
|                  |                         | Small frugivore abundance                                                           |
|                  |                         | Large frugivore abundance                                                           |
|                  |                         | Nectarivore abundance                                                               |
|                  |                         | Animalivore abundance                                                               |
|                  |                         | Sanguivore abundance                                                                |
| <b>Predictor</b> | Local variables         | Fruit: Sum of the fruit types<br>Canopy: Canopy mean height (m)                     |
|                  | Landscape composition   | Fragmentation: number of patches<br>Habitat amount (%)<br>Habitat diversity         |
|                  | Landscape configuration | Edge: Total edge (m)<br>Shape: Mean shape Index<br>Connectivity: Mean proximity (m) |

#### *Multiscaled landscape metrics*

We estimated a set of metrics for six scales of response: 0.5, 1, 1.5, 2, 2.5 and 5 km, these distances correspond to the radii around landscape centroids. Three composition metrics and three configuration metrics were computed for each landscape and for each spatial scale (Table 1.) Total edge represents the amount of edge length in meters; Mean shape index (MSI) measures the complexity of average patch shape in the landscape compared to circular reference based in perimeter area relationships, where MSI higher than 1 points to shapes more complex than a circle. We used mean proximity index a proxy for connectivity and is the sum of distances between

fragments divided by the square of mean distance from the focal patch. High proximity values indicate high habitat connectivity. We used forest cover as a surrogate for adequate habitat amount and we refer to adequate habitat amount as *habitat amount*.

As variation in habitat composition can be confounded with area effects (Ricklefs and Lovette 1999), we assessed habitat diversity within the 15 landscapes considering Simpson's index of diversity (Magurran 2004). This index gives values ranging from one to six, considering the area occupied by our six types of vegetation classes as potential habitat for bat: cerrado, riparian forest, semi deciduous, secondary forest, forestry (*Pinus* and *Eucalyptus*) and fruit crops (banana and guava). We did not consider matrix (non-habitat) landscape metrics in the analysis, due to their homogeneity in all landscapes, since sugarcane was predominant. Metrics were calculated using the software FRAGSTATS 3.3 (McGarigal *et al.* 2002) and QGIS.

#### *Local variables*

We quantified presence of four families of plants widely consumed by frugivorous bats based on Muscarella and Fleming's (2007) top five: Solanaceae, Cecropiaceae, Moraceae and Piperaceae (Fig. S1). We counted all plant individuals with more than three branches and more than 1.5 m high, and used their sum as a surrogate for fruit abundance (referred as fruit). The families of plant *vouchers* were identified by Maria I. S. Lima (UFSCar). We also estimated information from vegetation structure and canopy height. We used canopy height as a surrogate for a physical structure of denser and older forests, which is a factor that potentially affects use of space by bats (Gorrensens and Willig 2004). Telescopic sticks were used to estimate canopy height. Always the same person stood near each set of mist nets (edge and forest) and measured the tree height of the highest tree that was possible in view from the set of mist nets. All variables were measured within a buffer of 5 m around the mist-nets *in tandem*. Temperature and humidity were measured using a thermohygrometer (Instrutherm TAL-300), which were taken each hour during each capture night (six samples per night) on edge and interior, always by the first mist net of the set. The vegetation description was defined based on a technical field guide (IBGE, 1992).

#### *Data analysis and model selection*

The list of predictor variables is shown in Table 1. The model selection process was performed in two steps: First, scale selection: choosing the best scales of response for each response variable as a function of each predictor variable. Second, choose which model was more

plausible among models including only one landscape variable or models including local and landscape predictors based on our hypothesis.

For the scale selection, a total of seven models were analyzed per each spatial scale and per each response variables (six scales and the null model). Before model fitting and selection we conducted a correlation analyses between all landscape variables to check for collinearity. All landscape variables included in the scale selection were not strongly correlated for a particular scale (with Pearson's  $r < 0.7$ ; Zuur *et al.* 2009), in exception for the same variable in different scales. For example total edge at 0.5 km scale is highly correlated with total edge at 1 km. Thus, we corrected for the effect of nestedness on scale by reducing collinearity of the same metric at different scales. We recasted each variable as a linear combination of the other scales for the same variable (following Zuur *et al.* 2009). After that, we checked for variance inflation (Zuur *et al.* 2009) for each variable (function *vif* in package *designGG*, values on Table S1.) to make sure that a decrease in collinearity was achieved for same variable at different scales.

We did not apply any transformation to the dataset for predictor variables or for abundance. We used the multivariate model selection with generalized additive mixed models (GAMM) with smoothness selection (Wood 2014). As response variables were counts, we modeled errors as Poisson distribution with a log link function. In each model we accounted for spatial autocorrelation among sampling points by including a term in each GAMM function that considers a spatial autocorrelation structure of the residuals adding a term of correlation with coordinates of sampling points (Methods S1).

We conducted the model selection based on restricted estimated maximum likelihood, using the Akaike's information criterion corrected for small number of observations (AICc; Burnham and Anderson 2002). For each response variable, we compared competing models following Burnham and Anderson (2002). We considered that models with  $\Delta AICc < 2$  are equally plausible to explain the observed pattern. We also used Akaike's information criterion weight (weight of evidence or  $w_i$ ) to assess model support. The weight of evidence varies from zero to one, and expresses the relative contribution of the model to explain the observed pattern. Thus, we selected models based on their  $\Delta AICc$  and Akaike weights (model contribution).

#### *Guild responses to local and landscape scales*

After choosing the best scale of response for each landscape variable, we used the original data for next step to allow easy interpretation when performing additive models with local

variables. The next step was performing additive models based on our predictions about interactions of factors (see base script on Methods S1). We built models accounting for interactions among landscape metrics at the most plausible scales of response and local variables. We did not use more than three predictive variables in each model to avoid over-fitting (see Burnham and Anderson, 2002, Freedman's paradox).

We also calculated bootstrap selection frequencies (Burnham and Anderson 2002) of second step models to assess inference uncertainty ( $\pi_i$ , 10,000 resamples). For this the data set is sampled with replacement 10,000 times, using the same sample size, we then used restricted maximum likelihood theory to provide estimates of the parameters for each of the models. Finally, model selection relative frequencies ( $\pi_i$ ) are computed as the sums of the frequencies where each model was selected as the best, divided by 10,000.

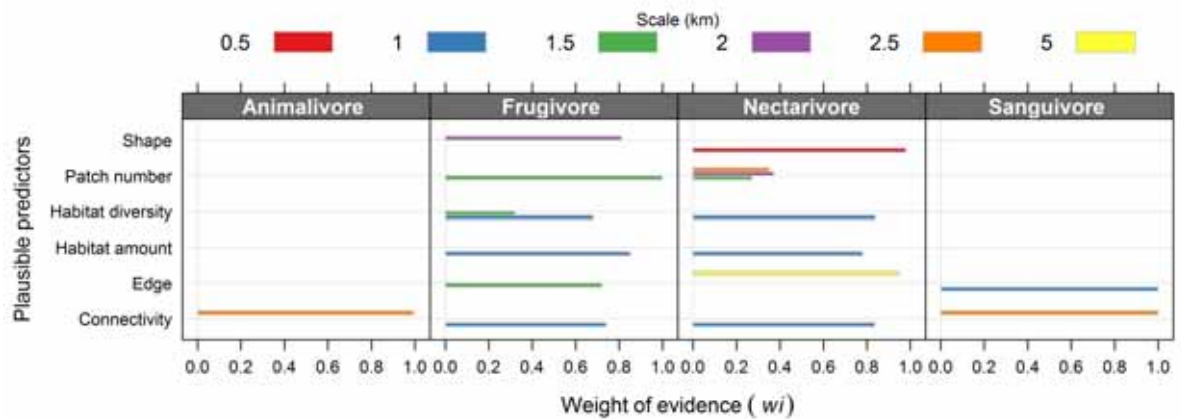
Residuals were examined and selected models were validated by visual inspection. The model selection process was performed in R 3.1.0 (R Development core team 2014) using the packages *mgcv* (Wood 2014), *bbmle* (Bolker *et al.* 2014), and *vegan* (Oskanen *et al.* 2010).

## Results

### *Multiscaled landscape metrics*

We caught a total of 1,482 bats, and 1,414 were from Phyllostomidae family (21 species). There were no differences in number of captures between summer and winter ( $t= 1.01$ ,  $p= 0.37$ ) and temperature was not correlated with bat abundance among samples (Spearman's correlation  $p= 0.86$ ,  $R^2=0.27$ ). The level of sampled completeness, phyllostomid richness and total abundance in the studied areas is on Table S2 and S3. We calculated the models with and without areas of low sample completeness (less than 70%), and we show the results for all areas when they were similar of the results without the low completeness areas data.

All plausible models for our first aim (scale selection) are showed in Fig. 3, Fig. S2. Table S3, and Methods S2 bring detailed information about the models. Guilds showed different responses to scale, but rarely the plausible models were at the coarser scale, so overall bats tend to respond better at intermediate and small scales.

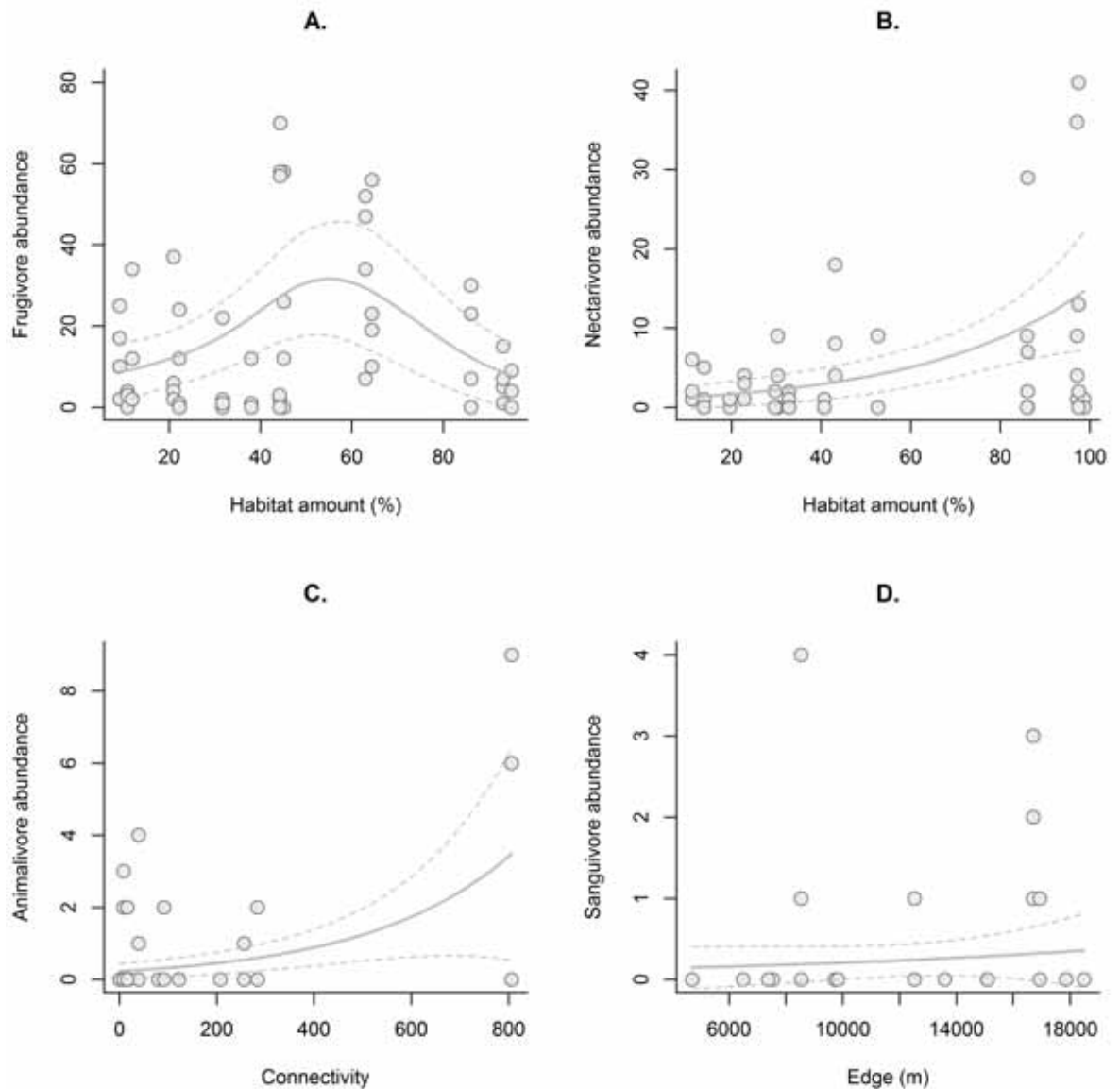


**Fig. 3.** Plausible models from the set of candidate models (GAMM) at six nested scales for phyllostomid bats in response to landscape variables within 15 landscapes of forest-savanna formations in southeastern Brazil. We considered plausible models those with  $\Delta AICc < 2$ . To see other groups, go to table S3 and Fig. S2.

Phyllostominae bats responded to connectivity, and sanguivores to edge amount and connectivity at intermediate scales. Edge amount and patch number were a important variables affecting frugivore abundance positively ( $w_i = 0.72$  and  $w_i = 0.99$ , respectively). Shape was weak to explain guilds occurrence (Table S3). Frugivore and nectarivore bats responded weakly to mean shape index at opposite scales, for the other groups, null model was the most plausible. Edge amount and habitat diversity were most related to frugivore abundance mainly at finer scales, but in a non-linear way.

Fig. 4 shows a synthesis of the models with better goodness of fit based on  $\Delta AICc$  and  $R^2$  for predicting each guild abundance in function of the landscape metrics. Habitat amount was the best model for nectarivore abundance at the fine scales. Habitat diversity and fragmentation played a weak negative effect on nectarivore abundance (Fig S4). Edge played a negative role on these bats abundance at small scales, in contrast with habitat amount.

*Desmodus rotundus* (the only captured sanguivore species captured) responded weakly to edge at the intermediate scale (2 km) and to connectivity (Fig. 4). The only plausible model for animalivores including landscape was connectivity: higher connectivity leads to higher animalivorous bat abundance.



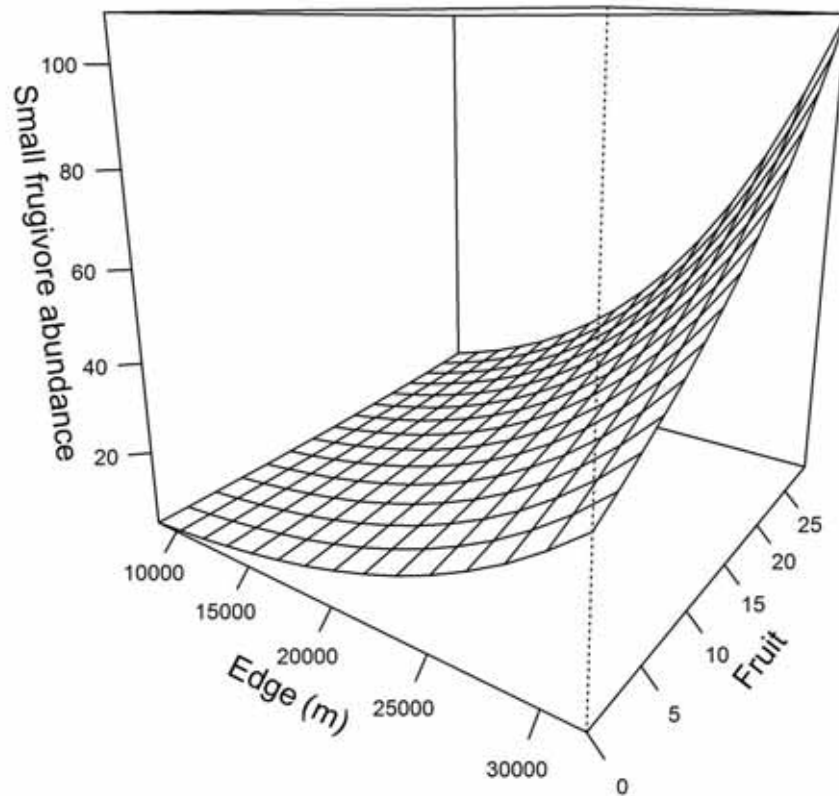
**Fig. 4.** Model predicting guilds abundance as a function of best predictors in best selected scale. A. Frugivores adjusted  $R^2 = 0.09$ ,  $p < 0.0001$ , B. Nectarivore adjusted  $R^2 = 0.13$ ,  $p < 0.0001$ ; C. Animalivore adjusted  $R^2 = 0.29$ ,  $p < 0.0001$ ; D. Sanguivore adjusted  $R^2 = 0.03$ ,  $p = 0.16$ . All plausible models for frugivore and nectarivores on Fig. S3 and S4. Dashed lines represent 95% confidence bands.

#### *Guild responses to local and landscape scales*

This results are referent to frugivorous and animalivorous bats. Total habitat amount was not selected as a plausible model for animalivorous bats abundance, but connectivity was. Thus, we included an additive model combining only canopy and connectivity in model selection. Canopy height was chosen as the best model alone for animalivorous bats (Table 4),

but it was as plausible as the model that predicted animalivores as a function of connectivity and canopy height.

Responses were slightly different among small and large frugivores (Table 2) to fruit and edge amount. For small frugivores abundance, the best model was the additive model combining fruit and edge, with strong effects ( $w_i = 0.62$ ) of edge than fruit abundance (Fig. 5), while for large frugivores and total frugivore abundance the most plausible model was edge amount alone.



**Fig. 5.** Graph of predicted values from an additive mixed model (GAMM) including small frugivore abundance as a function of total edge and number of fruits. Adjusted  $R^2=0.51$ , smooth's  $p<0.0001$  for predictor variables.

**Table 2.** Additive mixed model's results for bat guilds in response to local and landscape variables sampled within 15 landscapes of forest-savanna formations in southeastern Brazil. The p-value for each component's smooth I to III in order.  $R^2$  is adjusted  $R^2$ . df is degrees of freedom of the model. AICc is corrected Akaike Information Criteria,  $\Delta AICc$  is Akaike differences,  $w_i$  is Akaike weights,  $\pi_i$  selection frequencies (10,000 resamples). Plausible models are in bold.

| Response variable      | Model                      | AICc         | $\Delta AICc$ | df       | $w_i$        | p I            | p II          | p III | $R^2$       | $\pi_i$     |
|------------------------|----------------------------|--------------|---------------|----------|--------------|----------------|---------------|-------|-------------|-------------|
| <b>Frugivore</b>       |                            |              |               |          |              |                |               |       |             |             |
|                        | <b>Edge</b>                | <b>195.9</b> | <b>0</b>      | <b>5</b> | <b>0.95</b>  | <b>0</b>       | -             | -     | <b>0.41</b> | <b>0.98</b> |
|                        | Edge+Fruit                 | 202.6        | 6.7           | 7        | 0.034        | 0              | 0.04          | -     | 0.41        | <0.001      |
|                        | Edge+Fruit+Habitat amount  | 204          | 8.1           | 9        | 0.016        | 0              | 0.02          | 0.2   | 0.42        | <0.001      |
|                        | Habitat amount+fruit       | 215.2        | 19.3          | 7        | <0.001       | 0.14           | 0.0006        | -     | 0.35        | <0.001      |
|                        | Null                       | 566          | 370.1         | 3        | <0.001       | -              | -             | -     | -           | 0           |
| <b>Small frugivore</b> |                            |              |               |          |              |                |               |       |             |             |
|                        | <b>Edge+fruit</b>          | <b>210.7</b> | <b>0</b>      | <b>7</b> | <b>0.62</b>  | <b>0</b>       | <b>0.0006</b> | -     | <b>0.51</b> | <b>0.27</b> |
|                        | Edge+fruit+habitat amount  | 212.8        | 2.1           | 9        | 0.222        | 0              | 0.00004       | 0.22  | 0.53        | 0.67        |
|                        | Edge                       | 214.7        | 4             | 5        | 0.085        | 0              | -             | -     | 0.43        | 0           |
|                        | Fruit                      | 215.4        | 4.6           | 5        | 0.061        | 0              | -             | -     | 0.47        | 0           |
|                        | Habitat amount+fruit       | 218.9        | 8.2           | 7        | 0.01         | 0.68           | 0             | -     | 0.46        | 0.06        |
|                        | Null                       | 497.3        | 286.6         | 3        | <0.001       | -              | -             | -     | -           | 0.001       |
| <b>Large frugivore</b> |                            |              |               |          |              |                |               |       |             |             |
|                        | <b>Edge</b>                | <b>230.8</b> | <b>0</b>      | <b>5</b> | <b>0.961</b> | <b>0.00006</b> | -             | -     | <b>0.24</b> | <b>0.72</b> |
|                        | Edge+fruit                 | 237.2        | 6.4           | 7        | 0.039        | 0.001          | 0.11          | -     | 0.21        | 0.09        |
|                        | Fruit                      | 255.9        | 25.1          | 5        | <0.001       | 0.03           | -             | -     | -0.01       | 0.09        |
|                        | Edge+Fruit+Habitat amount  | 256.4        | 25.6          | 8        | <0.001       | 0.0009         | 0.85          | 0.26  | 0.25        | 0.09        |
|                        | Habitat amount+fruit       | 262.4        | 31.6          | 7        | <0.001       | 0.74           | 0.03          | -     | -0.02       | 0           |
|                        | Null                       | 503.6        | 272.9         | 3        | <0.001       | -              | -             | -     | -           | 0           |
| <b>Animalivore</b>     |                            |              |               |          |              |                |               |       |             |             |
|                        | <b>Canopy</b>              | <b>117.1</b> | <b>0</b>      | <b>2</b> | <b>0.58</b>  | <b>0</b>       | -             | -     | <b>0.24</b> | <b>0.52</b> |
|                        | <b>Canopy+Connectivity</b> | <b>117.7</b> | <b>0.6</b>    | <b>3</b> | <b>0.42</b>  | <b>0.03</b>    | <b>0.03</b>   | -     | <b>0.3</b>  | <b>0.19</b> |
|                        | Connectivity               | 228.7        | 12.9          | 2        | <0.001       | -              | -             | -     | 0.28        | 0           |
|                        | Null                       | 228.1        | 111           | 3        | <0.001       | 0.00001        | -             | -     | -           | 0.29        |

## Discussion

This study found evidence of guild-specific responses to scales, and that bats respond at different scales to landscape composition and configuration. Moreover, despite differences in responses, we found common patterns of response for small and large frugivores to fragmentation and local variables.

### *Responses to multiscaled landscape metrics*

The responses of guilds to landscape attributes occurred mainly at small and intermediate scales. Different guilds did not respond similarly to scales, like in other studies (Pinto and Keitt 2008, Klingbeil and Willig 2009), and we found little contribution of coarse scale, an element little explored in landscape studies on different animal groups and specifically for bats, where frequently the study design and high spatial autocorrelation among landscapes impedes a test of broader scales (for example Gorrensens and Willig 2004, Gorrensens *et al.* 2005, Pinto and Keitt 2008, Klingbeil and Willig 2009).

It is expected that the responses reflect those of the most common species, such as nectarivore *Glossophaga soricina* and large frugivore *Artibeus lituratus*. Interestingly these two species show different patterns of responses to landscape. These two very abundant and widespread bat species respond differently to landscape, emphasizing that total assemblage abundance provides only limited information when dealing with such an ecologically diverse group as bats. Habitat amount was a strong predictive model for nectarivore abundance at the smaller scales, reflecting *Glossophaga soricina*'s abundance and their relatively short dispersal distances (Lemke 1984).

Interestingly, small and large frugivores presented similar responses to scale, differently from other study that found that larger frugivore from the genus *Artibeus* responded to habitat amount at broader scales than the smaller frugivores *Carollia* sp. and *Sturnira* sp. (Pinto and Keitt 2008). Though, it is important to verge that Pinto and Keitt (2008) focused on species level analysis and the present study focused on guilds. Moreover, the other study was conducted on lowland neotropical rainforest, with large proportions of primary rainforests nearby. Maybe bats on highly fragmented landscapes tend to respond to broader scales, since they might be selected and adapted to use the space broadly in search of resources.

Studies on bat responses to landscape characteristics mostly use three scales of response in analysis, and it has become a trend on these studies (Gorrensens and Willig 2004, Gorrensens *et al.* 2005, Henry *et al.* 2010, Avila-Cabadilla *et al.* 2012). To improve the predictability and

understanding of scale-dependent ecological processes, information about spatial responses across numerous scales of the ecological patterns is needed (Fortin and Dale 2005). This is especially important because scale at which many ecological processes act is unknown (Gustafson 1998) and many times scale definition is arbitrarily imposed by sampling design or types of analysis (Fortin and Dale 2005). But there is a problem rarely considered when analyzing multiple spatial scales: they are nested and frequently show significant collinearity (Zuur 2009).

When we correct for the effect of the nested pattern on scales, the pattern of landscapes' condition (for example high amount of habitat) is maintained at largest and smaller scales (up to 60% of habitat amount for largest scales instead of up to 100% at smaller scale in the present study) due to spatial dependence, but the coarse scale showed to be too rough to explain the occurrence of most bat guilds. It would be interesting to compare if our approach to analyze scale responses matches with the other approaches that totally exclude dependence among them or not exclude at all. For example, several studies simply do not account for this nestedness (for example Lyra-Jorge *et al.* 2010, Pinto and Keitt 2008), what could lead to biased results. This could be evaluated if a comparison between the (1) same approach we used here, (2) the approach of not correct for nestedness or (3) the approach that most reduces dependency. The third one considers areas of broader scales excluding the areas nested within them (like a donut shape for each scale and a small circle for the smallest extent scale) and thus calculates all landscape metrics inside these parts. This could clear our comprehension of scales and provide more reliable evidences about ecological patterns.

#### *Responses to local and landscape scales combined*

This study found two main landscape determinants of bat abundance: habitat amount and edge. Local variables also played an important role explaining frugivores and animalivores, the selected guilds for our second step analysis, where we tested our main hypothesis: Edge for frugivores and Forest for animalivores.

We found evidences that partly corroborate these working hypotheses combining landscape and local variables. The working hypothesis, *Forest for animalivorous* bats was partly supported, because canopy height alone was the best model explaining animalivore abundance, but was as plausible as the model combining canopy and connectivity, and both models had similar weights. We suggest that models including canopy height and other forest structure characteristics and landscape attributes should be investigated across more intensively sampled areas. This would

better inform our understanding of these bats sensitiveness, which is assumed to be related to edge avoidance (Meyer *et al.* 2008, Farneda 2013).

Also, studies that highlight independent responses of these forest bats species to savanna formations and other tropical forest amounts might elucidate possible confounding effects of deforestation and cerrado presence for these bats. It is unclear how Phyllostominae bats use cerrado remnants, because most landscape studies that considered these bats were developed in Atlantic and in moist tropical forests (Fenton *et al.* 1992, Medellín *et al.* 2000, Gorrensens *et al.* 2005, Faria 2006, Meyer *et al.* 2008).

Frugivores abundance increased mainly in areas with intermediate levels of habitat amount. We suggest that it happens because there is higher edge amount when habitat amount is at intermediate levels and thus, higher abundance of pioneer fruits nearby. Even knowing that we had only one selected model combining local and landscape attributes (small bats abundance as a function of fruit and edge), we need to point out that since the simplest model not always is the most parsimonious (Aho *et al.* 2014), we believe that additive and non-linear models are good tools to enlighten associations among bats, landscape and local factors in a more realistic way. Although small scale variables can bring noise and high variability to samples (Fortin and Dale 2005), as resource availability can be very important determinants for habitat occupancy (Dunning *et al.* 1992), it is desirable to know how landscape characteristics affect patterns of animal groups and their resources distribution across landscapes.

Interestingly, small and large frugivores responded similarly to landscape structure. The response of frugivore abundance to habitat amount seems to be strictly related to edge behavior in gradients of fragmentation. The bell-shaped curve is reflecting the nonlinear behavior of edge in landscapes, since edge is maximum when we have intermediate level of habitat amount (see Fahrig 2003), and indeed our maximum level of edge was near 50% of habitat amount at intermediate scales.

The presence of local effects such as fruits for frugivores might reflect landscape effect determining presence and distribution of bat dispersed fruits, so the presence of fruits *per se* should reflect amounts of edge (see plot on Fig. S5). This highlights the importance of studying the effect of resources availability on species occurrence. We can think of a study on resource availability as we did with buffers around mist nets. We performed a mosaic-level sampling with sample points in a single type of patch (*sensu* Bennet *et al.* 2006). We had four points per landscape but ideally

having more points per landscape would allow us to remove the effect of focal patches on plants and elucidate the effects of landscape on resource availability. Are these plants strongly responding to edge even when we control for amount of secondary vegetation? Are edges the big hubs for seed dispersers in fragmented landscapes?

Some bats prefer fruits of pioneer plants typically found in disturbed areas (Lobova *et al.* 2009). These species tend to persist a long time in the seed bank and grow fast, offering fruits all year long. They might be not of great quality in terms of biodiversity, but attract a lot of seed dispersers from far away, promoting links between more mature forests and these disturbed areas (Henry *et al.* 2007). Frugivorous bats are functional links, bringing with them a high diversity of seeds (Lobova *et al.* 2009) besides the pioneer ones and thus promote “restoration for free” on highly fragmented landscapes. Moreover, bats might benefit from or depend of landscape complementation (Dunning *et al.* 1992) in some degree, since they can fly considerable distances to find food resources on disturbed areas (Trevelin *et al.* 2013) and may later roost inside older or more preserved forest patches. But the question is: what is more important to maintain the number of fruit bats: high connectivity promoted by high quality areas such as riparian forests or increase connectivity throughout pioneer vegetation on edges and secondary forests?

These two ways of thinking about connectivity might help restoration strategies in highly deforested landscapes, such as those in southeastern Brazil. These areas were deforested more than 40 years ago (Durigan *et al.* 2007), and today they are included as high priority areas for restoration and increases in connectivity (Joly *et al.* 2010). Considering bats as efficient seed dispersers of many plants, understanding how they respond to landscape alterations might elucidate how predictable is the outcome of such a service in fragmented landscapes. Many restoration initiatives use very common plant species as *Cecropia* sp. (Leal Filho *et al.* 2013), which attract bats to colonize new areas.

This is the first study accessing bat responses to landscape and local factors in Neotropical savanna areas. We found strong guild responses to landscape attributes in landscapes that have been fragmented for a long time. We also demonstrate that small and intermediate scales are adequate for analyzing phyllostomid bat guilds response to landscape. Our results point out to the importance of landscape composition for the conservation of Neotropical bats, which can play an important role on resilience in fragmented landscapes.

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## Supplements

**Table S1.** Variance inflation of each variable diminished and verified with *vif* function (package *vif*) applied after a generalized linear model including all variables at six different scales.

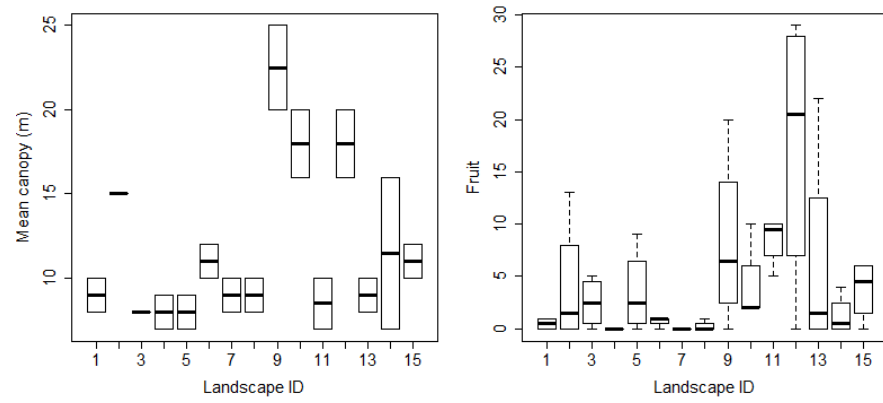
| Variance inflation | Scale (km) | % Habitat | Edge  | Habitat diversity | Shape | Patch number | Connectivity |
|--------------------|------------|-----------|-------|-------------------|-------|--------------|--------------|
| <b>Before</b>      | 0.5        | 12.52     | 16.49 | 22.56             | 1.46  | 7.78         | 1.2          |
|                    | 1          | 102.67    | 42.09 | 47.12             | 1.81  | 54.63        | 1.3          |
|                    | 1.5        | 215.84    | 15.03 | 14.32             | 2.25  | 40.53        | 164.51       |
|                    | 2          | 181.57    | 3.73  | 10.53             | 1.52  | 51.37        | 278.15       |
|                    | 2.5        | 50.3      | 6.41  | 10.59             | 3.34  | 21.3         | 87.18        |
|                    | 5          | 3.47      | 1.21  | 5.45              | 1.53  | 30.86        | 7.54         |
| <b>After</b>       | 0.5        | 5.05      | 4.83  | 2.54              | 47.75 | 1.99         | 1.21         |
|                    | 1          | 14.99     | 17.49 | 3.42              | 20.78 | 33.27        | 1.3          |
|                    | 1.5        | 87.51     | 11.06 | 2                 | 36.95 | 35.35        | 164.6        |
|                    | 2          | 142.85    | 3.39  | 1.89              | 19.24 | 45.94        | 276.96       |
|                    | 2.5        | 50.6      | 5.69  | 2.8               | 68.41 | 20.22        | 81.87        |
|                    | 5          | 13.13     | 1.21  | 3.47              | 32.28 | 30.28        | 7.81         |

**Table S2.** Descriptive information of landscapes and phyllostomids. The landscapes were sorted by amount of habitat based at 5 km scale. % Jackknife is sample completeness.

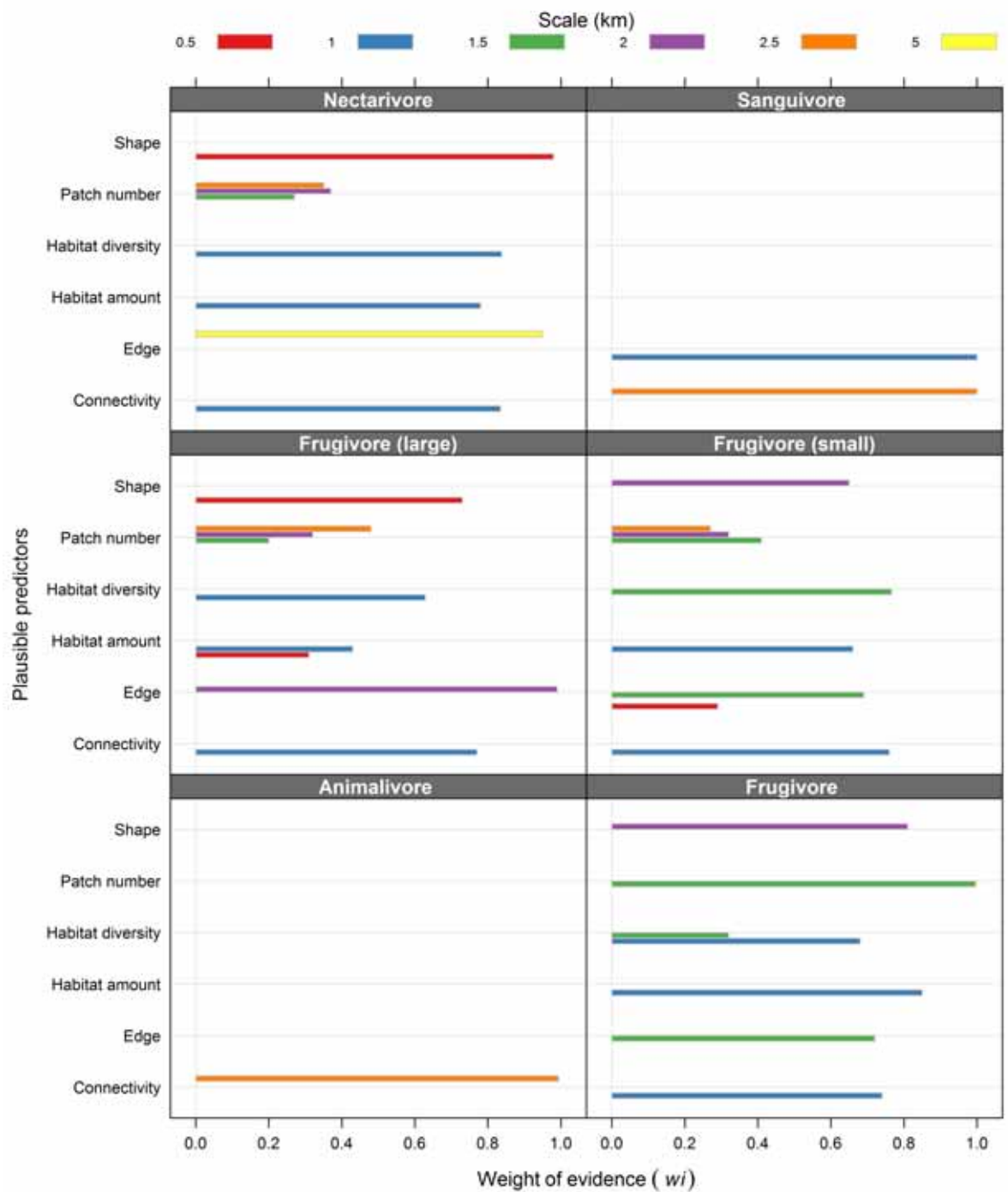
| Landscape | UTMy           | UTMx          | Name           | Municipality        | %Jackknife | Richness  | Abundance  |
|-----------|----------------|---------------|----------------|---------------------|------------|-----------|------------|
| 1         | 7534276        | 177944        | sabia          | Brotas              | 90         | 8         | 81         |
| 2         | 7559393        | 247296        | aguabr         | Pirassununga        | 82         | 8         | 66         |
| 3         | 7705137        | 237697        | batatais       | Batatais            | 100        | 7         | 61         |
| 4         | 7530303        | 178885        | losano         | Brotas              | 80         | 10        | 40         |
| 5         | 7538049        | 222831        | karl           | Corumbataí          | 87         | 3         | 13         |
| <b>6</b>  | <b>7545549</b> | <b>204365</b> | <b>botelho</b> | <b>Itirapina</b>    | <b>57</b>  | <b>4</b>  | <b>16</b>  |
| 7         | 7548542        | 226893        | cuscuzeiro     | Analândia           | 73         | 6         | 19         |
| 8         | 7568217        | 202636        | ufscar         | São Carlos          | 94         | 11        | 156        |
| 9         | 7581818        | 249698        | Pf             | Porto-Ferreira      | 77         | 14        | 167        |
| 10        | 7613422        | 217123        | bordaleste     | Luiz Antônio        | 70         | 10        | 107        |
| 11        | 7645669        | 255908        | cajuru         | Cajuru              | 86         | 9         | 57         |
| 12        | 7534912        | 168799        | tapeirao       | Jaú                 | 86         | 11        | 374        |
| 13        | 7606427        | 228130        | gigante        | Santa Rita          | 73         | 3         | 113        |
| 14        | 7616172        | 207457        | cachorro       | Luiz Antônio        | 70         | 9         | 83         |
| <b>15</b> | <b>7608246</b> | <b>208784</b> | <b>mogi</b>    | <b>Luiz Antônio</b> | <b>65</b>  | <b>15</b> | <b>129</b> |

**Table S3.** Plausible models ( $\Delta AICc < 2$ ) from the set of candidate mixed models (GAMM) in six nested spatial scales for guilds and assemblage responses of Phyllostomidae bats to landscape variables in southeastern Brazil. Abbreviations: AICc is corrected Akaike Information Criteria,  $\Delta AICc$  Akaike differences,  $w_i$  is Akaike weights.

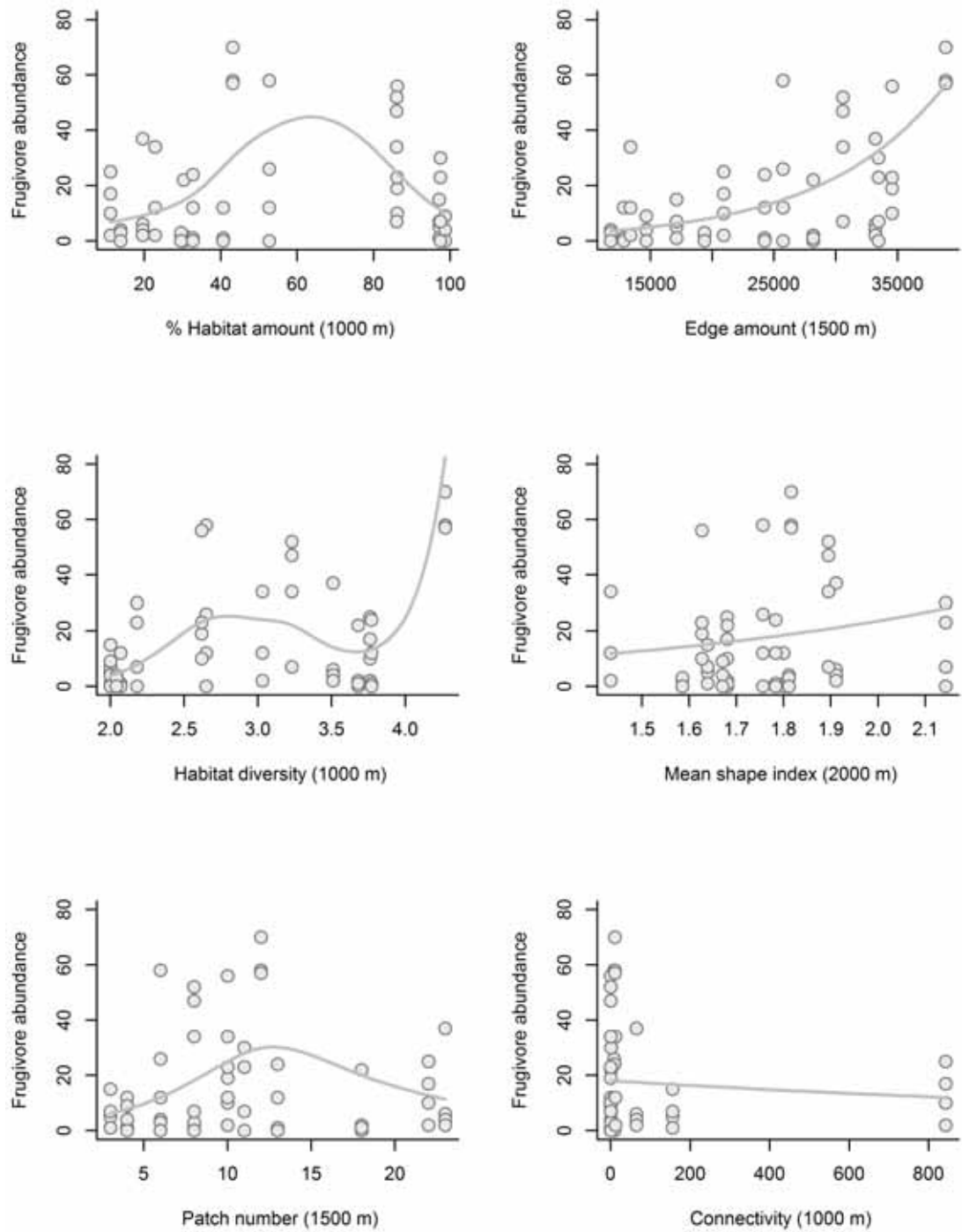
| Response variable        | Plausible models  | Scale (km) | AICc         | $\Delta AICc$ | $w_i$       |
|--------------------------|-------------------|------------|--------------|---------------|-------------|
| <b>Animalivore</b>       | Proximity         | 2.5        | 217.4        | 0             | 0.99        |
| <b>Sanguivore</b>        | Total edge        | 1          | 124.6        | 0             | 1           |
|                          | Proximity         | 2.5        | 125.9        | 0             | 1           |
| <b>Frugivorous</b>       | Total edge        | 1.5        | 197.8        | 0             | 0.72        |
|                          | Habitat amount    | 1          | 222          | 0             | 0.85        |
|                          | Habitat diversity | 1          | 204.1        | 0             | 0.68        |
|                          |                   | 1.5        | 205.6        | 1.6           | 0.32        |
|                          | Patch number      | 1.5        | 211.6        | 0             | 0.99        |
|                          | Proximity         | 1          | 222.8        | 0             | 0.74        |
|                          | Mean Shape Index  | 2          | 212.9        | 0             | 0.81        |
|                          | Habitat amount    | 1          | 221.4        | 0             | 0.66        |
| <b>Small frugivorous</b> | Total edge        | 1.5        | 215.1        | 0             | 0.69        |
|                          |                   | 0.5        | 216.8        | 1.7           | 0.29        |
|                          | Habitat diversity | 1.5        | 219.5        | 0             | 0.76        |
|                          |                   | 1.5        | 226          | 0             | 0.41        |
|                          | Patch number      | 2          | 226.5        | 0.5           | 0.32        |
|                          |                   | 2.5        | 226.9        | 0.9           | 0.27        |
|                          | Proximity         | 1          | 223.7        | 0             | 0.76        |
|                          | Mean Shape Index  | 2          | 220.5        | 0             | 0.65        |
| <b>Large frugivorous</b> | Habitat amount    | 1          | 257.2        | 0             | 0.43        |
|                          |                   | 0.5        | 257.9        | 0.7           | 0.31        |
|                          | Total edge        | 2          | 231.8        | 0             | 0.99        |
|                          | Habitat diversity | 1          | 246.4        | 0             | 0.62        |
|                          | Mean Shape Index  | 0.5        | 251.7        | 0             | 0.73        |
|                          |                   | 2.5        | 255.8        | 0             | 0.48        |
|                          | Patch number      | 2          | 256.6        | 0.8           | 0.32        |
|                          |                   | 1.5        | 257.4        | 1.7           | 0.2         |
| <b>Nectarivorous</b>     | Proximity         | 1          | 255.8        | 0             | 0.77        |
|                          | Habitat amount    | 1          | <b>273.3</b> | <b>0</b>      | <b>0.78</b> |
|                          | Total edge        | 5          | 281          | 0             | 0.95        |
|                          | Habitat diversity | 1          | 284.5        | 0             | 0.83        |
|                          |                   | 2          | 282.4        | 0             | 0.37        |
|                          | Patch number      | 2.5        | 282.5        | 0.1           | 0.35        |
|                          |                   | 1.5        | 283.1        | 0.6           | 0.27        |
|                          | Proximity         | 1          | 289.6        | 0             | 0.83        |
|                          | Mean Shape Index  | 0.5        | 269          | 0             | 0.98        |
|                          |                   |            |              |               |             |



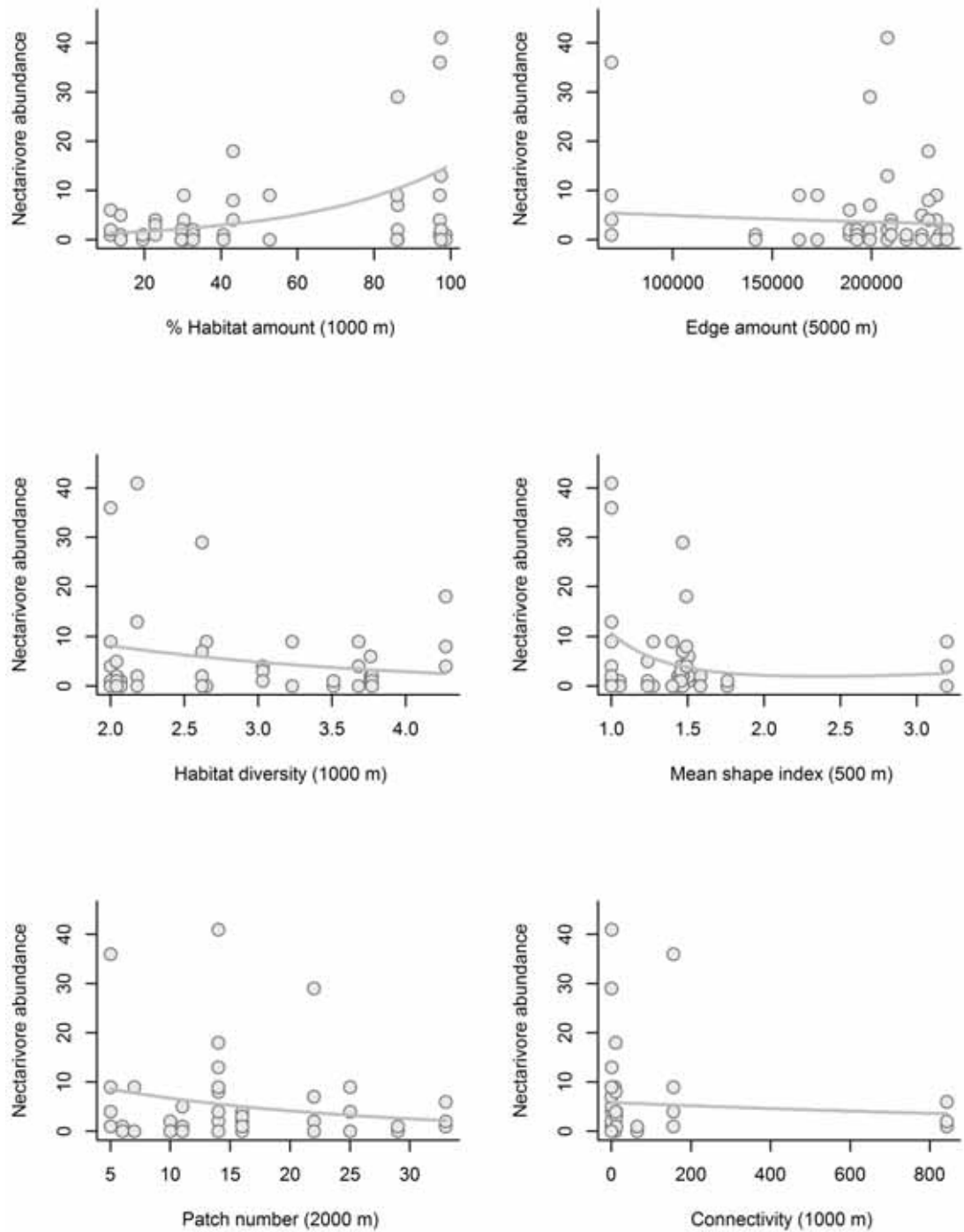
**Fig. S1.** Local variables and their variation among landscapes. Each landscape had 4 sampling points (n=60) where bats were sampled.



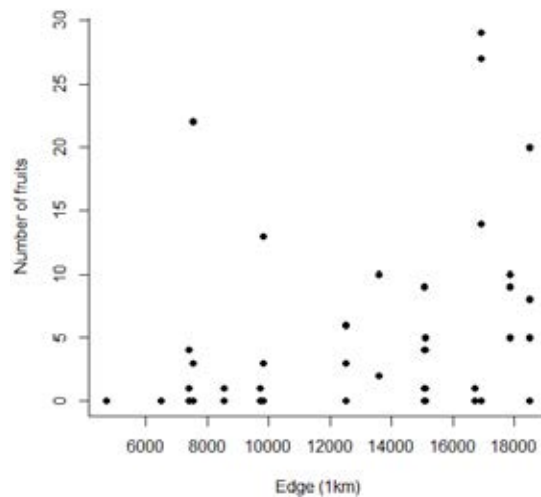
**Fig. S2.** Plausible models from the set of candidate models (GAMM) showing the contribution of scale for phyllostomid bats in response to landscape variables within 15 landscapes of forest-savanna formations in southeastern Brazil. We considered plausible models those with  $\Delta AIC_c < 2$ .



**Fig. S3.** Plausible models at the best scale of response predicting frugivore abundance as a function of a set of landscape structure metrics.



**Fig. S4.** Plausible models at the best scale of response predicting nectarivore abundance as a function of a set of landscape structure metrics.



**Fig. S5.** Plot of edge (m) and number of fruits among landscapes per each sampling point (n=60).

#### **Methods S1 Basic script in R:**

```
require(mgcv)

gamm_Abundance_frugivorous_HD_5000<-gamm(
  Abundance_frugivorous~s(HD_5000, fx=F, k=-1), cor=corExp(form=~long+lat, nugget=F),
  family= poisson, data=cutebats, method="REML")
```

#### **Methods S2**

Results of the generalized additive mixed models (GAMM) showing most plausible model fits' and their random (LME) and fixed (GAM) effects. We used package *mgcv* and function *gamm* in R 3.1.0. The random effect part accounted for spatial autocorrelation among sampling points (four sampling points per landscape). The response variables were bat abundance.

#### **Fugivores**

**Ab\_fru~VEG\_1500:**

**VEG\_1500: habitat amount at 1.5 m scale**

**Ab\_fru: Frugivore abundance**

#### **LME**

Linear mixed-effects model fit by maximum likelihood

Data: data

Log-likelihood: -100.8582

Fixed: fixed

X(Intercept) Xs(VEG\_1500)Fx1

2.7305478 -0.3414276

Random effects:

Formula: ~Xr - 1 | g

Structure: pdIdnot

| Xr1 | Xr2 | Xr3 | Xr4 | Xr5 | Xr6 | Xr7 | Xr8 | Residual |
|-----|-----|-----|-----|-----|-----|-----|-----|----------|
|-----|-----|-----|-----|-----|-----|-----|-----|----------|

|                  |          |          |          |          |          |          |          |          |
|------------------|----------|----------|----------|----------|----------|----------|----------|----------|
| StdDev: 4.332305 | 4.332305 | 4.332305 | 4.332305 | 4.332305 | 4.332305 | 4.332305 | 4.332305 | 4.332305 |
|------------------|----------|----------|----------|----------|----------|----------|----------|----------|

4.997215

Correlation Structure: Exponential spatial correlation

Formula: ~long + lat | g

Parameter estimate(s):

range

9.057197e-08

Variance function:

Structure: fixed weights

Formula: ~invwt

Number of Observations: 60

Number of Groups: 1

**GAM**

Family: poisson

Link function: log

Formula:

Ab\_fru ~ s(VEG\_1500, fx = F, k = -1)

Estimated degrees of freedom: 2.42 total = 3.42

**Nectarivore**

**Ab\_fru~VEG\_1000:**

**VEG\_1000: habitat amount at 1km scale**

**Ab\_fru: Frugivore abundance**

**LME**

Linear mixed-effects model fit by maximum likelihood

Data: data

Log-likelihood: -124.6344

Fixed: fixed

X(Intercept) Xs(VEG\_1000)Fx1

1.364024 0.876474

Random effects:

Formula: ~Xr - 1 | g

Structure: pdIdnot

|          | Xr1          | Xr2          | Xr3          | Xr4          | Xr5          | Xr6          | Xr7          | Xr8          |
|----------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| Residual |              |              |              |              |              |              |              |              |
| StdDev:  | 0.0001730415 | 0.0001730415 | 0.0001730415 | 0.0001730415 | 0.0001730415 | 0.0001730415 | 0.0001730415 | 0.0001730415 |
|          | 0.0001730415 | 0.0001730415 | 0.0001730415 | 3.82024      |              |              |              |              |

Correlation Structure: Exponential spatial correlation

Formula: ~long + lat | g

Parameter estimate(s):

range

1.329519e-10

Variance function:

Structure: fixed weights

Formula: ~invwt

Number of Observations: 60

Number of Groups: 1

## GAM

gamm\_Ab\_nectar\_VEG\_1000\$gam

Family: poisson

Link function: log

Formula:

Ab\_nectar ~ s(VEG\_1000, fx = F, k = -1)

Estimated degrees of freedom: total = 2

## Animalivore abundance

**Ab\_fru~VEG\_1000:**

**PROX\_2500: Proximity index at 1km scale**

**Ab\_anim: Animalivore abundance**

## LME

Linear mixed-effects model fit by maximum likelihood

Data: data

Log-likelihood: -145.0947

Fixed: fixed

X(Intercept) Xs(PROX\_2500)Fx1

-1.0257043      0.6814771

Random effects:

Formula: ~Xr - 1 | g

Structure: pdIdnot

|          | Xr1 | Xr2 | Xr3 | Xr4 | Xr5 | Xr6 | Xr7 | Xr8 |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|
| Residual |     |     |     |     |     |     |     |     |

StdDev: 0.0001285391 0.0001285391 0.0001285391 0.0001285391 0.0001285391  
0.0001285391 0.0001285391 0.0001285391 1.626552

Correlation Structure: Exponential spatial correlation

Formula: ~long + lat | g

Parameter estimate(s):

range

1.497383e-10

Variance function:

Structure: fixed weights

Formula: ~invwt

Number of Observations: 60

Number of Groups: 1

Family: poisson

Link function: log

Formula:

Ab\_anim ~ s(PROX\_2500, fx = F, k = -1)

Estimated degrees of freedom: 1 total = 2

### **Sanguivore abundance**

**Ab\_vamp~VEG\_1000:**

**PROX\_2500: Total edge at 1 km scale**

**Ab\_vamp: Sanguivore abundance**

**LME**

Linear mixed-effects model fit by maximum likelihood

Data: data

Log-likelihood: -142.324

Fixed: fixed

X(Intercept) Xs(TE\_1000)Fx1

-1.445904 0.283818

Random effects:

Formula:  $\sim Xr - 1 \mid g$

Structure: pdIdnot

|          | Xr1 | Xr2 | Xr3 | Xr4 | Xr5 | Xr6 | Xr7 | Xr8 |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|
| Residual |     |     |     |     |     |     |     |     |

|         |              |              |              |              |              |              |              |              |
|---------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| StdDev: | 0.0002772796 | 0.0002772796 | 0.0002772796 | 0.0002772796 | 0.0002772796 | 0.0002772796 | 0.0002772796 | 0.0002772796 |
|         | 0.0002772796 | 0.0002772796 | 0.0002772796 | 1.500039     |              |              |              |              |

Correlation Structure: Exponential spatial correlation

Formula:  $\sim \text{long} + \text{lat} \mid g$

Parameter estimate(s):

range

5.205743e-05

Variance function:

Structure: fixed weights

Formula:  $\sim \text{invwt}$

Number of Observations: 60

Number of Groups: 1

## **GAM**

Family: poisson

Link function: log

Formula:

$\text{Ab\_vamp} \sim s(\text{TE\_1000})$

Estimated degrees of freedom: 1 total = 2

## **Sanguivore abundance**

**Ab\_vamp~PROX\_2500:**

**PROX\_2500: Total edfe at 1 km scale**

**Ab\_vamp: sanguivore abundance**

## LME

Linear mixed-effects model fit by maximum likelihood

Data: data

Log-likelihood: -140.2562

Fixed: fixed

X(Intercept) Xs(PROX\_2500)Fx1

-1.5204520      -0.5489095

Random effects:

Formula: ~Xr - 1 | g

Structure: pdIdnot

|          | Xr1 | Xr2 | Xr3 | Xr4 | Xr5 | Xr6 | Xr7 | Xr8 |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|
| Residual |     |     |     |     |     |     |     |     |

StdDev: 0.0006385498 0.0006385498 0.0006385498 0.0006385498 0.0006385498  
0.0006385498 0.0006385498 0.0006385498 1.400507

Correlation Structure: Exponential spatial correlation

Formula: ~long + lat | g

Parameter estimate(s):

range 5.789123e-05

Variance function:

Structure: fixed weights

Formula: ~invwt

Number of Observations: 60

Number of Groups: 1

Family: poisson

Link function: log

Formula: Ab\_vamp ~ s(PROX\_2500, fx = F, k = -1)

Estimated degrees of freedom: 1 total = 2

## **CHAPTER 2: THRESHOLD EFFECT OF HABITAT LOSS ON BAT RICHNESS IN SAVANNA–FOREST LANDSCAPES**

# THRESHOLD EFFECT OF HABITAT LOSS ON BAT RICHNESS IN SAVANNA– FOREST LANDSCAPES

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The knowledge about which factors determine biodiversity on the current conditions of habitat loss and fragmentation are essential to the development of strategies for species conservation. Up to now, there is no consensus about the response to landscape effects in bat diversity and distribution. Some studies have verified that there are some population decline and species loss in impacted areas, although it is unknown the magnitude of these effects on bat community. There is a fragmentation threshold theory to explain fragmentation effects on diversity, where an accentuated drop in biodiversity and species persistence occurs below a level around 30% of habitat amount in landscape. In this study, we tested if there are response thresholds on bat diversity in function of habitat amount. The study was conducted in a set of 15 landscapes distributed on a habitat amount gradient (from 9 up to 80%) in southeastern Brazil at a 2 km scale, in dense cerrado (Brazilian savanna) formations. We sampled bat diversity through mist nets over two years, on fragments and their respective edges. To verify threshold on the species composition we used a multiple concurrent hypothesis model selection approach based on Akaike information's theory. The threshold value was estimated at 47% of habitat amount and the response was not associated to abundance effects. Different guilds responded differently to habitat class, with nonlinear effects of higher contribution of forestry to frugivores, cerrado to nectarivores and Phyllostominae bats and semideciduous forest amount to sanguivorous bats. We suggest that restoration strategies should increase the connectivity of landscapes, since the study region is in a context of landscape low or moderate resilience.

**Keywords:** Fragmentation threshold, habitat amount, Chiroptera, responses to habitat degradation.

## Introduction

Habitat loss and fragmentation threatens species survival, in particular on tropical region (Brooks *et al.* 2002). It is imperative to determine which species in different taxonomic groups respond to anthropogenic alterations and how they persist in fragmented environments (Gardner *et al.* 2009, Sutherland *et al.* 2013). Based on this information it is possible to create guidelines for planning more efficient conservation strategies. Biodiversity not always respond linearly to local and landscape characteristics (Fahrig 2002). In several cases there are threshold responses among these factors (Fahrig 2002), what can influence species persistence, abundance, richness and a variety of ecological processes. Also, different types of habitat may present variable contribution to a better understanding of biodiversity changes (Tilman 2000).

Many studies have verified that landscape structure characteristics contribute to explain biodiversity and its loss, which may cause negative changes on key ecological processes, such as seed dispersal (Galetti *et al.* 2013) and pollination (Aguillar *et al.* 2006). As consequence these changes can have serious impacts on ecosystem functions and services (Rosenfeld 2002, Larsen *et al.* 2005). Patch size, connectivity, edge effect and habitat conservation have direct effect on species distribution and diversity (Pardini *et al.* 2005, Uezu *et al.* 2005, Martensen *et al.* 2008, Lyra–Jorge *et al.* 2010). However, until now there is no consensus about which variables govern the presence and distribution of species, what remains as the greatest challenges to management of highly disturbed landscapes (Gardner *et al.* 2009). Studies that address these questions can provide insights into effects of habitat fragmentation (McGarigal and Cushman 2002).

Landscape structure may substantially influence occupation patterns by vertebrates (Swihart *et al.* 2006). On other hand, species traits allow adaptability to use different landscape elements in response to changes in the spatial arrangement of resources due to deforestation (Gascón *et al.* 1999). For example, the high mobility of several bat species allows them to persist in highly fragmented landscapes (Montiel *et al.* 2006, Meyer *et al.* 2008a), since they are capable to transpose the matrices that isolate fragments, such as pasture or crop fields (Fahrig and Merriam 1985). This behavior flexibility of bats increases functional connectivity of landscapes (Estrada *et al.* 1993, Bianconi *et al.* 2004, Henry *et al.* 2010).

Regarding to Neotropical bats, there is no consensus about the influence of landscape structure and habitat fragmentation on assemblages; some studies recorded positive effects (Medellín *et al.* 2000), negative effects (Fenton *et al.* 1992, Brosset *et al.* 1996, Cosson *et al.* 1999), or even absence of effect

(Estrada *et al.* 1993). The idiosyncrasy of studies (Cunto and Bernard 2012) does not allow making general conclusions or describing a common pattern of bat responses to habitat loss.

Despite this idiosyncrasy, bats compose a promising group for studies about responses to fragmentation and due to their diversity, high abundance and relative easy sampling (Medellín *et al.* 2000). Moreover, studies in different biomes verified that there is population decline, species loss and turnover in impacted areas, although the magnitude of these effects on community is highly variable (Brosset *et al.*, 1996, Jones *et al.* 2003, Safi and Kerth 2004, Saldaña-Vasquez 2014). Also, the presence or persistence of certain bat subfamilies or species can indicate ecosystem integrity (Fenton *et al.* 1992, Brosset *et al.* 1996 on Neotropics and Duchamp and Swihart 2008 in temperate forests). Besides, the magnitude of importance of these animal groups to ecological functions is still unclear (Sutherland *et al.* 2013), which stimulate studies either about their role in predation (Boyles *et al.* 2011), mutualisms (Muylaert *et al.* 2013) and coexistence (Weber *et al.* 2011), but also about their sensitivity and persistence in different habitats (Martensen *et al.* 2012). This information allied with a priori descriptive knowledge of species characteristic are surrogates for evaluation of each species' or groups' importance to ecosystem functioning. Thus, this information is needed, since the absence of groups that perform key ecological functions would accentuate the impact caused by perturbations as deforestation and fragmentation.

Among species that respond to landscape changes, gleaner animalivores are supposed to be highly edge-sensitive, and to respond negatively to disturbance and forest fragmentation (Fenton *et al.* 1992; Medellín *et al.* 2000; Meyer *et al.* 2008). Such a pattern may not be pervasive, since a positive and significant association with edge density was found for those bats in Peruvian Amazonia (Klingbeil and Willig 2009). But those results also deserve a cautious interpretation since the broad context of the studied area (Iquitos, Peru) are immerse in a large block of continuous forest. In a context of highly fragmented landscapes, which have been fragmented for a long time, it is mister to better understand the Phyllostominae responses to landscape attributes.

Changes on vegetation cover and configuration of fragments can alter species composition and ecological processes (Fahrig 2003), pointed as relevant factors to biodiversity maintenance to distinct animal groups. Knowledge about these alterations has direct implications on the definitions of strategies of landscape management for biodiversity conservation and habitat restoration (Lindenmayer *et al.* 2008, Rodrigues *et al.* 2009, Gama *et al.* 2013, Tambosi *et al.* 2013). In fact, among the landscape properties, the quantity of remaining habitat is the one that better explains the ecological responses related to ecosystem functions for many organisms (Fahrig 2013).

## *Landscape thresholds influencing biodiversity*

Considering that fragmentation process and loss of natural habitats can lead to irreversible changes in biodiversity and species interactions (Chapin *et al.* 2000), the concept of thresholds can be helpful to support conservation initiatives. The broad concept means that "small changes in an environmental driver produce large responses in the ecosystem" when there is a threshold relationship (Groffman *et al.* 2006). Thus, a threshold is a region or a point (also called breaking point) when a sharp change occurs from one condition to another (Hugget 2005).

There appear to be thresholds at which a small change in spatial structure can produce an abrupt shift in ecological responses. For example, the abundance and distribution of birds and non-flying mammals are more susceptible to changes in landscapes with less than 30% of habitat amount, due to effects of isolation and how patches are distributed (Andrén 1994, Pardini *et al.* 2010). This point is referred as Andrén's fragmentation threshold (*sensu* Pardini *et al.* 2010) in the total amount of remnant vegetation in the landscape.

Furthermore, a recent study about responses of Neotropical understory birds to connectivity and habitat amount observed that richness decline significantly below 50% of forest cover, and that landscapes with 10% and 30% of forest cover behave similarly (Martensen *et al.* 2012). This might mean that for some groups, having 10% or 30% of habitat amount in landscape are two similar conditions in terms of biodiversity loss. Thus, identifying whether there are fragmentation thresholds for other animal groups becomes fundamental to better understand ecosystems in a fragmented world, since knowing if there are similarities in threshold responses of biodiversity to landscape is a desirable and useful information for conservation planning (Hugget 2005).

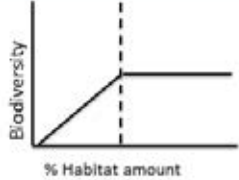
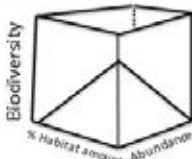
It has been observed strong variation on bat species composition in heterogeneous forested habitats and in adjacent non forested areas as fruit crops (Estrada *et al.* 1993, Medellín *et al.* 2000) and forest edges (Swihart *et al.* 2006). Furthermore, bats use different landscape elements as a way to reach resources (e.g. Fahrig and Merriam 1985), but inhabit forests much more frequently (Estrada *et al.* 1993). This reinforces the hypothesis of a threshold relationship, with higher bat diversity following higher proportions of habitat amount, with an expected abrupt change on bat diversity below a certain level of habitat amount.

Here, we investigated the contribution of quantity of different suitable habitat types in the landscape on bat abundance, and if accounting for individual habitat types is as plausible as total habitat amount to explain the occurrence of frugivores, nectarivores, animalivores and sanguivores. Our expectations for responses of these groups to different habitat types are showed in Table 1 . Then, we evaluated whether

there is a threshold on the response of bat diversity (assessed as taxonomic richness) as a function of habitat loss in Cerrado landscapes. We predicted that: 1) there is a threshold for biodiversity in function of habitat amount; 2) Landscapes among a gradient of habitat amount will present drop in diversity in lower habitat proportions (Fig. 1).

**Table. 1.** Our hypothesis for explaining abundance of bat guilds as a function of amount of different habitat types within fragmented landscapes in southeastern Brazil.

| <b>Response variable</b>                     | <b>Hypothesis and motivation</b>                                                                                                                                                                                                                                                    |
|----------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Frugivore abundance                          | Frugivorous bat abundance is plausibly explained several habitat types, but in a bell-shaped pattern, increasing abundances in intermediate levels of habitat amount, probably following higher amounts of edge in landscape ( <i>sensu</i> Muylaert, Ribeiro and Stevens in prep.) |
| Nectarivore and<br>Animalivore<br>abundances | Nectarivorous and animalivorous bat abundance are better explained by native habitat amount, since these bats roost in these areas and are more sensitive to habitat loss (Meyer <i>et al.</i> 2008, Muylaert, Ribeiro and Stevens in prep).                                        |
| Sanguivore abundance                         | Sanguivore abundance will be not be affected by habitat amount, since these bats are very common on disturbed areas (Fenton <i>et al.</i> 1992)                                                                                                                                     |

| Hypotheses             | Description                                                                                                                                      | Visual representation                                                                |
|------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|
| Linear                 | Biodiversity increases on a linear trend in response to changes in total habitat amount of landscape                                             |   |
| Biodiversity Threshold | Biodiversity increases on a non linear trend in response to changes in total habitat amount of landscape, including a threshold point around 30% |   |
| Neutral                | Biodiversity increases in response to changes in total habitat amount of landscape, and this effect is proportional to an increase of abundance  |   |
| Null                   | Biodiversity does not vary in function of habitat amount                                                                                         |  |

**Fig. 1** Working hypotheses for bat diversity in response to habitat amount within fragmented landscapes of southeastern Brazil.

### *Cerrado domain and bats*

We adopted the term Cerrado as the set of forest-like savannah formations together with riparian forests and other physiognomies, as semi deciduous forests (Coutinho 2006). The Cerrado, second largest Brazilian phytogeographic domain, actually is the most devastated biome of São Paulo state, being restrict to 0.81% of its original area (Kronka *et al.* 2005), and one of world's conservation hotspots (Ratter *et al.* 1997). As consequence of the anthropic activity, biodiversity of Cerrado is strongly threatened, because, only 20% of its areas remain not disturbed in the entire biome, and only 1.2% is within protected areas (Myers *et al.* 2000).

The Cerrado domain spreads over an important region of geographic dispersion of bats, due to its heterogeneity of habitats, and because it extends through central Brazil, linking other biomes such as Pantanal, Atlantic Forest and Amazon (Bordignon 2006). At least 103 bat species occur in the biome (Aguilar and Zortea 2008), composing half of mammal species number registered, and corresponding to

almost 61% of Brazilian bat species (Marinho-Filho 1996). Maintaining the cerrado diversity depends on the knowledge of composition and dynamics of species interaction, to develop strategies for their conservation and restoration of remaining fragments.

## Methods

### *Landscape selection and habitat amount calculation*

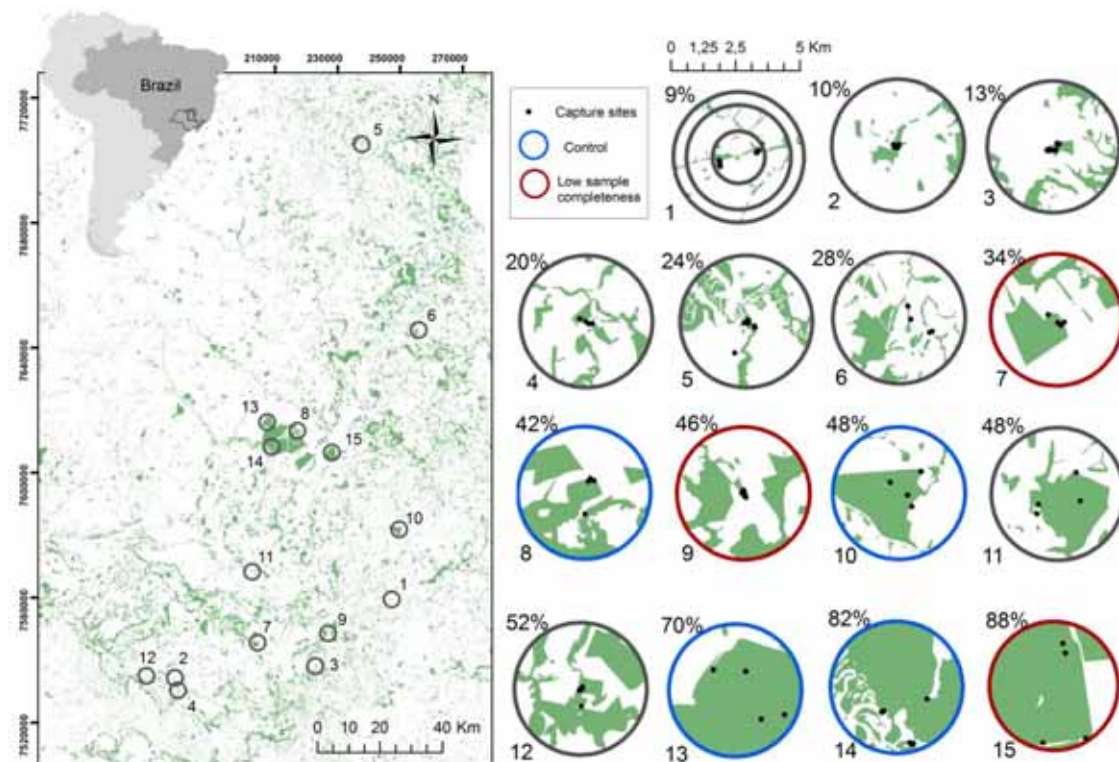
We selected 15 landscapes on a gradient from 8% to 80% of habitat amount at a 2.5 km scale comprising the radius of a circular buffer (Table S1, Fig. 2). Here, we define scale as the spatial extent of a measured landscape, as a surrogate for the extent of realized dispersal of bats within a landscape (Wu and Hobbs 2007).

On the region there are very small patches (Durigan *et al.* 2004), with more than 80% of patches <50 ha (Ribeiro *et al.* 2011). But the region still harbor the largest cerrado area of São Paulo state, (Pires 1995), located on the Jataí Ecological Station (21° 33' S; 47° 45' W), with 10,000 ha. This allowed us to select landscapes across the desirable gradient of habitat amount. We selected four control landscapes (areas 8, 10, 13 and 14, Fig. 2), that were located at the following protected areas: the Jataí Ecological Station and Porto-Ferreira State Park, due to their better conservation status (high quantities of habitat amount within protected areas) and presence of cerrado.

The surrounding of the sampled remnants included mostly sugarcane plantations, but also forestry (*Eucalyptus* spp. and *Pinus* spp.), and less frequently fruit crops (as *Citrus* and banana), cattle pasture, dams and urban areas (Coutinho 1978, Pires 1995). Although the region harbors different vegetation formations, such as semideciduous forest, open cerrado, *sensu stricto* cerrado and cerradão forests (a woodland cerrado, Coutinho 1978, Pires 1995), the selection of the central landscapes position were mainly on cerrado fragments with different patch sizes, within forest-like physiognomies like Cerradão (Eiten 1979). Also, none of the landscapes are located in boundaries of any sampled bats species' distribution range, to avoid errors related to biogeographical distribution. The climate is Tropical of Central Brazil, presenting two defined seasons, one hot and rainy from October to April, another cold and dry, between May and September (Pires 1995).

We used forest cover as a surrogate for adequate habitat amount, hereafter *habitat amount*. Habitat amount is a measure of landscape composition, where the total quantity of remaining vegetation is evaluated, not mattering its spatial organization (habitat quantity, size and distribution of the fragments, border effect and shape). Here, we used habitat amount as surrogates for landscape degradation by anthropic impacts: the higher the habitat amount in a landscape, the lower the landscape degradation (see Fahrig 2003). Using a vegetation cover map, the habitat amount was estimated for each landscape,

dividing its area within a buffer of the respective scale by the total circular area of the buffer. The metrics were calculated throughout Quantum GIS version 2.0.1 (QGIS Development Team 2014). The landcover map was derived from a georeferenced Landsat satellite image (acquired on 2010, spatial resolution of 30 m, cloud free). The landscape classification procedure for generate the landcover map followed three steps: (1) identification of the vegetation types according to the map of remaining vegetation of São Paulo state (resolution of 30 m, Kronka *et al.* 2005); (2) map editing and (3) field validation. The map-editing used high resolution images available at Google Earth throughout the Open Layer plug-in in QGIS 2.0.1 (cartographic data from 2013, QGIS Development Team 2014), where different textures of vegetation types were discriminated. The working scale using open layer was set up to 1:8.000 on screen. The vegetation classes used for analysis were: total vegetation amount, native vegetation amount, cerrado, semideciduous forest, riparian forest, forestry (mainly *Eucalyptus* sp.) and matrix (open anthropogenic areas, such as sugarcane, pasture and agriculture).



**Fig. 2.** Spatial distribution of 15 landscapes with the scales represented as buffers with dimensions of 2.5, 2, and 1 km in southeastern Brazil, where bats were sampled with mist nets. The green areas are the vegetation patches, and at the upper left of each landscape we present the percent of habitat amount. The geographic coordinates of the centroids are presented on S1. Coordinates in UTM.

#### *Data sampling of bat diversity*

Fieldwork was carried out under research permits granted by the Chico Mendes Institute for Conservation and Biodiversity (SISBIO #31163–1, #35901–1), São Paulo Forest Institute (IF/COTEC #260108-007.043 for sampling in protected areas), São Paulo State University (Ethics Committee) and campus Administration of Federal University of São Carlos (#022/07 DISG/PU). In the capture and handling of bats we followed the guidelines for the care and use of mammals in research suggested by the American Society of Mammalogists (Sikes *et al.* 2011).

Bats were identified to the species level in the field using a combination of taxonomic keys (Vizotto and Taddei 1973, Gardner 2008). The vouchers will be deposited at the Museum of Zoology (UFRRJ) and some were already deposited in the mammal collection of the Zoology Museum of São Paulo University and on the collection of Prof. Ariovaldo Cruz-Neto (UNESP).

We performed a mosaic-level sampling with sample points per landscape in a single type of habitat patch (*sensu* Bennet *et al.* 2006). We had four sampling points, two sampled in winter (2012) and two in summer (2013). Within each landscape, sampling points were at least 50 m distant from each other ( $287 \pm 107$  m). We selected the sampling points based on the centroids of previous selected landscapes. On each season one sampling point was set inside the cerrado patches and another was set on the nearest edge in contact with sugarcane matrix (Fig. S1). The position of mist nets in different portions of fragments increase the chances of bats capture (Kunz and Kurta 1990). We chose the sampling points based on the vegetation structure, always preferring to set nets on trails close to denser cerrado formations (with canopy height higher than 7 m) and within the focal fragment (where the landscape centroid was set). We estimated the canopy height for each sampling point with telescopic sticks (8 m). The edge nets were set also based on vegetation structure, always 1 m distant from the boundary with the native vegetation.

We conducted the captures on two sampling points per season, totalizing five capture nights per landscape (three nights on summer, two on winter). Each sampling night was comprised of 12 mist nets (model 716/7P, 12x 3 m; denier 70/2, mesh  $16 \times 16$  mm; Ecotone Inc., Gdynia, Poland) on each landscape. The nets remained open since the sunset for 6 h, once many Neotropical bats are more active on the first hours of night (Aguilar and Marinho-Filho 2004). We avoided to capturing on full moons because Neotropical bats can show lunar phobia (Mello 2013). We also avoided heavy rains, because bats frequently stop their activity on rainy nights (Thies *et al.* 2006). Sampling effort was calculate by multiplying the area and total exposition times of mist nets (Straube and Bianconi 2002).

We did not consider differences in species capture probabilities, because although mist nets are selective for phyllostomids (Kunz and Parsons 2009), apparently the capture of insectivorous bats from other families is facilitated in Cerrado due to its simplified vertical stratification (Aguirre 2002, Zortéa and Alho 2008). Thus, we included data of all bats captured to measure species richness. To assess differences between captures in summer and winter, we performed a t-test (Zar 1999).

### *Data analyses*

We achieved a satisfactory level of sample completeness (Magurran 2004) in the studied areas (Table S1, Fig S2), calculated by dividing the sampled richness by the mean of sums of estimated jackknife of first and second orders. We considered as low completeness, those areas with values of estimated completeness less than 75% (landscapes 7, 10, 11, 13, 14 and 15, Fig. 2, Fig.S1). Three of the four control landscapes (all within Jataí Ecological Station, 11, 13 and 14) had low completeness, but we kept them in the model selection since their species number followed the same pattern as other control area classified as with satisfactory sample completeness (Porto-Ferreira State Park, area 9). They were areas of relatively high diversity, as expected for a landscape with high habitat amount. Then, we present the results which consider the data of 15 landscapes when their correspondent models without the low sample completeness areas (7, 10 and 15) showed similar results.

### *Contribution of different habitat types to bat abundance*

It is important to consider that mist nets are selective, capturing mostly bats of the family Phyllostomidae, since Vespertilionidae and Molossidae bats have accurate echolocation and detect the net more easily (Kunz and Parsons 2009). Therefore, we conducted our analysis with only abundance of Phyllostomid guilds as response variables: frugivores, animalivores (Phyllostominae), nectarivores and sanguivores (adapted from Gardner *et al.* 2008, concept of guilds of Simberloff and Dayan 1991). Also, as we were interested in guild occurrence and not only on species richness, we ran the models with all sampling areas' data. We used number of bat captures (occurrence) as a surrogate of bat abundance. The dependent variables were estimated to assemblages as a whole as for each group: frugivores, nectarivores, animalivores and sanguivores. For frugivorous, nectarivorous and Phyllostominae bats, we used a fixed scale (1 km) and for Sanguivores we used 2.5 km scale to analyze class area contribution. We chose those scales because they were plausible to explain abundance on other study conducted within the same areas (Muylaert, Ribeiro and Stevens in prep).

Eight models were concurred to select if the presence of individual habitat types, or their sum was better to explain each guild occurrence (Table 2). The null model represents model with absence of effect. The neutral model represents that bat occurrence could receive influence of any habitat type, and then respond mainly to total habitat amount, than to specific habitat types. The best gradient of habitat represented in this study was the amount of Cerrado (Fig. S3, see Pearson's correlation among habitat types and total habitat amount). We only used in the analysis the types of habitat that did not present high collinearity, with exception of cerrado and native forest.

We used an approach of model selection by multiple concurrent hypothesis based on Akaike information theory (Burnham and Anderson 2002). As Phyllostomidae bat guilds may present non-linear responses to landscape attributes (Muylaert, Ribeiro and Stevens in prep), we applied generalized additive models assuming Poisson distribution. We consider best models the ones with best predictive accuracy by corrected AIC based on maximum likelihood estimates and selection frequencies ( $\pi_i$ , Burnham and Anderson 2002). To assess  $\pi_i$ , data set is sampled with replacement 10,000 times using the same sample size (bootstrap). Then, selection relative frequencies ( $\pi_i$ ) are computed as the sums of how many times each model was selected as the best ( $\Delta AIC_c=0$ ), divided by 10,000.

**Table 2** List of competing models to explain bat guild abundance as a function of amount of different types of habitat in landscape within fragmented landscapes in southeastern Brazil.

| Predictor habitat type in model | Description                                                                                                           |
|---------------------------------|-----------------------------------------------------------------------------------------------------------------------|
| Cerrado                         | Abundance is affected by cerrado amount                                                                               |
| Semideciduous forest            | Abundance is affected by semideciduous forest amount                                                                  |
| Riparian forest                 | Abundance is affected by riparian forest amount                                                                       |
| Forestry                        | Abundance is affected by riparian forest amount                                                                       |
| Secondary forest                | Abundance is affected by secondary forest amount                                                                      |
| Native vegetation               | Abundance is affected by native habitat amount                                                                        |
| Neutral                         | Abundance does not show selectivity among different habitat types, but is positively affected by total habitat amount |
| Null                            | Abundance is not affected by habitat amount                                                                           |

#### *Threshold between bat richness and habitat amount*

For this step, total richness was used as response variable, including all bat families besides Phyllostomidae. We ran models with richness as a surrogate of bat biodiversity. Before investigating the *threshold hypothesis*, generalized additive models were concurred including different classes of habitat to explain richness on our habitat amount gradient, similarly to the steps considering abundance.

We used data on native vegetation cover at 2 km spatial scale to conduct the model selection, following the most plausible scale to explain richness (*sensu* Muylaert, Ribeiro and Stevens *in prep*). The model selection procedure concurred among four types of models: piecewise, null, neutral and linear (Fig. 1). In this study we used neutral models with two different approaches: 1) One is related to total habitat amount in landscape (neutral model in the section *Contribution of different habitat types to explain bat occurrence*), and 2) the other one, which took into account the abundance of bats as a neutral factor associated with species number (neutral model in the section *Richness and habitat amount*).

Piecewise regressions are models that consider more than one line fit to the data, forming breaking points between them (Toms and Lesperance 2003). The piecewise regression of the *glm* is provided by iterative fitting procedure to estimate the model parameters (Muggeo 2011). Values of coefficients and breaking points are fitted repeatedly until the estimates lead to the maximum likelihood estimated values. Standard errors and confidence intervals of breaking points were obtained by the package *segmented* (Muggeo 2011). We used the R language (R Development core team 2014), model selection was made using *bbmle* (Bolker *et al.* 2014), and additive models used *gam* (Hastie, 2013). We analyzed the plausible models observing model weights ( $w_i$ ),  $\Delta AICc$  and selection frequencies ( $\pi_i$ ).

#### *Model validation and spatial autocorrelation*

All plausible models were validated following Zuur *et al.* (2009). We selected landscapes distant from each other to minimize spatial autocorrelation, but to verify if there was significant spatial autocorrelation we followed Fortin and Dale (2005), using the Pearson's residuals of the plausible models to build a Moran's I correlogram and test significance of spatial auto-correlation using 10,000 permutations. These analyses were made in the software SAM (Rangel *et al.* 2006) with six distance classes. If significant autocorrelation was detected in model residuals, we included additional model terms on the models to account for it.

## **Results**

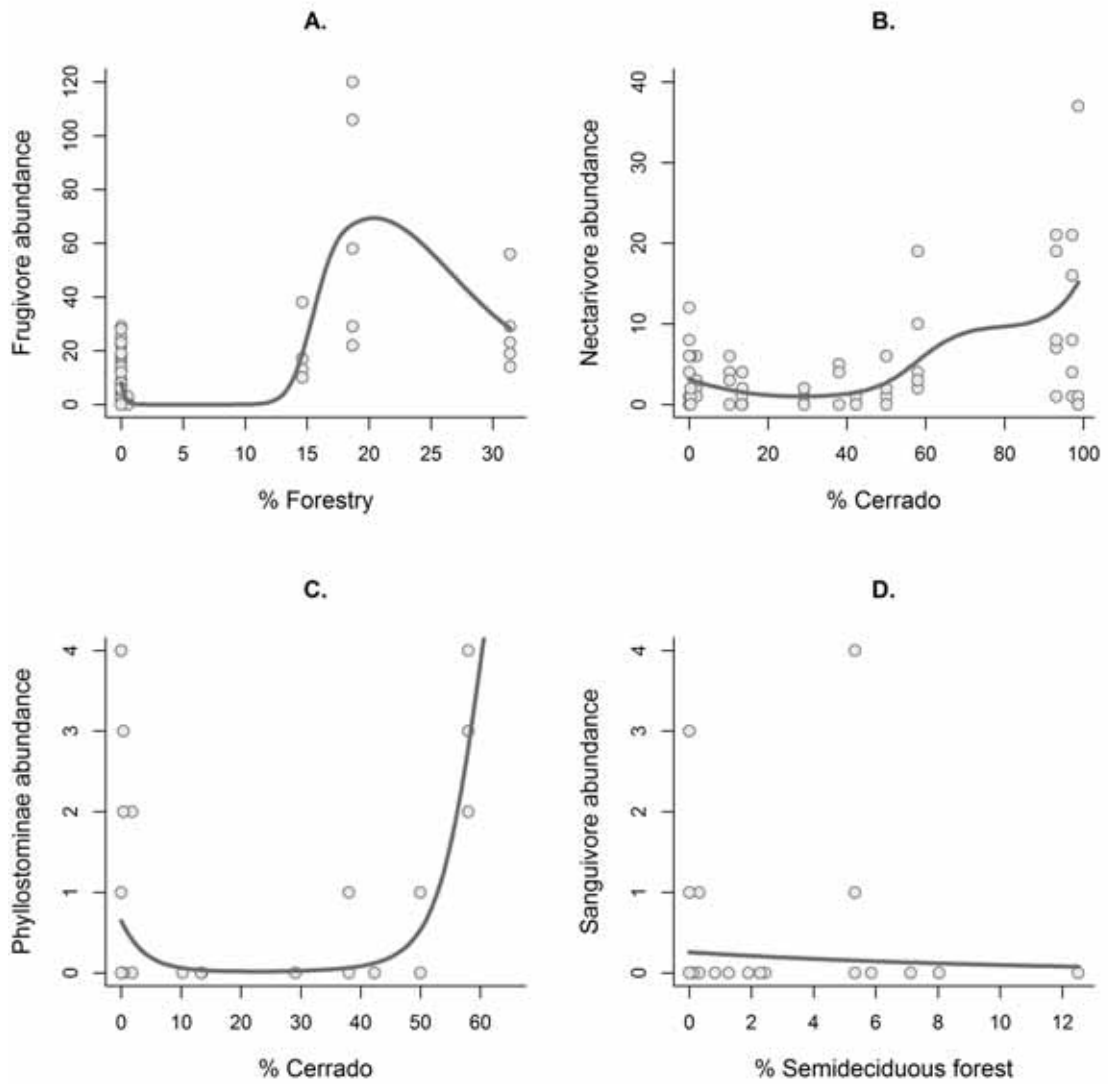
#### *Contribution of different habitats types to bat abundance*

We had a total effort of 162,000 m<sup>2</sup>.h and 1,484 captures. We sampled 34 species (Table S2), and 92% (n=1,362) of captures were phyllostomids (23 species, 67% of community samples, Table S2). There were no differences in captures among sites between summer and winter ( $t= 1.01$ ,  $p= 0.37$ ).

The contribution of different habitat types to explain bat occurrence varied among the guilds (Table 3, Fig. 3). For both nectarivorous and animalivorous bats, the best habitat model was cerrado amount ( $w_i=0.72$  and  $w_i= 0.98$ , respectively). The response of Sanguivore to all habitat types was weak, and the only plausible model was the one including semideciduous forest amount ( $w_i=0.45$ ). Frugivorous bats' occurrence responded to forestry on a bell-shaped pattern ( $w_i=1.00$ ).

**Table. 3** Models explaining abundance of bat guilds as a function of amount of different habitat types and their respective effect. AICc is corrected Akaike Information Criteria,  $\Delta AICc$  is Akaike differences,  $w_i$  is Akaike weights,  $\pi_i$  selection frequencies (10,000 resamples). The best models ( $\Delta AICc=0$ ) in bold and the plausible models as the best are in italic and bold.

| Spatial scale | Response variable (abundance) | Model                | AICc         | $\Delta AICc$ | $w_i$       | $\pi_i$     |
|---------------|-------------------------------|----------------------|--------------|---------------|-------------|-------------|
| 1 km          | <i><b>Frugivores</b></i>      |                      |              |               |             |             |
|               |                               | <b>Forestry</b>      | <b>872.4</b> | <b>0</b>      | <b>1</b>    | <b>0.93</b> |
|               |                               | Secondary            | 1038.6       | 166.2         | <0.001      | 0.05        |
|               |                               | Cerrado              | 1199.8       | 327.4         | <0.001      | 0.01        |
|               |                               | Riparian             | 1215.2       | 342.8         | <0.001      | 0.01        |
|               |                               | Neutral              | 1354         | 481.6         | <0.001      | 0           |
|               |                               | Native               | 1421.2       | 548.8         | <0.001      | 0           |
|               |                               | Semideciduous        | 1564.6       | 692.2         | <0.001      | 0           |
|               |                               | Null                 | 1689.5       | 817           | <0.001      | 0           |
|               | <i><b>Nectarivores</b></i>    |                      |              |               |             |             |
|               |                               | <b>Cerrado</b>       | <b>590.9</b> | <b>0</b>      | <b>0.72</b> | <b>0.36</b> |
|               |                               | <b>Native</b>        | <b>592.8</b> | <b>1.9</b>    | <b>0.28</b> | <b>0.2</b>  |
|               |                               | Neutral              | 613          | 22.1          | <0.001      | 0.02        |
|               |                               | Riparian             | 818.2        | 227.3         | <0.001      | 0.33        |
|               |                               | Semideciduous        | 821.8        | 230.9         | <0.001      | 0.04        |
|               |                               | Forestry             | 835.3        | 244.4         | <0.001      | 0.03        |
|               |                               | Secondary            | 849.6        | 258.7         | <0.001      | 0           |
|               |                               | Null                 | 882.4        | 291.4         | <0.001      | 0           |
|               | <i><b>Animalivores</b></i>    |                      |              |               |             |             |
|               |                               | <b>Cerrado</b>       | <b>101.2</b> | <b>0</b>      | <b>0.98</b> | <b>0.6</b>  |
|               |                               | Secondary            | 109.4        | 8.3           | 0.02        | 0.27        |
|               |                               | Semideciduous        | 112.6        | 11.5          | 0           | 0.01        |
|               |                               | Native               | 113.6        | 12.5          | 0           | 0           |
|               |                               | Neutral              | 130.5        | 29.3          | <0.001      | 0.04        |
|               |                               | Riparian             | 144.3        | 43.1          | <0.001      | 0.06        |
|               |                               | Forestry             | 152.5        | 51.3          | <0.001      | 0           |
|               |                               | Null                 | 152.8        | 51.6          | <0.001      | 0           |
| 2.5 km        | <i><b>Sanguivores</b></i>     |                      |              |               |             |             |
|               |                               | <b>Semideciduous</b> | <b>78.6</b>  | <b>0</b>      | <b>0.66</b> | <b>0.45</b> |
|               |                               | Forestry             | 81.8         | 3.2           | 0.13        | 0.44        |
|               |                               | Neutral              | 82.5         | 3.9           | 0.1         | 0.05        |
|               |                               | Cerrado              | 83.1         | 4.5           | 0.07        | 0.04        |
|               |                               | Riparian             | 85.4         | 6.7           | 0.02        | 0           |
|               |                               | Native               | 86.8         | 8.2           | 0.01        | 0.03        |
|               |                               | Secondary            | 89.5         | 10.9          | 0           | 0           |
|               |                               | Null                 | 92.3         | 13.7          | <0.001      | 0           |



**Fig. 3** Plausible non-linear models (gam) explaining bat occurrence in a gradient of habitat amount within 15 fragmented landscapes of Brazil. Landscape metrics were measured at 1 km scale for frugivorous, nectarivorous and Phyllostominae bats, and at 2 km for sanguivorous bats. Adjusted values (p is p for smooth's parametric effects and F values for smooth's parametric F-test) and  $R^2$  is adjusted  $R^2$ : A. Frugivores  $p < 0.0001$ ,  $F = 65.73$ ,  $R^2 = 0.42$ ; B. Nectarivores  $p < 0.0001$ ,  $F = 34.67$ ,  $R^2 = 0.26$ ; C. Phyllostominae bats  $p = 0.04$ ,  $F = 4.07$ ,  $R^2 = 0.33$ ; D. Sanguivore  $p < 0.0001$ ,  $F = 10.88$ ,  $R^2 = 0.02$ .

#### *Threshold between bat richness and habitat amount*

Richness was best explained by total habitat amount ( $w_i = 0.32$ ), but with plausible contributions of cerrado and riparian forest (Table 4, Fig. S4). Of total recorded species, 44% ( $n = 15$ ) were exclusive of landscapes above the theoretical threshold ( $\psi = 30\%$  of habitat, Andr n 1994), while only four species were exclusive of areas below the lower level of Andr n's threshold (10%, Andr n, 1994).

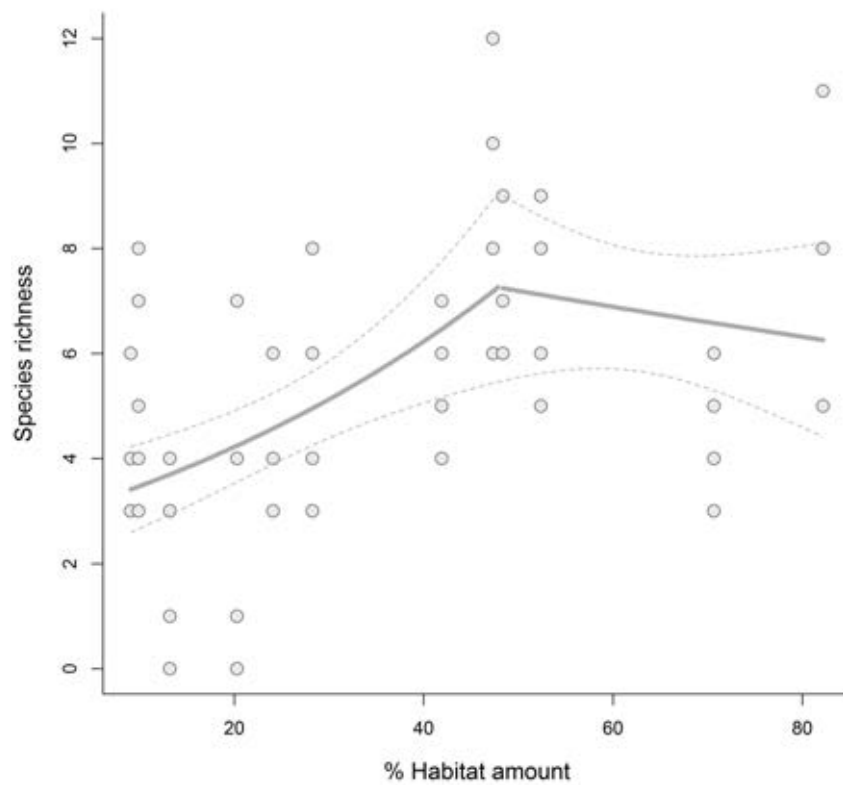
**Table 4** Generalized additive model's results for bat richness in response to habitat amount sampled within 15 landscapes of forest–savanna formations in southeastern Brazil. Df: degrees of freedom of the model. AICc is corrected Akaike Information Criteria,  $\Delta$ AICc is Akaike differences,  $w_i$  is Akaike weights,  $\pi_i$  selection frequencies (10,000 bootstraps). The best model ( $\Delta$ AICc=0) are in bold. Plausible models in bold and italic.

| Model                          | AICc        | $\Delta$ AICc | df       | $w_i$         | $\pi_i$       |
|--------------------------------|-------------|---------------|----------|---------------|---------------|
| <b>Neutral (Total habitat)</b> | <b>62</b>   | <b>0</b>      | <b>2</b> | <b>0.3233</b> | <b>0.9987</b> |
| <b><i>Cerrado</i></b>          | <b>62.7</b> | <b>0.7</b>    | <b>3</b> | <b>0.2259</b> | <b>0</b>      |
| <b><i>Riparian</i></b>         | <b>64</b>   | <b>2</b>      | <b>3</b> | <b>0.1181</b> | <b>0</b>      |
| Semideciduous                  | 64          | 2.1           | 3        | 0.1135        | 0             |
| Secondary                      | 64.8        | 2.8           | 3        | 0.0796        | 0             |
| Forestry                       | 65.5        | 3.6           | 3        | 0.0536        | 0             |
| Native                         | 65.5        | 3.6           | 3        | 0.0536        | 0             |
| Null                           | 73.2        | 11.2          | 3        | 0.0012        | 0.0013        |

Comparing the models, the most plausible to explain richness was the piecewise model ( $w_i = 0.86$ ,  $\pi_i=0.99$ , Table 5). The estimated threshold was at 47.81% of habitat amount for richness at the 2 km scale (Fig. 4, Table S2). The piece-wise model had  $\Delta$ AICc equal to zero and weight of 0.92, being better to explain the relation between richness and habitat amount than the linear model ( $\Delta$ AICc=6,7,  $w_i= 0,03$ ), and the null and neutral model were weak. The piecewise best model for richness did not show significant spatial auto–correlation for the residuals (Table S3, model validation in Fig S5).

**Table 5** Generalized linear models explaining bat richness in response to habitat amount sampled within 15 landscapes of forest–savanna formations in southeastern Brazil.  $R^2$  is adjusted  $R^2$ , df is degrees of freedom. AICc is corrected Akaike Information Criteria,  $\Delta$ AICc is Akaike differences,  $w_i$  is Akaike weights,  $\pi_i$  selection frequencies (10,000 bootstraps). The best models ( $\Delta$ AICc=0) are in bold. See model coefficients in Table S4.

| Model            | AICc         | $\Delta$ AICc | df       | $w_i$       | $R^2$       | $\pi_i$     | p            |
|------------------|--------------|---------------|----------|-------------|-------------|-------------|--------------|
| <b>Piecewise</b> | <b>252.1</b> | <b>0</b>      | <b>5</b> | <b>0.86</b> | <b>0.60</b> | <b>0.99</b> | <b>0.002</b> |
| Linear           | 258.8        | 6.7           | 4        | 0.08        | 0.44        | 0.01        | 0.00006      |
| Neutral          | 261.1        | 9             | 3        | 0.05        | 0.45        | 0.00        | 0.0005       |
| Null             | 269.7        | 17.7          | 3        | <0.001      | 0.39        | 0.00        | 0.72         |



**Fig. 4.** Piecewise regression model highlighting that there is a threshold in bat richness as a function of suitable habitat amount. The estimated breaking-point at 47% ( $p_{\psi} = 0.03$ ,  $SE_{\psi} 7.51$ ) of total habitat amount remaining in landscape. There is a rapid decline of bat richness at the breaking point. The study was conducted among 15 landscapes in southeastern Brazil. Dashed lines indicate 95% confidence intervals of fitted values.

## Discussion

Our results suggest that bats respond to habitat loss, despite the high variability of our data. Different habitat types on landscape influenced differently each bat guild. As expected, this indicates that among bat groups there are different sensitivities to environmental degradation. The threshold hypothesis was corroborated in the present study, and it is substantially above than previously thought (Andr n 1994). Native and non-native vegetation types did not similarly affect bat occurrence, but habitat types tend to affect richness on a neutral way, since total habitat amount is the most plausible model to explain bat taxonomic richness. This means that what matters for an increased richness is the total habitat amount within the landscape, at least considering just landscape composition in a broad gradient (8–80% of habitat amount).

### *Relative contribution of different habitat types to explain bat occurrence*

The present study points that bats with different feeding habits respond negatively to habitat loss and, variation in amount of different habitat types are perceived differently among guilds. Also, this response is not simply to total suitable habitat quantity, emphasizing the role of other aspects of landscape structure determining bat abundance, such as landscape heterogeneity. Different guilds tend to respond more positively to higher amounts of native vegetation, and not as strongly as to forestry and secondary forests (see  $w_i$  values in Table 3). Since heterogeneity seems to be important for the persistence of guilds, the quality and permeability of habitats must be taken into account when protected areas are planned, modified or created on sugarcane dominated landscapes.

Frugivorous bat abundance was better explained by forestry amount, with higher abundances at intermediate levels. Other models were not equally plausible as the model that considered forestry, and thus, frugivores might be benefiting from exotic forest plantations, which frequently have native understory (Silva *et al.* 1995) with many chiropterochoric plants. This pattern probably also follows higher amounts of edge in landscape at intermediate levels of forestry or total habitat amount (*sensu* Muijlaert, Ribeiro and Stevens in prep., in a study conducted at the same areas). The persistence of frugivorous bat species not caring much for the native vegetation proportion means high adaptability to environmental changes, at least considering short term responses.

Nectarivores were the guild most strongly affected by habitat loss (Fig. 3). Phyllostomines also responded positively to habitat amount, what corroborates our hypothesis that these two groups are more sensitive to fragmentation. In relation to sanguivorous bat abundance, the models were very weak (adjusted  $R^2 = 0.01$  for the best model), showing just a tendency to increased occurrences on more degraded landscapes. We suggest that this happens due to our sample design, that prioritized areas mostly surrounded by sugarcane, and not pasture, where these bats tend to be more abundant (del Pietro *et al.* 1992).

We expected that animalivorous bats (subfamily Phyllostominae) would be affected, due to their small home ranges for some species and their characteristic foraging strategies (Cosson 1999). We found these bats on both low habitat landscapes and more frequently in high habitat landscapes, but with low abundances. Due to the extensive fragmentation process occurred in São Paulo state (Durigan *et al.* 2007), it is possible that rare species became absent of landscapes with lower levels of forest cover, and even locally extinct. As phyllostomines were not abundant in this study, and under sampling could mask

habitat loss effects, we recommend that a broader analysis of the response of this group should be performed for the Cerrado and other biomes where information of long term sampling is available.

#### *Richness, habitat amount and fragmentation threshold*

The breaking point at 47% of habitat amount influencing richness found in this study is above the threshold proposed by Andrén (1994), of 20 up to 30%. It is also above the threshold found for other groups. As example, for small mammals, the value was at 30% of remaining forest (Estavillo and Pardini 2013), but it was between 30-50% for understory birds in Atlantic forest (Martensen *et al* 2012), forming a threshold zone. Other works did not corroborate the threshold hypothesis at all. For example, Parker and MacNally (2002) studying invertebrates, and Lindenmayer *et al.* (2005) studying bird and reptiles. The reason for that is suggested to be due to diversity in individual species traits and the possibility that even ecologically similar species might respond differently to landscape changes (Lindenmayer *et al.* 2005). Although, much more evidence supports that in most landscapes, the total suitable habitat amount will be of great importance for species persistence (Fahrig 2013).

There is evidence of both positive and negative effects of native vegetation loss on organisms abundance (Fahrig 2002). However, in a community perspective, fragmentation can have strong influence on biodiversity persistence, and can be a major cause of extinction (Fahrig 2002). Most works on thresholds in response to habitat loss were performed considering taxonomic groups (Andrén 1994) separately, for example, considering woodland birds (Redford *et al.* 2005, Betts *et al.* 2007). Since the loss of species can be preceded by loss of interactions (Estes *et al.* 2011), it would be interesting investigate fragmentation thresholds on key ecological processes, such as pollination (Aguilar *et al* 2006) or decomposition (Hooper *et al.* 2012), instead of focusing a particular group. With this approach, the consistency of the threshold concept, and also the mechanisms driving responses to habitat loss could be clarified. Thus, stronger evidence for conservation could be generated if fragmentation thresholds were detected on ecological key interactions.

#### *Threshold and bat conservation*

In relation to the second neutral model (richness as a function of habitat amount and abundance), our results did not point that with higher abundances, higher will be the species number. Instead, we found a piecewise pattern, where two straight lines have different slopes, being one almost parallel to the x axis (low variation in species number at landscapes with higher habitat amount), and the other one is more leaning, with an accentuated decrease in species number at low habitat amount landscapes. The threshold above the theoretical threshold proposed by Andrén (1994) is an alarming result since even

among bats, a group with many highly mobile species, there is a decrease in number of species and abundance in degraded landscapes. We believe the bat assemblages of these landscapes, fragmented for more than 40 years (Durigan *et al.* 2007), might be impoverished in number sensitive species, compared to more preserved areas. For example, in a well preserved cerrado area on the center–west of Brazil (Zortéa and Alho 2008), with a total effort of 60 nights of capture, 25 bat species were registered, and eight species were phyllostomines (Zortéa and Alho 2008). In our study we registered only five species of Phyllostominae bats, and we sampled more areas (n=15), with higher effort. We performed 75 capture nights, *versus* 60 with less hours of sample *per* night on Zortéa and Alho (2008). Thus, we suggest that the bat communities on São Paulo’s interior are impoverished in comparison to well preserved cerrados. Restoration strategies must seek increasing the connectivity of fragmented landscapes, since great part of this region presents low or moderate landscape resilience (Tambosi *et al.* 2013).

Meyer *et al.* (2008) found that habitat loss rather than fragmentation in islands is the main process after isolation underlying phyllostomid responses on islands. Here, we did not account for other fragmentation effects, but surely enlightens the importance of habitat amount to explain bat biodiversity. This agrees with a recent review by Fahrig (2003), who argued that in most studies, the effects of fragmentation *per se* are absent, too weak to be detected or may only become apparent at low levels of habitat amount. It suggests that conservation efforts that attempt to minimize fragmentation effects for a given amount of habitat may often be inadequate. We believe that for bat conservation efforts, combining habitat amount and the concept of thresholds is a simple and useful for evaluating landscapes that still have considerable quantities of habitat amount. Moreover, landscape composition rather than configuration should be driving biodiversity on these landscapes (Fahrig *et al.* 2003). Thus, configuration must be more important in low–resilience landscapes, where restoration initiatives would not compensate the efforts compared to moderate–resilience landscapes (*sensu* Tambosi *et al.* 2012). Furthermore, the high vulnerability to fragmentation in bats is associated mostly with high edge–sensitivity (Meyer *et al.* 2008a), a menacing information, since moderated fragmented landscapes present very high amounts of edge (Fahrig 2003).

This study corroborates that bats of subfamily Phyllostominae and nectarivores are scarce on disturbed regions (see Fenton *et al.* 1992, Wilson *et al.* 1996, Medellín *et al.* 2000), whereas these guilds could be indicators of ecosystem integrity (Raport 1992). We believe that together with the studies that have been published for more than 20 years (Fenton *et al.* 1992, Meyer *et al.* 2008a, Meyer *et al.* 2008b, Meyer *et al.* 2009, Farneda 2013) we are forming a robust background of evidence about the high sensitivity of bat groups in the Neotropics.

The decreased species number in landscapes with low quantity of habitat amount might support conservation strategies definitions, as identifying areas with major restoring potentials and landscape resilience. Bats play an interesting role in this sense, whereas they can be sensitive as the forest Phyllostominae bats and the small sized nectarivores, but in the other extreme, frugivores can be allies to restoration in future projects related, since they are persistent and very abundant in fragmented landscapes. For example Bianconi *et al.* (2009) used fruit essential oils to attract frugivorous bats to fragments and obtained success, which is promising to facilitate the colonization of new areas by seed dispersers. As bats are among the main responsible for seed dispersal of many plants (Lobova *et al.* 2009), they seem to be important agents for restoration (Kelm *et al.* 2008), what makes their conservation highly desirable.

While diverse studies had proposed to relate bat diversity with patch size (Faria 2006, Cosson *et al.* 1999, Estrada *et al.* 1993, Schulze *et al.* 2000), this is a pioneer study that confirmed the existence of fragmentation threshold with a landscape perspective. We consider that studies addressing spatial and temporal parameters that affect the distribution and occurrence of species are an advance on the uptake of ecosystems balance, bringing more plainness for decisions related to environmental issues. The observed patterns can contribute to amplify our predictive knowledge of consequences of alterations on landscape to animals.

Our research highlights the effects of habitat loss and landscape composition on a highly abundant animal group. Native vegetation cover, particularly cerrado amount on landscape was important to explain two most sensitive groups to fragmentation: animalivores and frugivores. We suggest that threshold relationships in biotic responses in response to landscape characteristics should be broadly investigated, in order to clearly understand effects of habitat loss on organisms distributions and also on ecological processes. Moreover, species loss might be occurring more severely bellow a threshold level, but it does not exclude species loss on areas with higher levels of habitat amount (Mönkkönen and Reunanen 1999), since other mechanisms can lead to species loss (Turner *et al.* 1989, Chapín *et al.* 2000), and even a high threshold point might be underestimating the magnitude in which there is species loss in highly fragmented landscapes.

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Supplementary material



**Fig. S1** Examples of sampling sites position in edge and interior, where mist nets were used to capture bats. A. Edge with sugarcane (Photo credit: Calebe Mendes) at Batatais municipality (São Paulo, Brazil). B. Patch interior, a dense cerrado formation (Photo credit: Pavel Dodonov), at Santa Rita do Passa Quatro municipality (São Paulo, Brazil).

**Table S1** Information of 15 landscapes where bats were sampled in southeastern Brazil. Sample completeness was calculated by dividing the sampled richness by the mean of sums of estimated jackknife of first and second orders, following Magurran (2004). Habitat amount calculated at a 2 km scale. We considered low completeness sampled the areas with sample completeness below 75% (areas with \*). We kept the control areas in model selection despite their low sample completeness. ID is landscape identification number.

| ID | UTM x  | UTM y   | Name        | Municipality   | % Completeness | Richness | Abundance | % Habitat |
|----|--------|---------|-------------|----------------|----------------|----------|-----------|-----------|
| 1  | 247296 | 7559393 | aguabr      | Pirassununga   | 82             | 8        | 66        | 9.05      |
| 2  | 177944 | 7534276 | sabia       | Brotas         | 90             | 11       | 81        | 9.88      |
| 3  | 222831 | 7538049 | karl        | Corumbataí     | 87             | 4        | 13        | 13.2      |
| 4  | 178885 | 7530303 | losano      | Brotas         | 80             | 10       | 40        | 20.29     |
| 5  | 237697 | 7705137 | batatais    | Batatais       | 100            | 8        | 61        | 24.1      |
| 6  | 255908 | 7645669 | cajuru      | Cajuru         | 86             | 12       | 57        | 28.26     |
| 7  | 204365 | 7545549 | botelho*    | Itirapina      | 57             | 5        | 16        | 34.83     |
| 8  | 217123 | 7613422 | bordaleste* | Luiz Antônio   | 70             | 12       | 107       | 41.92     |
| 9  | 226893 | 7548542 | cuscuzeiro* | Analândia      | 73             | 8        | 19        | 46.36     |
| 10 | 249698 | 7581818 | pf          | Porto-Ferreira | 77             | 19       | 167       | 47.33     |
| 11 | 202636 | 7568217 | ufscar      | São Carlos     | 94             | 15       | 156       | 48.37     |
| 12 | 168799 | 7534912 | tapeirao    | Jaú            | 86             | 11       | 374       | 52.4      |
| 13 | 207457 | 7616172 | cachorro*   | Luiz Antônio   | 70             | 13       | 83        | 70.66     |
| 14 | 208784 | 7608246 | mogi*       | Luiz Antônio   | 65             | 13       | 129       | 82.2      |
| 15 | 228130 | 7606427 | gigante*    | Santa Rita     | 73             | 9        | 113       | 88.19     |

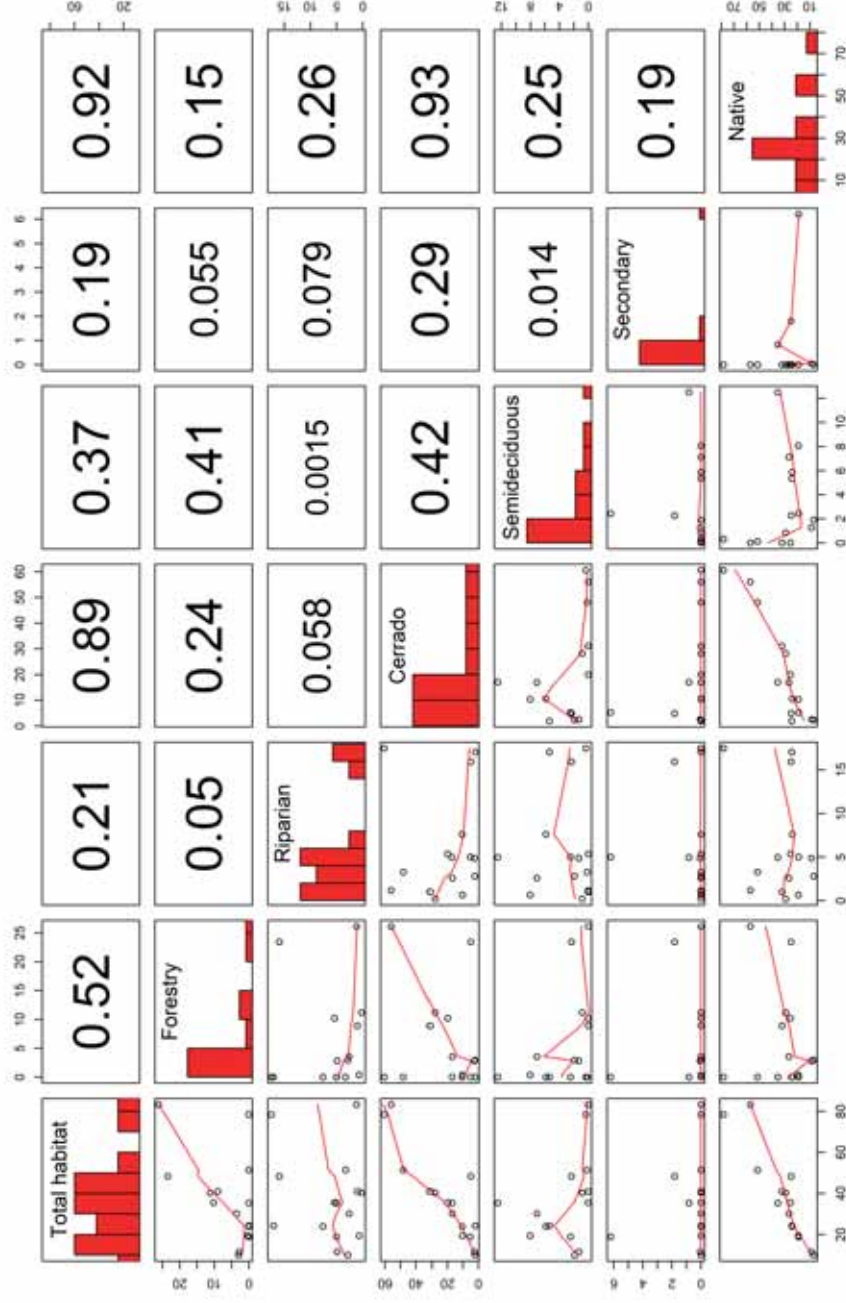
**Table S2** Bat species sampled at 15 landscapes considering five nights of capture in São Paulo, southeastern Brazil (2012 and 2013).

| Species                          | Voucher | DNA sample |
|----------------------------------|---------|------------|
| <i>Anoura caudifer</i>           | Y       | Y          |
| <i>Anoura geoffroyi</i>          | Y       | Y          |
| <i>Anoura sp</i>                 | N       | Y          |
| <i>Artibeus fimbriatus</i>       | Y       | Y          |
| <i>Artibeus lituratus</i>        | Y       | Y          |
| <i>Artibeus planirostris</i>     | Y       | Y          |
| <i>Carollia brevicauda</i>       | Y       | Y          |
| <i>Carollia perspicillata</i>    | Y       | Y          |
| <i>Chiroderma doriae</i>         | Y       | Y          |
| <i>Chiroderma trinitatum cf.</i> | N       | Y          |
| <i>Chrotopterus auritus</i>      | N       | Y          |
| <i>Cynomops planirostris</i>     | Y       | Y          |
| <i>Desmodus rotundus</i>         | Y       | Y          |
| <i>Eptesicus brasiliensis</i>    | Y       | Y          |
| <i>Eptesicus diminutus</i>       | Y       | Y          |
| <i>Eptesicus furinalis cf.</i>   | Y       | Y          |
| <i>Eptesicus sp.</i>             | Y       | Y          |
| <i>Glossophaga soricina</i>      | Y       | Y          |
| <i>Lasiurus blossevillii</i>     | Y       | Y          |
| <i>Micronycteris megalotis</i>   | N       | Y          |
| <i>Micronycteris minuta</i>      | N       | Y          |
| <i>Molossus molossus</i>         | Y       | Y          |
| <i>Myotis albescens</i>          | Y       | Y          |
| <i>Myotis nigricans</i>          | Y       | Y          |
| <i>Myotis riparius</i>           | Y       | Y          |
| <i>Myotis ruber cf.</i>          | N       | Y          |
| <i>Noctilio albiventris</i>      | N       | Y          |
| <i>Phyllostomus discolor</i>     | N       | Y          |
| <i>Phyllostomus hastatus</i>     | Y       | Y          |
| <i>Platyrrhinus lineatus</i>     | Y       | Y          |
| <i>Sturnira lilium</i>           | Y       | Y          |
| <i>Sturnira tildae</i>           | Y       | Y          |
| <i>Uroderma bilobatum</i>        | N       | Y          |
| <i>Vampyressa pusilla</i>        | Y       | Y          |

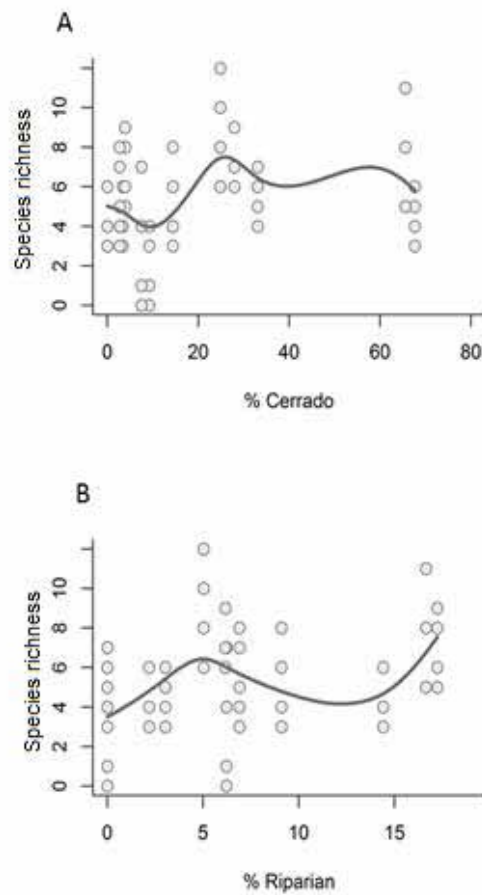


**Table S4** Estimated model coefficient statistics for the threshold model selection with bat richness as a function of habitat amount in the landscape. SE: standard error.  $\Psi$ : estimated breaking point. The model selection was based on maximum likelihood estimation.

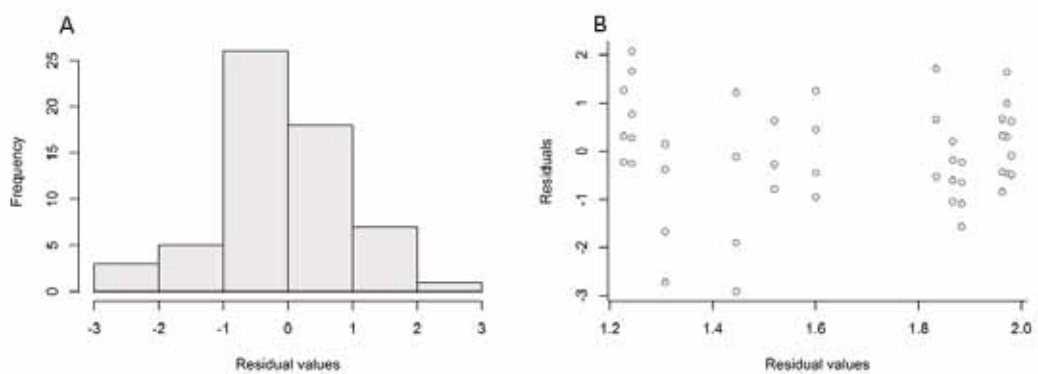
| Model      | Coefficient                     | SE    | t     | P      |
|------------|---------------------------------|-------|-------|--------|
| Piece-wise | $\beta_0$                       | 1.07  | 2.05  | 0.05   |
|            | $\beta_1$                       | 0.05  | 1.93  | 0.05   |
|            | $\Psi$                          | 7.51  | 0     | 0.03   |
|            | $\beta_2$                       | 0.06  | -2.21 | 0.03   |
| Linear     | $\beta_0$                       | 0.59  | 5.79  | 0.001  |
|            | $\beta_2$                       | 0.01  | 3.88  | <0.001 |
| Neutral    | $\beta_0$                       | 0.13  | 9.69  | <0.001 |
|            | $\beta_{\text{Habitat amount}}$ | 0.002 | 4.03  | <0.001 |
|            | $\beta_{\text{Abundance}}$      | 0.002 | 0.51  | 0.6    |
| Null       | $\beta_0$                       | 0.68  | 6.93  | <0.001 |
|            | $\beta_1$                       | 1.22  | 1.19  | 0.23   |



**Fig. S3** Scatterplot of percentage of each habitat types. The upper panel shows Pearson's correlation among the proportions of each habitat class on 15 landscapes in a context of cerrado in southeastern Brazil. The font size is proportional to correlation value. The diagonal panel shows histograms representing the frequency of each interval of values of habitat amount for each habitat class and for total habitat amount. For example, low number of landscapes presented high quantities of total habitat amount (Total habitat). The lower panel shows scatterplots among variables and a LOESS smoother fitted.



**Fig. S4** Contribution of habitat types to explain bat richness at a 2 km scales **A.** Cerrado denser formations (Brazilian savanna). **B.** Riparian forest. Fitted values ( $R^2$  is adjusted  $R^2$ , p-value is for smooth's parametric F-test): Cerrado:  $p = 0.04$ ,  $F = 4.25$ ,  $R^2 = 0.34$ ; Riparian:  $P = 0.01$ ,  $F = 6$ ,  $R^2 = 0.26$ .



**Fig. S5 A.** Histogram of residuals of a piecewise model predicting bat richness. **B.** Residuals of the piece-wise model and richness in function of fitted values at a scale of 2 km around landscape centroid.

## CONCLUSÃO

A presente dissertação apresenta quatro considerações principais:

- 1) **Limiar da fragmentação:** Encontramos um limiar da fragmentação para morcegos em 47% de habitat remanescente na paisagem, acima do valor sugerido pela hipótese de Andrén (1994). Isto corrobora o encontrado por Martensen *et al.* (2012), para aves em paisagens fragmentadas da Mata Atlântica, que também registrou redução significativa para paisagens acima e abaixo (10% e 30%) do limiar de 50% de habitat. Nosso estudo destaca os efeitos da perda de habitat e composição da paisagem em um grupo de animais muito abundantes. Cobertura vegetal nativa, particularmente quantidade cerrado na paisagem, foi importante para explicar variação da abundância de dois grupos mais sensíveis à fragmentação: morcegos da subfamília Phyllostominae e nectarívoros. Sugerimos que limiares em características bióticas em resposta às características da paisagem devem ser amplamente investigados, a fim de entender claramente efeitos da perda de habitat sobre a distribuição e persistência das espécies e de processos ecológicos. Além disso, a perda de espécies pode estar ocorrendo mais severamente abaixo de um nível limiar, mas isso não exclui que a perda de espécies esteja ocorrendo em áreas com maiores níveis de quantidade habitat (Mönkkönen and Reunanen 1999), uma vez que outros mecanismos podem levar à perda de espécies (Turner *et al.* 1989 , Chapín *et al.*, 2000). Além disso, até mesmo um alto valor de limiar pode estar subestimando a magnitude em que ocorre a perda de espécies em paisagens fragmentadas. Os padrões observados podem contribuir para ampliar o conhecimento preditivo das consequências de alterações na paisagem para os animais.
- 2) **Efeito das escalas espaciais:** Observamos que morcegos filostomídeos em geral respondem em escalas mais finas (1 km no entorno dos pontos amostrais) às características de paisagens fragmentadas. Além disso, grupos troficamente similares, como pequenos e grandes frugívoros, responderam de forma bem semelhante às características da paisagem.

- 3) **Frugívoros na borda:** A quantidade de borda pode ser um fator determinante na ocorrência de frugívoros, o que pode estar associado a uma maior disponibilidade de frutos quiropterocóricos na paisagem. Essa resposta nos faz repensar a importância de diferentes tipos de habitat na paisagem para o grupo. O que será mais importante para morcegos frugívoros e como pensar em conectividade da paisagem para este grupo? Talvez morcegos frugívoros dependam em certo grau ou estejam se beneficiando da presença de vegetação pioneira na paisagem em proporções similares a matas ripárias e mais preservadas. Neste caso, estudar o processo de *landscape complementation* para esse grupo pode contribuir para o entendimento do papel dos morcegos frugívoros na restauração florestal, já que estes morcegos desempenham amplamente a dispersão de sementes em áreas degradadas (Lobova et al. 2009).
- 4) **Animalívoros, nectarívoros e conectividade:** Animalívoros e nectarívoros mostraram-se os mais sensíveis à fragmentação. Ainda que muitas espécies de nectarívoros sejam abundantes, a presença desse grupo e de animalívoros na paisagem pode ser um indicador de integridade ecossistêmica. Dessa maneira, esses grupos devem ser bons modelos para se estudar negativos efeitos da fragmentação em animais ou processos ecológicos, como a polinização, no caso de nectarívoros. A conectividade do habitat na paisagem foi um fator importante para explicar a abundância de animalívoros na paisagem. Sendo assim, sugerimos que mais estudos explorando essa característica de configuração da paisagem devem ser feitos, tendo em vista a sensibilidade desse grupo à perda de habitat e a suas respostas positivas a quantidade de vegetação nativa.

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