

**UNIVERSIDADE FEDERAL DE GOIÁS**  
**INSTITUTO DE CIÊNCIAS BIOLÓGICAS**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO**

Poliana Mendes

**Consequências da perda e fragmentação de habitat em morcegos**

Tese apresentada à Universidade Federal de Goiás como parte das exigências do programa de Pós-graduação em Ecologia e Evolução para obtenção do título de doutor.

Orientador: Dr. Paulo De Marco Júnior

Goiânia, Goiás

Maio, 2015

Poliana Mendes

Consequências da perda de habitat e fragmentação em morcegos

Tese apresentada à Universidade Federal de Goiás como parte das exigências do programa de Pós-graduação em Ecologia e Evolução para obtenção do título de doutor.

Banca avaliadora:

---

Prof. Dr. Daniel Brito

Banca avaliadora

---

Prof. Dr. Rafael Loyola

Banca avaliadora

---

Prof. Dr. Milton C. Ribeiro

Banca avaliadora

---

Prof. Dr. Adriano Paglia

Banca avaliadora

---

Dr. Paulo De Marco Júnior

Orientador- presidente da banca avaliadora

Goiânia, Goiás

Maio, 2015

A todas as pequenas criaturas  
voadoras que foram abduzidas  
para a criação dessa tese, o meu  
perdão e agradecimento.

*“Twinkle, twinkle, little bat!  
How I wonder what you're at!  
Up above the world you fly,  
Like a tea tray in the sky.”*

Lewis Carroll em Alice no País das Maravilhas

## AGRADECIMENTOS

Quatro anos (mais três meses de prorrogação) são suficientes para receber ajuda de um grande número de pessoas e instituições. Primeiramente gostaria de agradecer a Universidade Federal de Goiás (UFG) e o Programa de Pós-graduação em Ecologia e Evolução (PPGEE), pela oportunidade de desenvolver essa tese e pela estrutura física e intelectual oferecida. Agradeço ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pela bolsa de doutorado, e à Coordenação de aperfeiçoamento de pessoal de nível Superior (CAPES) pela bolsa de doutorado-sanduche no exterior. Agradeço também aos membros da banca por aceitarem o convite de usarem horas de seus trabalhos para avaliar e se possível dar sugestões para a melhora desse trabalho.

O trabalho de campo realizado contou com ajuda financeira e pessoal de diversas fontes. O trabalho de campo recebeu auxílio financeiro do CNPq (várias fontes), PPGEE, International Foundation for Science (IFS) e Anglo American. Agradeço ao Instituto Chico Mendes pela emissão das licenças para o trabalho de campo. Agradeço também a todos os proprietários que gentilmente permitiram a realização dos trabalhos de campo, mesmo sabendo que iríamos passar de madrugada na propriedade acordando todos os animais da vizinhança. Também agradeço ao diretor da FLONA de Silvânia e da PARNA Emas junto ao projeto PELD que além de permitirem a realização do estudo ofereceram locais para a estadia durante as pesquisas. Ao Renato César de Miranda, diretor da FLONA de Silvânia, que ainda permitiu a minha participação na reunião sobre a elaboração do plano de manejo do Parque, além de incentivar a realização de uma pequena apresentação sobre os morcegos da FLONA para os proprietários rurais da região.

Algumas pessoas auxiliaram desde os primeiros passos do planejamento da amostragem até todos os problemas que surgiram no campo, dentre eles: Prof. Dr. Arthur A. Bispo, Shayana de Jesus e Paulo Vitor S. Bernardo. À Shayana e Paulinho, eu tenho muita sorte de ter encontrado vocês para dividir todas as alegrias e tensões desse trabalho de campo. Espero que vocês tenham a mesma

sensação de alívio, e também muitos artigos sobre os passarinhos. Agradeço a todas as pessoas que me auxiliaram nos trabalhos de campo, mas claro, com uma atenção especial ao Bruno C. Gomes, Pedro. H. C. Ramos, Cláudia W. Sobral, Pedro H. P. Braga e Lucas Camargos. Ao Dr. Rogério Bastos por gentilmente disponibilizar ajuda para os primeiros (e mais difíceis) campanhas. Agradeço aos pesquisadores que me deram importantes sugestões em 2011, quando ainda estava planejando como seria esse trabalho. Agradeço especialmente a Dra. Kimberly With que cedeu uma tarde de trabalho para me dar uma aula particular sobre ocupação, e por pacientemente iluminar a minha imatura proposta para o segundo capítulo. A Luciana, por me ensinar e me ajudar a cada dúvida sobre as análises de ocupação do segundo capítulo e também por topar essa parceria. Agradeço também Lilian Salles que pacientemente me deu sugestões sobre as análises de ocupação.

Agradeço a todo o pessoal do laboratório TheMetaland da UFG que me abrigou e me ensinou durante muitos anos. A todos que participaram da apresentação do meu projeto de tese em 2011 ou 2012 pelas sugestões e críticas. André pela ajuda na avaliação dos modelos de distribuição de espécie. Camila pelas dicas para o capítulo 3. Daniel pela leitura e comentários sobre o projeto de tese, qualificação, dentre outros textos e auxílio na busca por agências financiadoras. Renata pela leitura e correções da apresentação. Pedro H. P. Braga pela leitura e comentários de diversos projetos, textos, manuscritos e do terceiro capítulo da tese. A Sarah pelas valiosas dicas para o terceiro capítulo. Francine pelas conversas e companheirismo no laboratório. A Livia, por ler e cuidadosamente me ajudar a corrigir o terceiro capítulo. Ao Bruno, Pedro e Cláudia pelo imenso prazer de tentar introduzi-los ao mundo dos morcegos e por tudo que me ensinaram. Agradeço especialmente ao chefe do laboratório e orientador Paulo De Marco Jr. que pacientemente cuidou do meu doutorado, e nunca reclamou de mim, mesmo quando poderia. O Paulo é um exemplo de sensibilidade e preocupação com o próximo e com o mundo. Essa preocupação é focada em melhorar as pessoas e o mundo que o cerca, e gera um peso de responsabilidade muito grande em seus pensamentos. Agradeço a esta pessoa por ser um exemplo de cientista e agente de mudança.

Agradeço pelas gentis recomendações e sugestões ao desenvolvimento da tese. Por ter investido, tempo e dinheiro nessa idéia inicial de analisar os efeitos da fragmentação em morcegos. Agradeço também, por todas as conversas sobre o papel da ciência no mundo que nos cerca.

Também agradeço ao pessoal do “Geomatic and Landscape Ecology Lab (GLEL)” da Carleton University que me recebeu de braços abertos. Todos os “Friday meetings” foram de muita importância, assim como o aprendizado sobre uma segunda língua e sobre como sobreviver em temperaturas abaixo de -25°C. Um agradecimento especial a Genevieve, Ludmila (Luge), Sandra, Ivan, Fernandinha, Sarah, Paul e Alex, que tornaram a minha estadia no Canadá muito mais agradável do que eu poderia imaginar. Luge, por favor, fique longe de xícaras de chá. Agradeço também a Dra. Lenore Fahrig, orientadora do doutorado sanduiche, pelas valiosas dicas de como desenvolver uma pesquisa científica, como escrever um trabalho científico e principalmente por mostrar que é possível ser muito produtivo cientificamente e ainda fazer diferença em questões ecológicas essencialmente práticas, mesmo que eu não tenha conseguido absorver todas estas dicas ainda.

Aos grandes amigos que fiz em Goiânia, alguns continuam por aqui, outros já estão longe. Camila pela companhia em casa e no trabalho, por ser essa grande amiga, que já estou sentindo falta, desejo a ela muitas felicidades em Manaus. Livia, por sempre estar disposta a oferecer um ombro amigo mesmo com tese de doutorado e a Nalu para cuidar, por todas as longas conversas que já mudaram minha forma de ver a vida. Pedro, o mais chato de todos os amigos, mas que não consigo me desgrudar, aquele me perseguiu por 8.000 km, mas se esqueceu de voltar ao Brasil comigo, dois metros de altura não cabem todas as suas qualidades, obrigada pela amizade. Paulo Vitor, por me manter atualizada sobre todas as novidades da moda e Hollywood, e por todos os divertidos sextas e sábado à noite com ele e a Camis. Luciana, a mais doce de todas, também morando em terras distantes, aquela que prepara a melhor caipirinha do mundo, e olha que não gosto de caipirinha, por sentir falta dela, quero a visitar novamente no Goiás americano. Solana, que agora está morando em

Belém, aquela que me salvou de uma crise alérgica, e sempre foi uma querida amiga. Agradeço também a Ana Paula, que inicialmente seria só uma professora de inglês, mas, além disso, é psicóloga, conselheira, consultora de viagens ao exterior e ainda acalma pessoas desesperadas. Ao Cadu, que cuida tão bem da Camis, e me aceitou como vela durante tanto tempo, um ótimo roommate, desejo toda a felicidade nessa nova etapa da vida em Manaus. Welma, uma amizade mais nova e não menos importante, por todas as conversas sobre o sentido da vida, por todo apoio de final de tese, prometo que vou ao passeio ciclístico assim que defender. Renata, que também está longe, obrigada pela amizade. Franciele, por ser sempre tão prestativa e preocupada, uma amiga que tenho muito carinho, mesmo não conseguindo a ver com frequência.

Agora eu tenho que agradecer aos amigos antigos, aqueles que me fizeram vir morar no centro do Brasil. Agradeço a Monik, minha primeira orientadora, aquela que me conhece há 10 anos, me fez decidir trabalhar com morcegos. Sempre me ajudou e me apoiou em todas as etapas da minha vida acadêmica e pessoal. Pela leitura e comentários do segundo capítulo. Pela amizade incondicional, pelas viagens a Brasília, pela admirável bondade em ajudar todos esses gatinhos e cachorros abandonados por humanos. Agradeço também ao Daniel, que me incentivou e motivou a vir para Goiânia, pela orientação no mestrado, por todas as contribuições que recebo da sua parte desde a graduação no Espírito Santo. Por último, os agradecimentos pessoais e especiais. Agradeço a minha mãe pelo apoio incondicional, mesmo quando faço tudo ao contrário do que ela gostaria. Por sempre me trazer a realidade, quando eu me afasto da mesma. Por ter sido impressionantemente paciente comigo nos últimos meses, com o meu atraso na entrega da tese, com o atraso em ter um emprego, e pela pouca ajuda que dei durante a vida adulta, obrigada por não ter me cobrado nada. Agradeço também ao Benjamin pelos 10 meses de companheirismo que parecem anos, pela correção do inglês de todos esses capítulos, que deviam parecer muito chatos, mas ele sempre disse que são muito interessantes. Agradeço também por todo o apoio e incentivo, por ter me suportado, espero que ele já consiga ler esse agradecimento em português.

## SUMÁRIO

APRESENTAÇÃO .....	1
RESUMO .....	3
ABSTRACT .....	4
INTRODUÇÃO GERAL .....	5
Consequências da perda de habitat e fragmentação em morcegos....	<b>Erro! Indicador não definido.</b>
Referências .....	8
CHAPTER 1: Multiscale effects of landscape composition and configuration on bat abundance, richness and variance in biological traits .....	11
Abstract .....	12
Introduction .....	13
Methods .....	18
Overview .....	18
Study area and site selection.....	19
Landscape classification and explanatory variables .....	21
Bat sampling .....	22
Response variables .....	22
Statistical analyses .....	23
Potential confounding variables .....	25
Results .....	26
Discussion .....	34
Acknowledgements .....	38
References .....	38
CHAPTER 2: The relative importance of local and landscape variables on bat occupancy .....	55
Abstract .....	56
Introduction .....	57
Methods .....	61
Overview .....	61
Study area .....	62
Bat sampling and species selected.....	62
Predictor variables .....	63
Detection bias .....	64

Occupancy models.....	68
Results .....	69
Discussion .....	77
References .....	83
CHAPTER 3: Bat species vulnerability to land-use changes in Cerrado: integrating climatic suitable areas with deforestation data at a landscape scale .....	94
Abstract .....	95
Introduction .....	96
Methods.....	100
Overview .....	100
Occurrence data .....	100
Ecological niche modeling .....	102
Deforestation data.....	103
Exposure and Sensitivity scenarios .....	103
Empirical-derived sensitivity scenario .....	106
Results .....	107
Discussion .....	116
Acknowledges .....	120
References .....	121
CONSIDERAÇÕES FINAIS.....	127

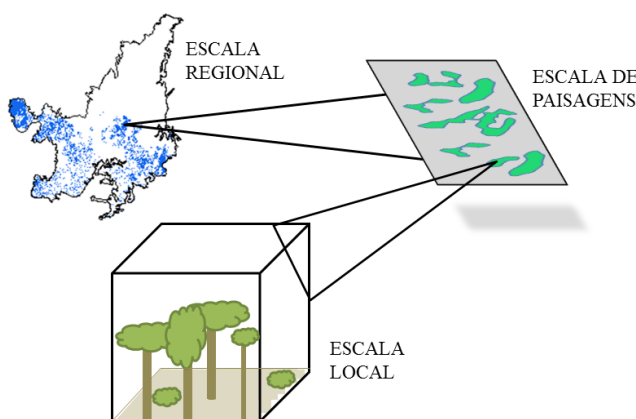
## 1 APRESENTAÇÃO

3 *“The scale of an investigation may have profound effects*  
4 *on the patterns one finds”* Wiens, 1989

6 A distribuição das espécies no espaço tanto geográfico quando ecológico poderia ser  
7 observada por lentes com poder de resolução e abertura óptica diferentes. Com maior abertura e  
8 menor resolução poderíamos ver, por exemplo, se a ocorrência de uma espécie de morcego  
9 insetívoro no continente americano está relacionada à temperatura média anual dessa região.  
10 Com menor abertura e maior resolução poderíamos observar se essa espécie tem preferência por  
11 forragear próximo a rios de águas calmas, em vez de turbulentas, pois isso significa menos ruídos,  
12 interferindo na detecção de insetos por ecolocalização. O primeiro exemplo estaria em uma escala  
13 regional, enquanto que o segundo, em uma escala local. A escala da paisagem é intermediária entre  
14 as duas citadas acima. Uma paisagem é grande o suficiente para abrigar vários elementos locais  
15 como, por exemplo, fragmentos com diferente uso do solo, e ao mesmo tempo ter resolução grande o  
16 bastante para permitir a distinção entre esses elementos (Figura 1).

17 Dentro desse contexto essa tese tem como foco principal explorar as consequências das  
18 mudanças que ocorrem nas paisagens sobre a ótica da diversidade de morcegos. **No primeiro**  
19 **capítulo**, foram explorados os efeitos das diferenças na estrutura da paisagem sobre a riqueza, a  
20 abundância total e a variação nas características biológicas de morcegos. A estrutura da paisagem,  
21 neste capítulo, foi dividida em dois componentes: a quantidade de habitat e a fragmentação do  
22 habitat. Após explorar como as variáveis na escala de paisagens afetam a diversidade de morcegos, a  
23 escala em que os morcegos estavam sendo observados foi reduzida, no segundo capítulo, para  
24 permitir uma contraposição entre os efeitos das variáveis locais e variáveis da paisagem na ocupação

1 de morcegos. **No segundo capítulo**, verificamos se variáveis locais como densidade de árvores,  
2 altura do sub-bosque, cobertura da copa e presença de lianas contrapostas à variáveis da paisagem  
3 como quantidade e fragmentação de habitat, podem ser preditoras da probabilidade de ocupação de  
4 oito espécies de morcegos em um local. O **terceiro capítulo** foi desenvolvido para todo o bioma  
5 cerrado, com uma visão mais ampla de como áreas climaticamente adequadas, para oito espécies de  
6 morcegos, seriam afetadas por alterações na escala de paisagem relacionadas à perda de habitat e a  
7 fragmentação nessas paisagens. Esses três passos permitiram uma visão diferenciada das ameaças  
8 que os morcegos podem sofrer devido a alterações na escala da paisagem, sem ignorar conexão entre  
9 as escalas e resoluções. Apesar da escala de paisagens ter sido o objeto central desse estudo, a  
10 conexão com múltiplas escalas permite um melhor entendimento dos processos que levam a perda de  
11 espécies e/ou a diminuição da abundância de morcegos decorrente das alterações nas paisagens.



**Figura 1:** A escala regional é representada por um estudo que desenvolveu um modelo de nicho ecológico para uma espécie no bioma Cerrado. A escala de paisagens compara paisagens com diferentes níveis de perda de habitat. A escala local explora características de um dos elementos da paisagem.

## RESUMO

Esse trabalho teve como objetivo explorar alguns componentes das respostas dos morcegos a mudanças na estrutura da paisagem. Morcegos foram amostrados em 18 fragmentos florestais durante quatro noites. Foram delimitadas paisagens com entre 500 metros e 10 km de raio a partir do local de amostragem. Métricas de dois componentes da paisagem foram medidas nestas paisagens: a quantidade de vegetação natural e a fragmentação dessa vegetação (medido como o número de manchas). No primeiro capítulo testamos o efeito desses dois componentes na abundância total, riqueza de espécies e variância em traços biológicos de morcegos. No segundo capítulo verificamos se essas variáveis eram mais importantes do que variáveis locais para determinar a probabilidade de ocupação de oito espécies de morcegos. As variáveis locais foram obtidas em três quadrantes no local de amostragem de morcegos, onde se obteve a densidade de árvores, altura do sub-bosque, quantidade de lianas e, cobertura do dossel. No terceiro capítulo, a adequabilidade climática das espécies no Cerrado foi contraposta com dados espacializados da quantidade de vegetação natural e fragmentação. Essa contraposição teve como o objetivo prever a vulnerabilidade de espécies se elas fossem sensíveis a um limiar de perda de habitat ou fragmentação na paisagem, além de mostrar de forma geral a exposição às mudanças na paisagem das áreas climaticamente adequadas para oito espécies de morcegos. Observa-se, de uma forma geral, padrões idiossincráticos de respostas a perda de habitat e fragmentação em morcegos. A abundância total é positivamente relacionada com a quantidade de habitat, enquanto que a riqueza de espécies, a variância na massa corporal e o número de guildas são negativamente relacionados com a fragmentação. A probabilidade de ocupação de *Sturnira lilium* é positivamente relacionada com a quantidade de habitat, enquanto que a probabilidade de ocupação de *Myotis nigricans* é negativamente relacionada com a fragmentação. Outras seis espécies não mostraram uma clara relação da probabilidade de ocupação com a estrutura da paisagem. Áreas do sul do Cerrado são locais com maiores valores de adequabilidade e, ao mesmo tempo, maiores exposições às mudanças na paisagem. Os resultados dos três capítulos fortalecem uma visão na literatura de que o padrão de respostas das espécies de morcegos à perda de habitat e fragmentação é específico para a espécie e para o componente de diversidade medido. Esta afirmação reforça o argumento de que um maior conhecimento sobre os fatores que determinam essas respostas é necessário, porém não inviabiliza o desenvolvimento de estratégias regionais de conservação utilizando o conhecimento já disponível na literatura.

## 1 ABSTRACT

2

3 Our aim was to explore some components of bat responses to land-use changes. Bats were sampled  
4 in 18 forest patches during four nights. Landscapes were delimited with 500 meter to 10km radius  
5 from sample site. We took metrics of two different landscape components: natural vegetation amount  
6 and fragmentation (measured as number of patches). In the first chapter we tested the effect of such  
7 components in total abundance, species richness and variance in biological traits of bats. In the  
8 second chapter we verified if those variables were more important than local ones to determine  
9 occupancy probability of eight bat species. Local variables were tree density, understory height, liana  
10 quantity, and canopy cover. In the third chapter we counterposed species climatic suitable areas with  
11 spatial data about habitat loss and fragmentation in Cerrado. We predicted species vulnerability  
12 creating scenarios in which they were sensitive to habitat loss and/or fragmentation, furthermore we  
13 showed an overview of species suitable areas exposure to land-use changes to eight bat species. We  
14 observed idiosyncratic patterns of responses to habitat loss and fragmentation in bats. Abundance is  
15 positively related to habitat amount, whereas species richness, variance in body mass and number of  
16 guilds is negatively related to fragmentation. Occupancy probability of *Sturnira lilium* is positively  
17 related to habitat amount, whereas occupancy probability of *Myotis nigricans* is negatively related to  
18 fragmentation. Six other species did not show any clear relationship between occupancy and  
19 landscape structure. South areas of Cerrado are locales with higher climatic suitability, while still  
20 having higher exposure level to land-use changes. Our results strengthen the view that species  
21 response patterns to habitat loss and fragmentation are species-specific and also diversity metric  
22 specific. Such assertion reinforces that it is necessary an improvement in knowledge about factors  
23 that determine those responses, however it does not mean that the development of regional  
24 conservation strategies is unfeasible when using the current available knowledge in literature.

## 1 INTRODUÇÃO GERAL

2  
3 Os efeitos da expansão da exploração do solo sob as espécies foram amplamente abordados,  
4 utilizando o arcabouço teórico do equilíbrio insular, na Biogeografia (Haila 2002). Segundo esse  
5 arcabouço, o tamanho das manchas de habitat e o isolamento das mesmas são tratados como as  
6 principais variáveis explanatórias do impacto das mudanças do uso da terra sob as espécies. Esta  
7 abordagem permitiu um grande avanço no entendimento das consequências da expansão agrícola nas  
8 comunidades naturais. Entretanto, um problema questionado na literatura com relação a essa  
9 abordagem é o pressuposto de que a mancha possui uma comunidade delimitada (Fahrig 2013;  
10 Ricklefs 2008), por considerar eventos de imigração e emigração entre manchas de habitat, mas não  
11 movimentos diários ou sazonais entre as manchas. Recentemente, a proposta de que os efeitos do uso  
12 da terra deveriam ser abordados na escala da paisagem ao invés da escala da mancha tem recebido  
13 cada vez mais atenção (Fahrig 2013), embora ainda seja tema de controvérsias.

14 A ecologia de paisagens tem como principal objetivo a compreensão dos efeitos da estrutura  
15 das paisagens sobre a biodiversidade (Turner 2005). A estrutura das paisagens poderia ser dividida  
16 em dois componentes principais: composição e configuração da paisagem (Fahrig 2005). A  
17 composição da paisagem é a proporção relativa de elementos da paisagem; por exemplo, cobertura  
18 florestal ou quantidade de rodovias. A configuração da paisagem é a distribuição desses elementos  
19 na paisagem, por exemplo, número de fragmentos e a forma dos fragmentos. Sendo assim, a perda de  
20 habitat representa uma mudança na composição da paisagem, enquanto que a fragmentação, ou a  
21 subdivisão do habitat, representa uma mudança na configuração da paisagem. A expansão do uso da  
22 terra por humanos é um dos principais causadores de perda de espécies no mundo (Murphy &  
23 Romanuk 2014). Essa expansão é acompanhada tanto pela perda de habitat

quanto pela fragmentação de habitat, porém existe alguma polêmica na literatura sobre os efeitos desses dois componentes em separado nas comunidades (Fahrig 2013; Villard & Metzger 2014).

Como consequência das tendências citadas acima, estudos sobre os efeitos das mudanças no uso do solo nas espécies de morcegos estão repletos de uma miscelânea de conceitos, métodos, métricas de paisagem e escalas. Muitos estudos compararam a diversidade de morcegos em áreas contínuas, fragmentos e na matriz antropizada (Estrada & Coates-estrada 2002; Faria *et al.* 2006; Henry *et al.* 2007; Medellín *et al.* 2000). Estes estudos reuniram importantes informações sobre a permeabilidade da matriz e sobre preferências de habitat para morcegos, mas tiveram grandes divergências nos resultados, tanto para diferentes táxons, quanto para diferentes localidades. García-Morales *et al.* (2013), em uma meta-análise sobre o tema encontrou poucos padrões que pareciam congruentes, um exemplo é que morcegos insetívoros e carnívoros são mais dependentes de ambientes florestais do que frugívoros e nectarívoros. Nos últimos anos houve uma tendência<sup>1</sup> de desenvolvimento de estudos utilizando a escala da mancha, da paisagem ou ambas para avaliar os efeitos da fragmentação e perda de habitat nos morcegos (e.g. Cisneros *et al.* 2014; Duchamp & Swihart 2008; Ethier & Fahrig 2011; Mendenhall *et al.* 2014). Novamente, esses estudos mostraram resultados com grandes disparidades, dificultando a obtenção de uma regra geral para o efeito das mudanças nas paisagens nos morcegos. A grande quantidade de métricas de estrutura de paisagens disponíveis aumenta ainda mais a diversidade de possíveis resultados.

Efeitos positivos da quantidade de habitat em comunidades de morcegos são encontrados frequentemente (Avila-Cabadilla *et al.* 2012; Duchamp & Swihart 2008; Ethier & Fahrig 2011; Ripperger *et al.* 2013), apesar de comuns os estudos que mostram nenhum efeito dessa variável ou

<sup>1</sup> tendências nos estudos sobre os efeitos da mudança na estrutura da paisagem em morcegos foram avaliadas através de uma busca na base de dados “ISI Web of Science” (Institute for Scientific Information), utilizando as palavras-chave: “‘bat OR bats OR Chiroptera’ AND ‘fragmentation OR habitat loss OR land-use OR landscape\*’”, para os últimos 10 anos (entre 2004 e 2015). Foram encontrados 1124 estudos, mas após uma avaliação cuidadosa, restaram somente 42 trabalhos empíricos sobre o tema.

1 mesmo efeitos negativos (Klingbeil & Willig 2010; Mendenhall *et al.* 2014). Na ausência de uma  
2 relação positiva da quantidade de habitat com a abundância ou riqueza de espécies, as explicações  
3 mais comuns englobam o possível uso da matriz como fonte de recursos pela espécie e uso das  
4 bordas como fonte de recursos. Efeitos negativos e positivos da fragmentação em morcegos são  
5 encontrados em uma frequência similar entre os estudos (Ethier & Fahrig 2011; Frey-Ehrenbold *et*  
6 *al.* 2013; Gorresen *et al.* 2005). Efeitos negativos são associados com sensibilidade à borda,  
7 dependência de fragmentos grandes ou baixa capacidade de atravessar a matriz para explorar a  
8 paisagem (Klingbeil & Willig 2010). Efeitos positivos incluem o aumento da heterogeneidade da  
9 paisagem que pode contribuir para um aumento dos recursos ou mesmo a diminuição da distância  
10 entre recursos (Ethier & Fahrig 2011). Essa variedade de resultados é ainda mais interessante quando  
11 notamos que a maioria dos estudos empíricos<sup>1</sup> sobre os efeitos das mudanças no uso da terra em  
12 morcegos foram realizados com dados da região Neotropical (e.g. Cisneros *et al.* 2014; Gorresen *et*  
13 *al.* 2005; Klingbeil & Willig 2010; Mendenhall *et al.* 2014).

14 Um problema adicional nos estudos que usam a escala da paisagem é a delimitação do  
15 tamanho da paisagem em questão. Uma solução interessante ao problema é o uso de um tamanho de  
16 paisagem que faça sentido com o organismo em questão, e que seja congruente com o tamanho da  
17 área de vida (Jackson & Fahrig 2012). Outra solução é utilizar múltiplas escalas de forma a encontrar  
18 a melhor escala para relacionar variáveis da paisagem com o organismo (Martin & Fahrig 2012). Os  
19 estudos com morcegos têm grandes diferenças no tamanho das paisagens medidas<sup>1</sup>, desde 100  
20 metros até 25 km de raio (Frey-Ehrenbold *et al.* 2013; López-González *et al.* 2014). Os estudos que  
21 avaliaram várias escalas mostraram resultados divergentes para diferentes escalas, enfatizando a

<sup>1</sup> tendências nos estudos sobre os efeitos da mudança na estrutura da paisagem em morcegos foram avaliadas através de uma busca na base de dados “ISI Web of Science” (Institute for Scientific Information), utilizando as palavras-chave: “‘bat OR bats OR Chiroptera’ AND ‘fragmentation OR habitat loss OR land-use OR landscape\*’”, para os últimos 10 anos (entre 2004 e 2015). Foram encontrados 1124 estudos, mas após uma avaliação cuidadosa, restaram somente 42 trabalhos empíricos sobre o tema.

1 possibilidade da existência de resultados espúrios em estudos que podem ter utilizado escalas não  
2 adequadas.

3 Variáveis ambientais medidas na escala da paisagem ou local podem ter um poder de  
4 explicação maior do que variáveis climáticas na diversidade de morcegos (Estrada-Villegas *et al.*  
5 2012; López-González *et al.* 2014; Mehr *et al.* 2011). Estas evidências reforçam a importância do  
6 entendimento de como os morcegos respondem as mudanças atuais no uso do solo e qualidade de  
7 habitat. As mudanças no uso do solo incluem a diminuição da quantidade de habitat e fragmentação  
8 do mesmo na paisagem (tratadas anteriormente). A qualidade de habitat é espécie-dependente e pode  
9 incluir a cobertura do dossel, quantidade de árvores frutíferas, quantidade de abrigos disponíveis ou  
10 menor número de obstáculos para o voo (Estrada-Villegas *et al.* 2012; Scott *et al.* 2010). A  
11 importância relativa de variáveis locais e da paisagem nas comunidades de morcegos é ainda pouco  
12 explorada na literatura (e.g. Estrada-Villegas *et al.* 2012), mas de profunda importância para o  
13 entendimento da distribuição dos morcegos na paisagem.

14 A aplicação do conhecimento sobre o efeito da estrutura da paisagem nas espécies em  
15 estratégias regionais de conservação permitirá um considerável avanço nas técnicas de manejo para a  
16 conservação e priorização de regiões (Opdam & Wascher 2004). Alguns avanços já têm sido feitos  
17 integrando processos regionais com quaisquer dados sobre a estrutura da paisagem (Betts *et al.* 2014;  
18 Dawson *et al.* 2011; Faleiro *et al.* 2013; Reino *et al.* 2013), mas essa ainda é uma das áreas de estudo  
19 que deve se expandir no futuro próximo (Haddad *et al.* 2015). Ela depende, primeiramente, da  
20 obtenção de dados concisos sobre limiares de sensibilidade das espécies à mudanças na estrutura das  
21 paisagens, o que já representa um desafio para os estudos. Além disso, o desenvolvimento de  
22 técnicas metodológicas que permitam uma associação entre fatores que atuam em diferentes escalas  
23 é necessário para operacionalizar uma associação entre mudanças em escalas regionais e da  
24 paisagem, como modelos de distribuição de espécies (e.g. Elith *et al.* 2006) e dados de uso de solo  
25 (e.g. Sano *et al.* 2010).

## 1    **Referências**

- 2    Avila-Cabadilla LD, Sanchez-Azofeifa GA, Stoner KE, *et al.*, 2012. Local and landscape factors  
3        determining occurrence of phyllostomid bats in tropical secondary forests. *PLoS ONE*, 7(4).
- 4    Betts MG, Fahrig L, Hadley AS, *et al.*, 2014. A species-centered approach for uncovering  
5        generalities in organism responses to habitat loss and fragmentation. *Ecography*, 37(6):517–  
6        527.
- 7    Cisneros LM, Fagan ME & Willig MR, 2014. Effects of human-modified landscapes on taxonomic,  
8        functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*,  
9        21:523–533.
- 10   Dawson TP, Jackson ST, House JI, Prentice IC & Mace GM, 2011. Beyond predictions: biodiversity  
11        conservation in a changing climate. *Science (New York, N.Y.)*, 332(6025):53–58.
- 12   Duchamp JE & Swihart RK, 2008. Shifts in bat community structure related to evolved traits and  
13        features of human-altered landscapes. *Landscape Ecology*, 23(7):849–860.
- 14   Elith J, Graham CH, Anderson RP, *et al.*, 2006. Novel methods improve prediction of species’  
15        distributions from occurrence data. *Ecography*, 29(2):129–151.
- 16   Estrada A & Coates-estrada R, 2002. Bats in continuous forest , forest fragments and in an  
17        agricultural mosaic habitat-island at Los Tuxtlas , Mexico. *Biological Conservation*, 103:237–  
18        245.
- 19   Estrada-Villegas S, McGill BJ & Kalko EK V, 2012. Climate, habitat, and species interactions at  
20        different scales determine the structure of a Neotropical bat community. *Ecology*, 93(5):1183–  
21        93.
- 22   Ethier K & Fahrig L, 2011. Positive effects of forest fragmentation, independent of forest amount, on  
23        bat abundance in eastern Ontario, Canada. *Landscape Ecology*, 26(6):865–876.
- 24   Fahrig L, 2005. When is a landscape perspective important? In JA Wiens & MR Moss (eds.), *Issues*  
25        *and perspectives in landscape ecology*. . 1<sup>o</sup> ed., Cambridge University Press, p. 3–10.
- 26   Fahrig L, 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of*  
27        *Biogeography*, 40(9):1649–1663.
- 28   Faleiro F V, Machado RB & Loyola RD, 2013. Defining spatial conservation priorities in the face of  
29        land-use and climate change. *Biological Conservation*, 158:248–257.
- 30   Faria D, Laps RR, Baumgarten J & Cetra M, 2006. Bat and Bird Assemblages from Forests and  
31        Shade Cacao Plantations in Two Contrasting Landscapes in the Atlantic Forest of Southern  
32        Bahia, Brazil. *Biodiversity and Conservation*, 15(2):587–612.
- 33   Frey-Ehrenbold A, Bontadina F, Arlettaz R & Obrist MK, 2013. Landscape connectivity, habitat  
34        structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*,  
35        50(1):252–261.

- 1    García-Morales R, Badano EI & Moreno CE, 2013. Response of Neotropical Bat Assemblages to  
2        Human Land Use. *Conservation biology : the journal of the Society for Conservation Biology*,  
3        00(0):1–11.
- 4    Gorresen PM, Willig MR & Strauss RE, 2005. Multivariate analysis of scale-dependent associations  
5        between bats and landscape structure. *Ecological applications*, 15(6):2126–2136.
- 6    Haddad NM, Brudvig LA, Clobert J, *et al.*, 2015. Habitat fragmentation and its lasting impact on  
7        Earth’s ecosystems. *Science Advances*, 1(2):1–9.
- 8    Haila Y, 2002. A conceptual genealogy of fragmentation research: From island biogeography to  
9        landscape ecology. *Ecological Applications*, 12(2):321–334.
- 10   Henry M, Cosson J-F & Pons J-M, 2007. Abundance may be a misleading indicator of  
11        fragmentation-sensitivity: The case of fig-eating bats. *Biological Conservation*, 139(3-4):462–  
12        467.
- 13   Jackson HB & Fahrig L, 2012. What size is a biologically relevant landscape? *Landscape Ecology*,  
14        27(7):929–941.
- 15   Klingbeil BT & Willig MR, 2010. Seasonal differences in population-, ensemble- and community-  
16        level responses of bats to landscape structure in Amazonia. *Oikos*, 119(10):1654–1664.
- 17   López-González C, Presley SJ, Lozano A, Stevens RD & Higgins CL, 2014. Ecological  
18        biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta  
19        diversity, and environmental gradients to species richness and composition patterns. *Ecography*,  
20        37:1–12.
- 21   Martin AE & Fahrig L, 2012. Measuring and selecting scales of effect for landscape predictors in  
22        species – habitat models. *Ecological Applications*, 22(8):2277–2292.
- 23   Medellín RA, Equihua M & Amin MA, 2000. Bat Diversity and Abundance as Indicators of  
24        Disturbance in Neotropical Rainforests. 14(6):1666–1675.
- 25   Mehr M, Brandl R, Hothorn T, *et al.*, 2011. Land use is more important than climate for species  
26        richness and composition of bat assemblages on a regional scale. *Mammalian Biology -*  
27        *Zeitschrift für Säugetierkunde*, 76(4):451–460.
- 28   Mendenhall CD, Karp DS, Meyer CFJ, Hadly E a & Daily GC, 2014. Predicting biodiversity change  
29        and averting collapse in agricultural landscapes. *Nature*, 509(7499):213–7.
- 30   Murphy GEP & Romanuk TN, 2014. A meta-analysis of declines in local species richness from  
31        human disturbances. *Ecology and evolution*, 4(1):91–103.
- 32   Norberg UM & Rayner JM V, 1987. Ecological morphology and flight in bats (Mammalia;  
33        Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Society*,  
34        316(1179):335–427.

- 1 Opdam P & Wascher D, 2004. Climate change meets habitat fragmentation: linking landscape and  
2 biogeographical scale levels in research and conservation. *Biological Conservation*,  
3 117(3):285–297.
- 4 Reino L, Beja P, Araújo MB, Dray S & Segurado P, 2013. Does local habitat fragmentation affect  
5 large-scale distributions? The case of a specialist grassland bird. *Diversity and Distributions*,  
6 19(4):423–432.
- 7 Ricklefs RE, 2008. Disintegration of the ecological community. *The American naturalist*,  
8 172(6):741–50.
- 9 Ripperger SP, Tschapka M, Kalko EK V, Rodriguez-Herrera B & Mayer F, 2013. Life in a mosaic  
10 landscape: Anthropogenic habitat fragmentation affects genetic population structure in a  
11 frugivorous bat species. *Conservation Genetics*, 14(5):925–934.
- 12 Sano EE, Rosa R, Brito JLS & Ferreira LG, 2010. Land cover mapping of the tropical savanna  
13 region in Brazil. :113–124.
- 14 Scott SJ, McLaren G, Jones G & Harris S, 2010. The impact of riparian habitat quality on the  
15 foraging and activity of pipistrelle bats ( *Pipistrellus* spp.). *Journal of Zoology*, 280(4):371–378.
- 16 Turner MG, 2005. LANDSCAPE ECOLOGY: What Is the State of the Science? *Annual Review of*  
17 *Ecology, Evolution, and Systematics*, 36(1):319–344.
- 18 Villard M-A & Metzger JP, 2014. REVIEW: Beyond the fragmentation debate: a conceptual model  
19 to predict when habitat configuration really matters. *Journal of Applied Ecology*, 51(2):309–  
20 318.

21

22

1  
2  
3  
4  
5  
6  
7  
8

9   **CHAPTER 1: Multiscale effects of landscape composition and configuration on bat**  
10 **abundance, richness and biological trait variation**

11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27

**Student: Poliana Mendes**  
Programa de Pós-Graduação em Ecologia e Evolução  
Universidade Federal de Goiás  
**Advisor: Dr. Paulo De Marco Júnior**  
Universidade Federal de Goiás  
**Co-advisor (“sandwich” program): Dr. Lenore Fahrig**  
Carleton University

## Abstract

Changes in landscape composition (e.g. habitat loss) and configuration (e.g. fragmentation *per se*) have distinct effects on biodiversity. We predicted: (1) landscape composition has larger effects than landscape configuration on bat abundance and species richness; (2) variance in biological traits should decrease with habitat loss or fragmentation *per se*; (3) the spatial extent of landscape effects (the 'scale of effect') should be larger for effects on bat richness than for effects on bat abundance; and (4) phytophagous bats (frugivores and nectarivores) should show a larger scale of effect than animalivorous bats (carnivores and insectivores). We tested these predictions by sampling bats using mist nets in 18 landscapes in the Cerrado biome, Brazil. We used multi-model inference to compare the effects of habitat loss (measured as the natural vegetation amount) and fragmentation *per se* (measured as number of patches) calculated for six landscape sizes (500m to 10km) on (1) bat total abundance, (2) richness, (3) variance in body mass variance, (4) variance in the ratio wingspan to wing width, (5) variance in the ratio of ear size to body mass and (6) number of feeding guilds. We compared the scale of effect for abundance and species richness, as well as for phytophagous and animalivore abundance. Our first prediction was only partly supported. Bat total abundance was better explained by habitat loss than fragmentation *per se*, being negatively related to it. However, species richness, was negatively related to fragmentation *per se*. Our second prediction was corroborated, variance in body mass, and number of guilds were negatively related to fragmentation *per se*. Our results did not support our third and fourth predictions. Our results suggest that landscape composition is an important predictor of the number of individuals of bats that can reach a site, especially for phytophagous (frugivores and nectarivores), and that configuration affects persistence of some species, particularly carnivores and aerial insectivores. Our results also suggest that the scale of effect of the landscape structure on bats is much larger (~8km radius) than it is commonly used in bat studies. This implies that previous studies have likely under-estimated the effects of landscape structure on bats.

**Keywords:** Chiroptera, Habitat amount, number of patches, filtering hypothesis, scale of effect and Savanna.

## 1 Introduction

2  
3 Natural populations across the world have declined at alarming rates in the past few decades  
4 (Barnosky *et al.* 2011; Dirzo *et al.* 2014), mostly caused by natural habitat conversion to human-  
5 dominated land covers (Murphy & Romanuk 2014). Land conversion is accompanied by  
6 modifications in landscape structure, such as changes in landscape composition (e.g. habitat loss) and  
7 changes in landscape configuration (e.g. fragmentation *per se*) (Fahrig 2003). Habitat loss is widely  
8 recognized as an important impact reducing biodiversity (Cosson *et al.* 1999; Pardini *et al.* 2010;  
9 Quesnelle *et al.* 2013; Thornton *et al.* 2011; Trzcinski *et al.* 1999). Such impact reduces population  
10 sizes through reduced resource availability and environmental heterogeneity, and the resulting  
11 smaller populations are subject to higher local and regional extinction rates. Effects of fragmentation  
12 *per se*, i.e. the breaking up of a given amount of habitat into smaller units, are still controversial and  
13 in general weaker than habitat loss effects; both negative and positive effects have been found.  
14 Positive effects of fragmentation *per se* include increasing environmental heterogeneity, reduced risk  
15 of simultaneous extinction over the whole population, and escape from predators (Den Boer 1968,  
16 1981; Ethier & Fahrig 2011; Fahrig 2013). Fragmentation *per se* is also associated with an increase  
17 in edge density which can have either positive or negative effects depending on the species  
18 (Buchmann *et al.* 2013; Pardini 2004; Ries *et al.* 2004; Thornton *et al.* 2011; Villard & Metzger  
19 2014). Demonstrating the effects of fragmentation *per se* is a challenge because it requires *a priori*  
20 selection of sample sites that control habitat amount while varying fragmentation (e. g. Ethier &  
21 Fahrig 2011; Pasher *et al.* 2013; Silva & De Marco 2014; Trzcinski *et al.* 1999).

22 The ‘habitat amount hypothesis’ suggests that habitat configuration should have relatively  
23 little effect on biodiversity in comparison to habitat amount (Fahrig 2013). This hypothesis is based  
24 on the assumption that habitat patches do not contain bounded communities (Ricklefs 2008) and that  
25 movement through the landscape matrix is common. In this situation habitat loss reduces population

1 sizes and increases extinction, but the specific spatial configuration of that habitat loss is relatively  
2 unimportant. In apparent contrast to this, some studies suggest that habitat fragmentation is an  
3 important predictor of species richness or abundance (Buchmann *et al.* 2013; Henle *et al.* 2004;  
4 Pardini *et al.* 2010; Rueda *et al.* 2013; Thornton *et al.* 2011; Villard & Metzger 2014). However,  
5 most of the empirical evaluation of effects of habitat fragmentation quantified fragmentation in ways  
6 that are confounded with habitat loss, thus making fragmentation effects ambiguous (Fahrig 2003).  
7 For example, patch isolation is often considered to be a measure of habitat ‘configuration’ (e.g.  
8 Estrada-villegas *et al.* 2010; Ockinger *et al.* 2010; Prugh *et al.* 2008; Thomas *et al.* 2001; Thornton *et*  
9 *al.* 2011; Uezu & Metzger 2011). Nonetheless, the observed effects of patch isolation on biodiversity  
10 are likely due to the reduced population sizes caused by habitat loss (Fahrig 2013).

11         The Neotropical region is home to the highest number of bat species in the world  
12 (Mickleburgh *et al.* 2002). Neotropical bats play diverse environmental roles, e.g. as agents of seed  
13 dispersal (Jacomassa & Pizo 2010; Muscarella & Fleming 2007) and pollination (Muchhala 2002),  
14 and in insect population control (Jung & Kalko 2010; Kalka *et al.* 2008; Threlfall *et al.* 2012). Given  
15 these environmental services provided by bats, it is important to build improved understanding of bat  
16 species responses to human-altered landscapes. In addition, as the only flying mammals, bats are  
17 likely better able to cross a human-altered matrix than other similar-sized mammals (Norberg &  
18 Rayner 1987). We might therefore expect that habitat patches do not contain closed bat communities,  
19 and as such Neotropical bats meet the assumption of the habitat amount hypothesis, that habitat  
20 amount should have a larger effect on bat richness than habitat configuration.

21         The filtering hypothesis proposes that in altered locals, for example landscape with high  
22 habitat loss, communities should show lower variance in biological traits such as body mass and diet,  
23 than in undisturbed locals (Holdaway & Sparrow 2006; Petchey *et al.* 2007; Wiescher *et al.* 2012).  
24 This prediction would assume that habitat loss may act as a filter selecting species with traits that  
25 make them able to survive in deforested areas. Such traits might include larger body sizes, generalist

1 feeding habits and higher dispersal ability (Henle *et al.* 2004). Consequently, in disturbed landscapes  
2 a smaller variance in those biological traits should be observed (Flynn *et al.* 2008; Wiescher *et al.*  
3 2012). For bats, we expect lower variance in body size, wing shape (a predictor of dispersal ability),  
4 and food habits with declining habitat amount (Duchamp & Swihart 2008; Jones *et al.* 2003; Meyer  
5 *et al.* 2007). If true, this would suggest an erosion of the ecological services provided by bats in such  
6 landscapes (Flynn *et al.* 2008).

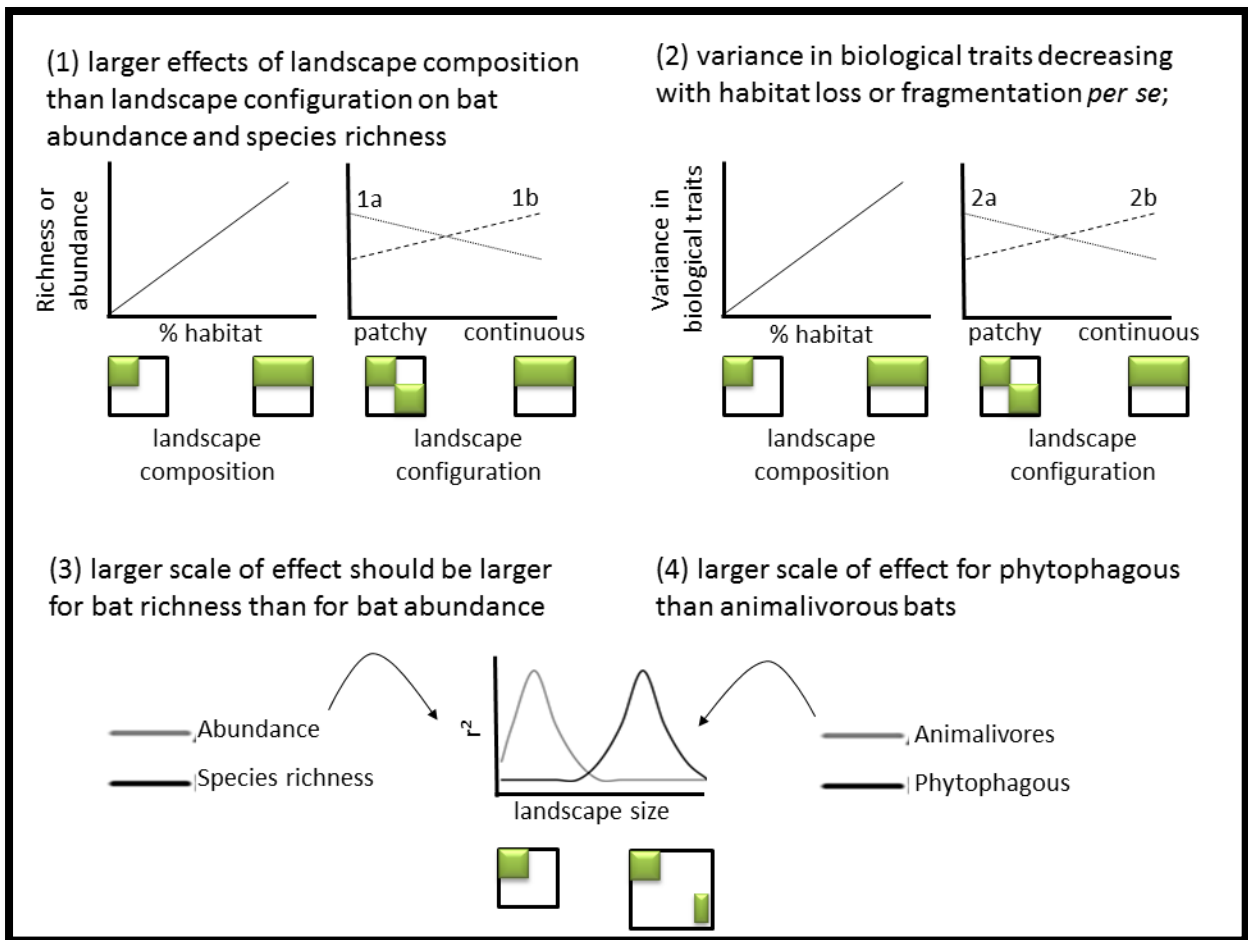
7         The distance within which the landscape structure influences an individual or population is  
8 known as the ‘scale of effect’ of landscape. The scale of effect is expected to increase with the  
9 movement range of the organism, and may be around 4 to 9 times the average movement distance of  
10 a species (Jackson & Fahrig 2012). Bat daily movements are, in general, greater than 1km, and for  
11 some species they reach up to 10km (Aguiar *et al.* 2014; Rollinson *et al.* 2013; Trevelin *et al.* 2013;  
12 Womack *et al.* 2013). As such, we might expect their populations and communities to be affected by  
13 environmental variables at large spatial extents, i.e. they should have a large scale of effect in the  
14 landscape context (e.g. Gorresen *et al.* 2005). Nevertheless, many of the landscape-scale studies on  
15 bats used landscapes with radius less than 5km (e.g. Duchamp & Swihart 2008; Mendenhall *et al.*  
16 2014). We might expect the scale of effect to depend on the biodiversity metric (Jackson & Fahrig  
17 2014), with larger scales for species richness and smaller scales for total abundance. The mechanism  
18 for this prediction is that the influence of the landscape on abundance occurs over a short time-scale  
19 through, immigration from nearby sites. In contrast, species richness is influenced by colonization  
20 and extinction events, which play out over a longer time scale and thus over a larger area (Jackson  
21 and Fahrig 2014).

22         Species that consume scarce or patchy resources are thought to be affected by the landscape  
23 structure over larger scales than species that use abundant or uniformly distributed resources  
24 (O’Neill *et al.* 1988; Wiens 1989), because the former must move farther to obtain required  
25 resources. For Neotropical bats, this suggests that phytophagous bats (frugivores and nectarivores)

should show a larger scale of effect than animalivorous bats (carnivores and insectivores). The food sources of phytophagous bats (fruits and flowers) are scattered in patches (e.g. individual trees) through the forest (Thies & Kalko 2004), and change location due to fruiting and flowering asynchrony (Poulin *et al.* 1999). This food distribution makes phytophagous bats wander widely through the forest searching for fruited or flowered trees (Henry *et al.* 2007). In contrast, animalivorous bats use food resources (small vertebrates and arthropods) that are more abundant and uniformly distributed, resulting in shorter searching movements by these bats. We thus predicted that the scale of effect of the landscape should be larger for phytophagous than for animalivorous.

We constructed four predictions of the effects of natural vegetation cover (a metric of landscape composition) and number of patches (a metric of landscape configuration representing fragmentation *per se*) on Neotropical bat species richness, abundance and variance in biological traits (Figure 1); (1) Natural vegetation cover should affect bat abundance and species richness more strongly than fragmentation *per se* as predicted by the ‘habitat amount hypothesis’. We expect a positive effect of natural vegetation cover, but based on the literature (Cisneros *et al.* 2014; Duchamp & Swihart 2008; Ethier & Fahrig 2011; Klingbeil & Willig 2010) we did not have an a priori prediction of whether the effects of fragmentation *per se* would be negative or positive. (2) Landscapes with lower natural vegetation cover should have communities with less variance in biological traits, such as body mass, wing span, wing width and diet, since this variance is calculated independent of species richness. For fragmentation *per se*, the direction of the effect of fragmentation *per se* on the variance of biological traits could be either positive or negative (Figure 1, part 2a and 2b), (3) Abundance will show a smaller scale of effect than species richness, and (4) Phytophagous bats (frugivores and nectarivores) will show larger scales of effect than animalivorous bats (carnivores and insectivores). These predictions are not independent because they are related to the same general process. For instance, the existence of landscape composition and configuration effects

- 1 on species richness (Prediction 1) suggests the possibility of a filtering process that will control the
- 2 variance of biological traits (Prediction 2).



3

4 **Figure 1-** Four predictions about how bats should respond to amount of natural vegetation (metric of

5 landscape composition) and number of patches (metric of landscape configuration) at different

6 landscape sizes. In the first prediction we expect that abundance and species richness will respond

7 more strongly to the amount of natural vegetation in a landscape than to fragmentation *per se*. Based

8 on the literature (Cisneros *et al.* 2014; Duchamp & Swihart 2008; Ethier & Fahrig 2011; Klingbeil &

9 Willig 2010) we did not have an a priori prediction of whether the effects of fragmentation *per se*

10 would be negative or positive (1a and 1b). In the second, prediction, we expect an increasing of

11 variance in biological traits, independent of species richness, with amount of natural vegetation.

12 However the direction of response to fragmentation *per se* will depend on the whether the effect of

fragmentation *per se* on species richness is negative or positive (2a or 2b). In the third prediction, we expect that the scale of effect of landscape structure, even habitat loss or fragmentation *per se*, on abundance will be smaller than on species richness. In the fourth prediction, we expect that the scale of effect of landscape structure on the abundance of animalivorous (carnivores and insectivores) will be smaller than on phytophagous (frugivores and nectarivores). The scale of effect represents the spatial extent at which the effect of landscape structure (amount of natural vegetation or number of patches) is strongest.

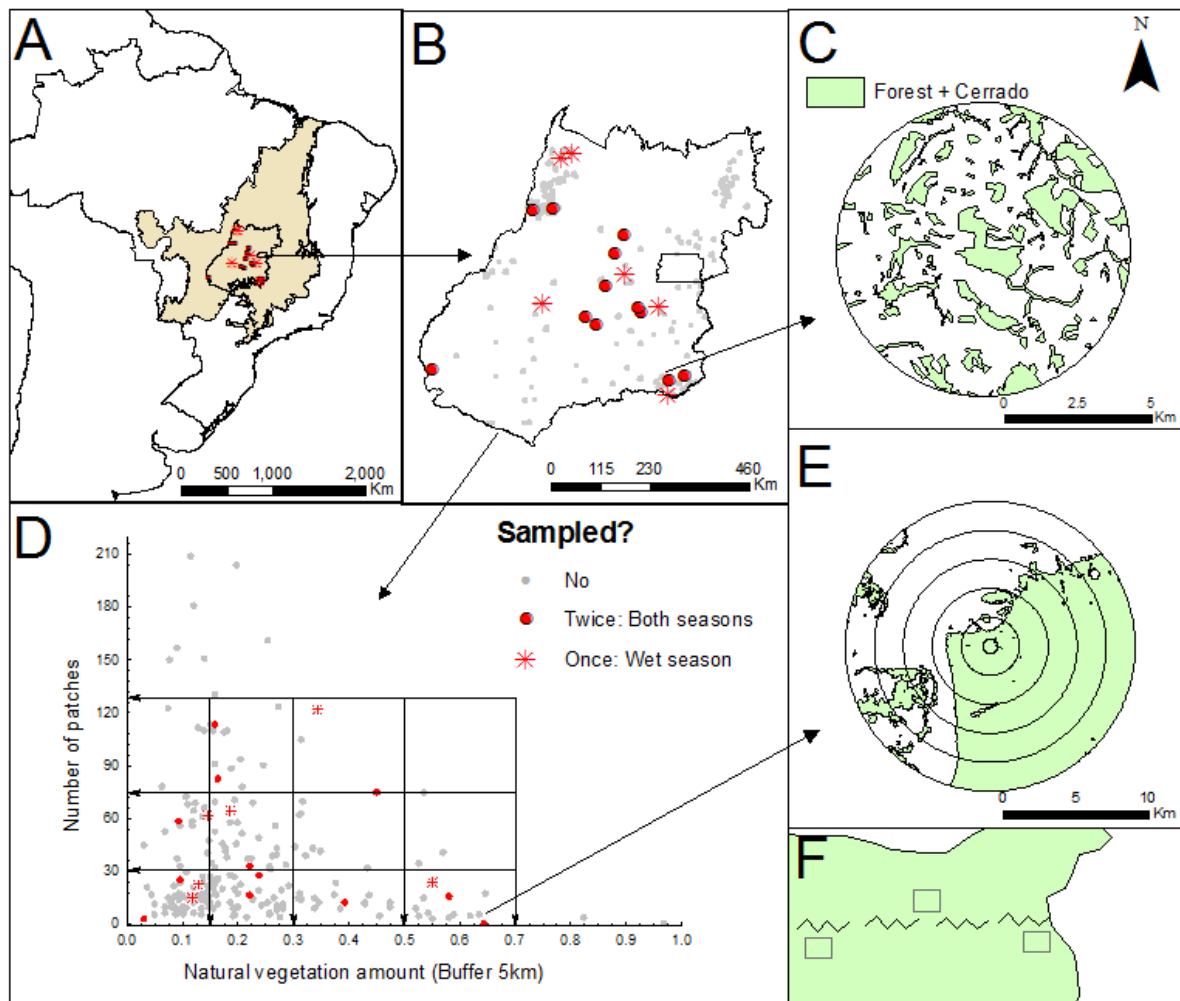
## Methods

### *Overview*

We sampled bats in 18 forest patches with varying surrounding natural vegetation cover and number of patches. Species richness and abundance (number of bats captured) were related to two landscape predictors: natural vegetation cover and inverse number of patches in the landscape (the last one representing habitat configuration in a gradient, patchy to continuous landscape). This analysis was performed for six landscape scales ranging from 0.5 to 10km radius around the bat sampling sites. To test the second prediction, we related the variance in biological traits, independent of species richness, for each community, to the same predictors: natural vegetation cover and number of patches. To test the third prediction, the best scale of effect of the two predictors for abundance and species richness were compared. To test the fourth prediction, the best scale of effect of the two landscape predictors for phytophagous abundance and animalivorous abundance were compared.

## 1 *Study area and site selection*

2           We chose 18 forest patches in the state of Goiás, central Brazil, using spatial data from the  
3 Ministry of Environment of Brazil (<http://mapas.mma.gov.br/>), for the year 2010. The area is in the  
4 Cerrado biome, a mosaic of natural vegetation formations, including dry forests, gallery forests,  
5 grasslands and wetlands (Sano *et al.* 2010). To control for potentially confounding variables, we  
6 selected fragments of similar size (90-400ha), with similar shape (Shape Index;  $SI < 2$ ) and similar  
7 vegetation type (dry and riparian forest). We chose only forest fragments to sample because in  
8 savannas they tend to have more bat species richness than other vegetation types (Gregorin *et al.*  
9 2011; Monadjem & Reside 2008). We found 209 forest patches in the State of Goiás following these  
10 criteria. We then calculated natural vegetation cover and number of natural patches within a buffer of  
11 5km around the centroid of each of these 209 forest patches, and sub-selected patches such that  
12 natural vegetation cover and number of patches were uncorrelated (Fahrig 2003). We did this by  
13 plotting natural vegetation cover vs. number of patches and then dividing the plot into 12 quadrants  
14 (Figure 2). Two patches were randomly chosen within each quadrant. We determined the  
15 accessibility of each patch, first using Google Earth (<http://www.google.com/earth/index.html>) and  
16 then by visiting them. If a fragment was inaccessible or the owner did not authorize the research, we  
17 chose a new fragment at random from the same quadrant. In the end, there were no patches in four of  
18 the quadrants and only one patch in one of them. This left us with 15 patches to sample, to which we  
19 added 3 patches in feasible quadrats, resulting in a total of 18 patches sampled.



1

2 **Figure 2-** A- Bat sample points in the state of Goiás, located within the Cerrado or savanna (light  
3 brown) of Brazil. B- Closer view of sample sites in Goiás state; red circles are forest patches sampled  
4 twice (both seasons, 12 units), red asterisks are forest patches sampled once (wet season, 6 units),  
5 gray circles are non-selected forest patches 90-400 ha each, and shape index <2). C- Sample 5-km  
6 radius landscape, centred on the centroid of the sample patch; the green indicates natural vegetation.  
7 D- Natural vegetation cover vs. number of patches for 209 forest patches with similar size (90-  
8 400ha) and shape (shape index<2) in the state of Goiás, central Brazil. The plot is divided into 12  
9 quadrants to allow selection of 24 bat sample sites such that predictors are uncorrelated. In the end,  
10 there were no patches in four of the quadrants and only one patch in one of them. This left us with 15  
11 patches to sample, to which we added 3 patches in feasible quadrats, resulting in a total of 18 patches

sampled (Appendix 1). E- Multi-sized nested landscapes, ranging from 500m to 10 km radius, i.e. 6 different landscape sizes, used in statistical analysis to relate bat richness and abundance to landscape metrics. F- 20 nets disposed from fragment edge through the interior in four groups of five nets and three quadrats which local environmental metrics were taken.

### *Landscape classification and explanatory variables*

We used satellite images from LANDSAT ETM+ from August 2013, 30m resolution, compositional bands 5, 4 and 3, to classify the land-use in the landscapes surrounding the 18 chosen sampling areas. These data were more recent than those used for site selection, allowing us to more closely link the landscape data to the bat data. We used images from the dry season to avoid clouds that could hamper classification. A supervised classification was performed to separate savanna+forest (natural vegetation) from all other land covers (matrix), within a 10 km radius area around each sample site. We combined savanna and forest as ‘habitat’ because while forest vegetation has more bat species (Gregorin *et al.* 2011; Monadjem & Reside 2008), many species use both savanna and forest to forage, roost or move (Aguirre 2002; Bernard & Fenton 2003). To perform the site selection, described above, we had to choose one radius size (5km), but to test our predictions (above) we needed to relate bat richness and abundance to habitat amount and fragmentation at multiple scales. The range of the scales tested was from 500m to 10km radius. The maximum (10km) was chosen because it is an approximation of maximum daily movement (Aguar *et al.* 2014; Rollinson *et al.* 2013; Trevelin *et al.* 2013; Womack *et al.* 2013).

We verified the supervised classification by comparing it to satellite images from LANDSAT ETM+ and Google Earth (<http://www.google.com/earth/index.html>). Any forest or savanna patch less than 0.09 ha was labeled matrix, as this represents the satellite image resolution. We used the Patch Analyst extension (Rempel *et al.* 2012) for ArcMap 9.3 (ESRI) to calculate the amount of

natural area and number of patches at 6 nested spatial scales, radii of 500m, 2km, 4km, 6km, 8km, and 10km around each sampling site (including the sampled patch). Pearson correlations between standardized natural vegetation cover and number of patches ranged from -0.266 (500m radius) to -0.466 (6km radius).

### *Bat sampling*

For each sampling patch, 20 mist nets (10X2.5m) were placed from the edge through the interior of the patch, in groups of five nets (Figure 1F), during four consecutive nights (six hours each, starting at sunset). The nets were not moved during these four consecutive days. We sampled 18 forest patches, one patch at a time. For 12 patches we sampled twice, once during the dry season and once during the wet season. For the remaining 6 patches we sampled once during the wet season (Figure 2). Sampling occurred between March 2012 and March 2014. We avoided sampling bats on full moon nights, because of reduced sampling success (Mello *et al.* 2013). Adult captured bats of more than 5 grams were marked using wing bands. All bats were identified to species.

### *Response variables*

To test the first prediction bat abundance and species richness were used as response variables. Total abundance was the number of captured bats. Species richness was the number of observed species of bats. Because only a subset of sites was sampled during both wet and dry seasons, we performed separated analysis for the wet season (18 sites) and both seasons (12 sites). To test the second prediction, the variances in biological traits were used as response variables. In this case, only the wet season data, with more sample units, was used. Biological traits were body mass, wing span to wing width ratio, ear size to body mass ratio and number of feeding habits. We chose these traits because they are related to species flight and foraging modes (Denzinger &

1 Schnitzler 2013; Kalko *et al.* 2008). Body mass was the mean obtained from all individuals captured.  
2 Wing span and wing width were obtained from wing photographs using the program ImageJ  
3 (Rasband 2014). Wing photographs were taken from captured bats, from one to ten individuals  
4 photographed per species, taken from different individuals. We used the ratio of wing span to wing  
5 width to represent wing shape. Bats flying in open areas generally have long, narrow wings, with the  
6 opposite for bats flying in cluttered spaces (Denzinger & Schnitzler 2013; Kalko *et al.* 2008). We  
7 used the size of the ear in relation to body mass as a predictor of the use of listening during foraging.  
8 Feeding habits were obtained from the literature (Denzinger & Schnitzler 2013; Kalko *et al.* 2008).  
9 Species were classified according to their most common food, in six categories: frugivores,  
10 nectarivores, edge-space aerial insectivores, gleaning insectivores, carnivores and hematophages.

11 To control for sample size in estimating variance in a biological trait, at each site we  
12 randomly sampled the same of number of individuals found in the site with the fewest individuals  
13 (3), and calculated the variance in the traits for those three individuals. We repeated this 100 times,  
14 for a mean variance for each trait in each sample site. In the case of feeding habit, the number of  
15 guilds (ranging from 1 to 3) was counted for each iteration. The sampling was run using R (R Core  
16 Team, 2014). To test the third predictions the response variable was the scale of effect of natural  
17 cover and number of patches on bat richness and abundance. To test the fourth prediction the  
18 response variable was the scale of effect of natural cover and number of patches on abundance of  
19 phytophagous (frugivores and nectarivores) and animalivorous (insectivores and carnivores). For the  
20 third and fourth predictions only the wet season data were used (n=18).

21

## 22 *Statistical analyses*

23 To assess the relative importance of natural cover and number of patches, to test the first  
24 prediction we used three complementary methods; (1) the partial regression coefficients in the most

parsimonious model, (2) the importance of each variable, and (3) the weighted average partial coefficient (Burnham & Anderson 1998; Grueber *et al.* 2011). We standardized all predictor variables. We fit the models at each of 6 spatial extents to determine the scale at which the landscape predictors had their strongest effects (their scales of effect), and to allow for the possibility of multiple scales of effect (Martin & Fahrig 2012). We used inverse of number of patches instead of actual number of patches to keep the direction of smaller values for patchy landscapes (with many patches) and continuous landscapes (with few patches).

For each model we calculated the Akaike information criterion corrected for finite samples sizes (Burnham & Anderson 1998). We extracted partial coefficients from the best model, weight and model-weighted partial coefficients from each variable. We used standardized partial regression coefficients as unbiased estimates of the relative effects of natural vegetation cover and inverse of number of patches (Smith *et al.* 2009). We calculated the importance of each variable as the sum of the weight of each model containing that variable (Burnham & Anderson 1998). The weight of the

Akaike criterion was:  $Weight_i = \frac{\exp(-\frac{1}{2}\Delta AICc_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta AICc_r)}$

$\Delta AICc_i$  is the difference between the corrected AIC for model  $i$  and the best model and  $\Delta AICc_r$  represents the difference between all models and the best model. Variables with weight are considered more important predictors.

The weighted averaged partial coefficient was calculated as the average of the partial coefficient for a certain variable in all models containing that variable weighted by the weight of that models (Burnham & Anderson 1998; Grueber *et al.* 2011). These analysis were performed using the package ‘MuMin’ version 1.10.5 (Barton 2014) in R (R Core Team, 2014). These analyses were repeated for each landscape size and response variable (total abundance or species richness).

1           The same statistical approach was used for the second prediction, with each trait analyzed  
2 separately. These analyses were also conducted at multiple spatial scales to ensure we evaluated the  
3 effects at the appropriate scales. To test the third prediction, we compared the scales of effect of the  
4 landscape predictors on richness vs. abundance. To test the fourth prediction we compared the scales  
5 of effect of the landscape predictors on abundance (number of captured bats) of animalivorous  
6 (insectivores and carnivores) and phytophagous (nectarivores and frugivores). Omnivores were  
7 excluded. Hematofages were excluded because, nowadays, they use mostly cattle (a non-native  
8 taxon) as a food resource, as opposed to other animalivorous that use mostly native resources as  
9 food.

#### 11 *Potential confounding variables*

12           Some local environmental variables can affect bat abundance and species richness (Estrada-  
13 Villegas *et al.* 2012). To assess whether the effects of the landscape variables, natural cover and  
14 number of patches, were confounded by effects of local environmental variables, we tested the  
15 correlations between them. Local environmental variables were sampled in three quadrats (10 X  
16 10m) in each sample patch, one quadrat near the edge, one near the end of the nets, and one between  
17 them (Figure 1F). In each quadrat we measured the number of trees, understory height, canopy  
18 density, and number of Lianas. Trees and understory vegetation indirectly represent resources for  
19 bats, such as food and shelter (Muscarella & Fleming 2007). Understorey height was measured with  
20 a 2 m pole divided into 10 equal parts; we counted how many parts of the pole were covered by  
21 understory, in each of the four corners of each quadrat. Canopy offers protection for some bats  
22 against predators, wind and rain. Canopy density was measured with a convex spherical densitometer  
23 in each corner and in the center of each quadrat. Lianas are obstacles for bats during flight, so we  
24 counted the number of lianas in each quadrat. We also collected data on mean temperature with an  
25 thermometer. We took note about presence of rain and presence of wind while bat were being

sampled. We standardized the mean values of each local variable and calculated Pearson correlations between the local variables and the landscape variables, natural cover and number of patches. To test for spatial autocorrelation in our bat response variables, we calculated Moran's I index in the software SAM with 199 permutations to estimate the p-value (Spatial Analysis in Macroecology) (Rangel *et al.* 2010).

## Results

We captured 989 individuals and 35 species of bats, within five families, Emballonoridae, Molossidae, Mormoopidae, Phyllostomidae, and Vespertilionidae (Appendix 2). The majority of captured bats were frugivores, with 799 captures. The most captured species was the understory frugivore *Carollia perspicillata*, with 479 captures. During the wet season we captured 744 bats of 33 species, and abundance in different landscapes ranged from 3 to 89 individuals. During the dry season we captured 247 individuals of 18 species, and abundance ranged from 1 to 85 individuals. Even with the differences in sample sizes between wet and dry seasons (18 landscapes for wet season and 12 for dry), the proportion of captures per sample in the wet season was substantially larger compared to the dry season, with an average of 41 individuals per sample site in the wet season, and 22 individuals per sample site in the dry season). There was no significant decline in spatial autocorrelation in species richness or abundance with distance, and there was no spatial autocorrelation at the scale of effect (8 km) (Appendix 3). There were no strong correlations between the landscape variables, natural cover and number of patches, and the local environmental variables; Pearson coefficient ranged from 0.01 to .36 (Appendix 4). Therefore, we did not include local variables as covariates in the analyses below.

The relative effects of natural cover and number of patches differed for species richness and total abundance: total bat abundance was better explained by natural vegetation cover (positive

effect) while species richness was better explained by the number of patches (negative effect) (Figure 3, Appendix 5). For both natural cover and number of patches the relationships were strongest at the 8km radius scale (Table 1). The relative importance of amount of natural area and number of patches for data collected for both seasons (12 sample sites) had a qualitatively similar pattern to the results for the wet season only (18 sample sites; Appendix 6, 7 and 8).

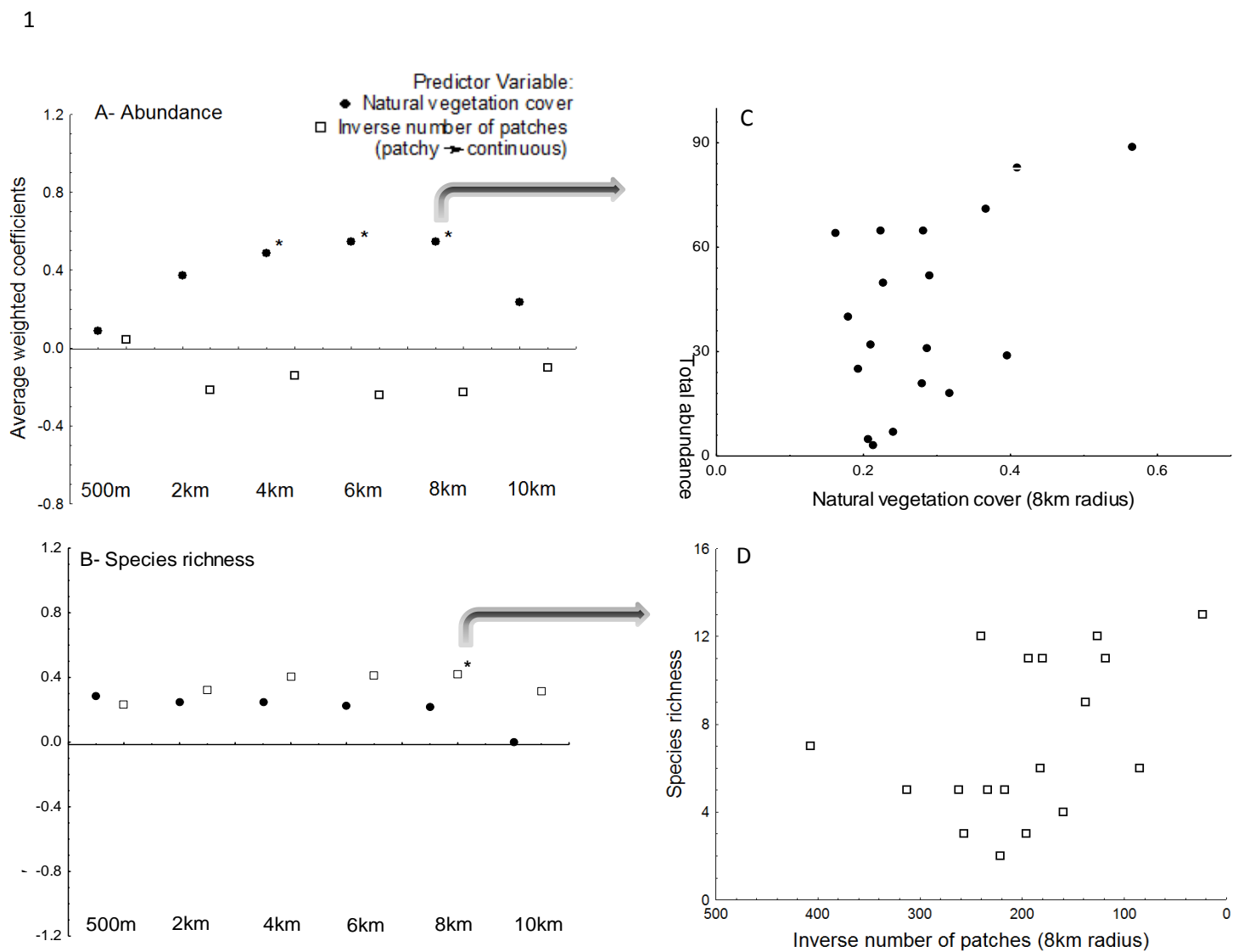
Fragmented landscapes (with more patches) had lower variance in body size and number of feeding habits, as predicted (Figure 4). Variance in wing shape (wingspan to wing width ratio) and in ear size to body mass ratio were not related to the landscape variables (Appendix 9, Table 2). Carnivores and aerial insectivores were disproportionately lost in very fragmented landscapes. Both smaller and larger species were disproportionately lost in fragmented landscapes (Figure 5a). Our results did not support our third prediction, as the scale of effect of the landscape variables on richness and abundance was the same, 8 km radius in both cases (Appendix 10, Table 3). Our results also did not support our fourth prediction, as there was no apparent difference in the scale of effect of the landscape variables on phytophagous and animalivorous (Figure 6).

1 **Table 1-** Importance of natural cover and number of patches in predicting total bat abundance and  
2 bat richness, for each landscape size. \* indicates that the 95% confidence interval of the weighted  
3 partial regression coefficient does not include zero.

<b>Radius of landscape</b>	<b>Total abundance</b>		<b>Species richness</b>	
	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>
500m	0.193	0.185	0.324	0.263
2km	0.442	0.248	0.277	0.366
4km	0.688*	0.212	0.266	0.502
6km	0.796*	0.272	0.253	0.517
8km	0.802*	0.261	0.247	0.540*
10km	0.267	0.196	0.184	0.362

4

5



16

17 **Figure 3-** Average of the weighted standardized partial coefficients of natural cover (solid circles)  
 18 and number of patches (open squares) for each landscape size, obtained using a multi-model  
 19 inference approach. Asterisks are 95% confidence intervals that do not span zero. A- weighted  
 20 standardized coefficients for total abundance; and B- for species richness; C- abundance vs. natural  
 21 cover at the scale of effect (8km); and D- richness vs. inverse number of patches at the scale of effect  
 22 (8km).

23

24

1 **Table 2-** Importance of natural cover and number of patches in predicting variance in traits, for each  
2 landscape size. Importance is the sum of weights of all models containing that variable. Response  
3 variables were variance in body size, variance in wingspan to wing width ratio, variance in ear size  
4 to body mass ratio and number of feeding habits sampled during the wet season. \* indicates that the  
5 95% confidence interval of the weighted partial regression coefficient does not span to zero.

<b>Radius of landscape</b>	<i>Variance Body Mass</i>		<i>Variance Wing Shape</i>	
	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>
500m	0.206	0.289	0.238	0.257
2km	0.470	0.280	0.237	0.276
4km	0.420	0.440	0.360	0.390
6km	0.350	0.590	0.350	0.370
8km	0.330	0.720*	0.350	0.350
10km	0.196	0.316	0.260	0.350

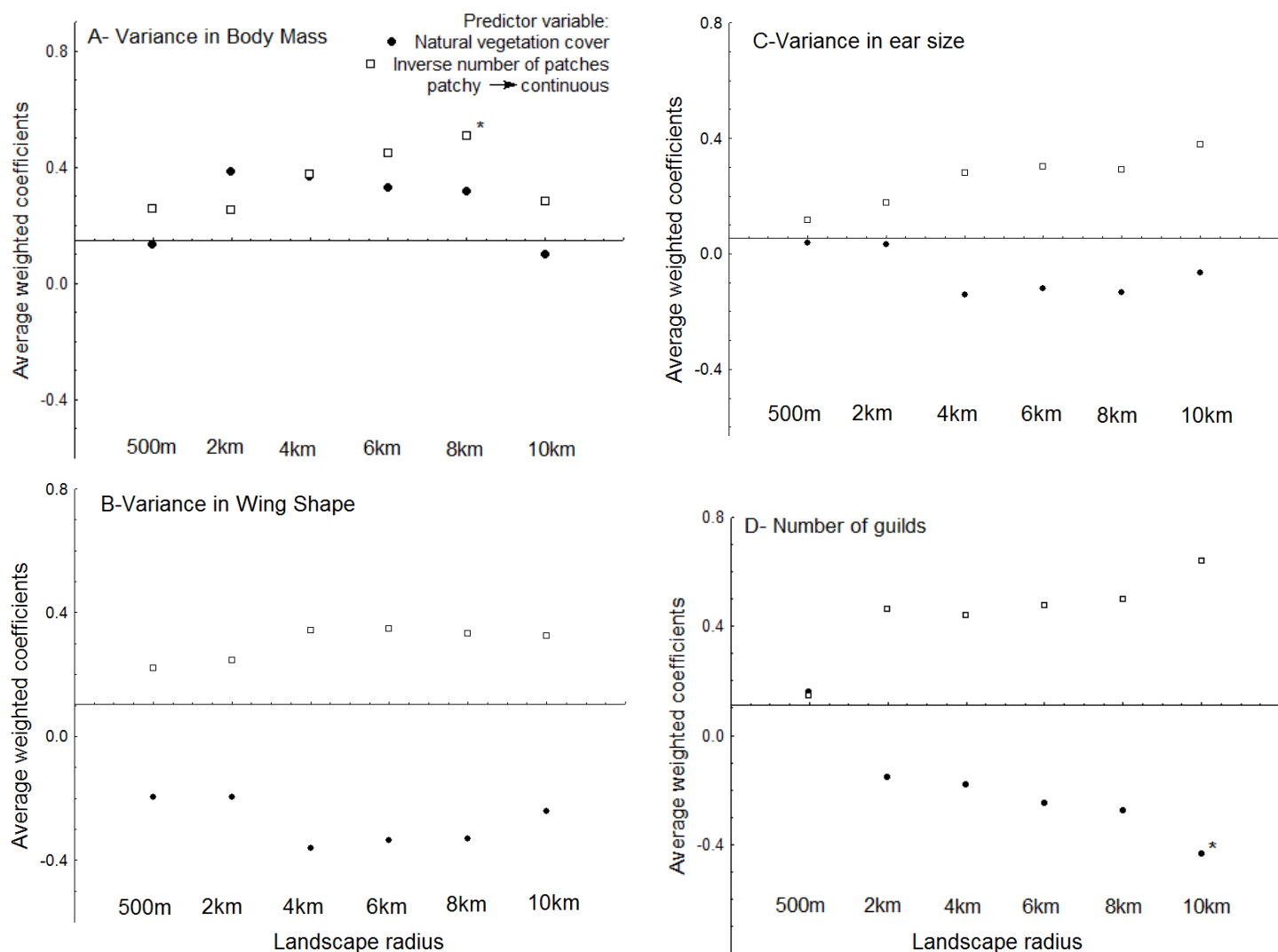
  

<b>Radius</b>	<i>Variance Ear</i>		<i>Number of Guilds</i>	
	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>
500m	0.185	0.202	0.220	0.212
2km	0.184	0.228	0.220	0.640
4km	0.210	0.307	0.230	0.570
6km	0.200	0.330	0.270	0.630
8km	0.210	0.320	0.300	0.680
10km	0.190	0.450	0.590	0.890*

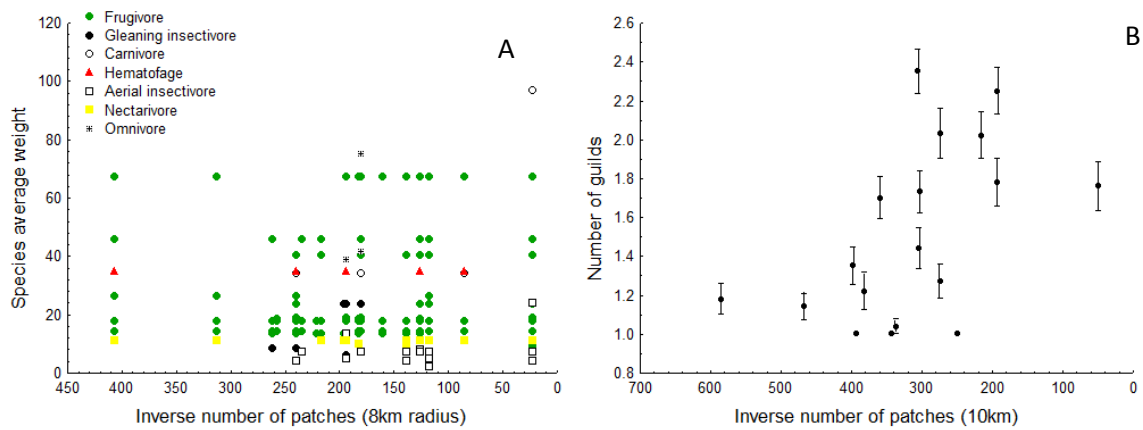
6

7

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16



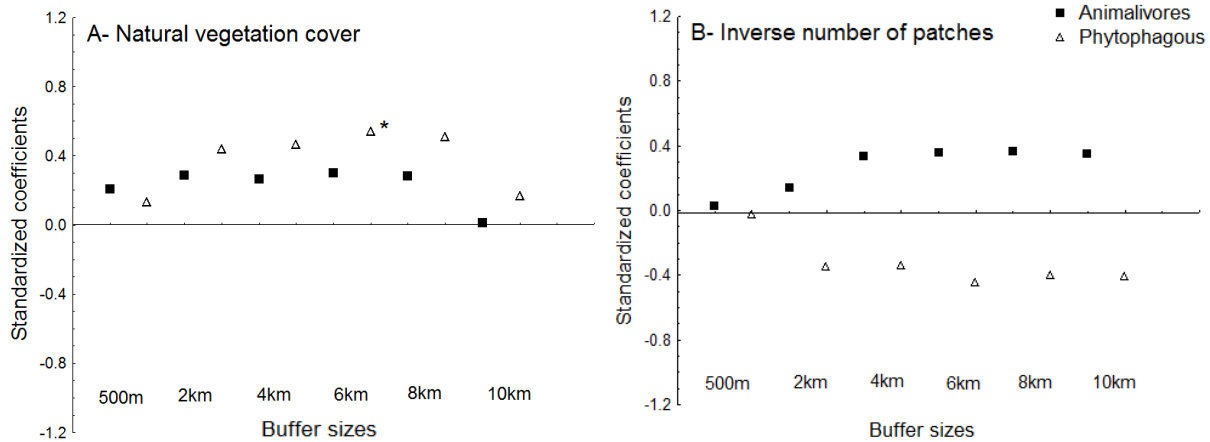
17 **Figure 4-** Average of the weighted standardized partial coefficients of variance in traits regressed on  
 18 natural cover (solid circles) and number of patches (open squares) for each landscape size, obtained  
 19 using a multi-model inference. Response variables are variance in body mass, variance winspan to  
 20 wing width ratio, variance in ear size to body mass ratio and number of guilds (see Methods).  
 21 Asterisks are 95% confidence intervals that do not span zero. A- weighted standardized coefficients  
 22 for variance in body mass; and B- weighted standardized coefficients for wing shape; C- weighted  
 23 standardized coefficients for ear size to body mass ratio; and D- weighted standardized coefficients  
 24 for number of guilds.



**Figure 5-** Identity of groups that were lost with fragmentation. A- Average of body mass of each species occurring in different landscapes related to inverse number of patches at the landscape size of 8km of radius. Inverse number of patches at the scale of 8km of radius was chosen because it is the best scale of effect of inverse number of patches on variance in body size. B- Number of guilds for landscape with confidence intervals. Inverse number of patches at the scale of 10km of radius was chosen because it is the best scale of effect of inverse number of patches on number of guilds.

**Table 3-** Importance of natural cover and number of patches in predicting phytophagous and animalivore abundances at each landscape size. Importance is the sum of weights of all models containing that variable. Phytophagous include frugivores and nectarivores; animalivorous include insectivores and carnivores. \* indicates that the 95% confidence interval of the weighted partial regression coefficient does not include zero.

	<b>Radius of the landscape</b>	<b>Natural vegetation cover</b>	<b>Inverse number of patches</b>
Animalivorous	500m	0.250	0.183
	2km	0.321	0.209
	4km	0.289	0.378
	6km	0.323	0.413
	8km	0.303	0.427
	10km	0.184	0.415
Phytophagous	500m	0.207	0.184
	2km	0.547	0.381
	4km	0.577	0.361
	6km	0.690*	0.524
	8km	0.641	0.437
	10km	0.222	0.510



**Figure 6-** Mean weighted standardized partial coefficients for the effects of natural cover and number of patches on abundances of phytophagous (open triangles) and animalivorous (black squares), for each landscape size. A- coefficients for natural vegetation amount; B- coefficients for inverse number of patches. Asterisks indicate 95% confidence that do not include zero.

## Discussion

Our results only partly supported our prediction that natural area effects would be stronger than effects of fragmentation per se. Natural area had the larger effect on total bat abundance but fragmentation per se (number of patches) had the larger effect on species richness. Bats, in general, have high mobility (Norberg & Rayner 1987), and large home-ranges (Womack *et al.* 2013). Consequently, bat ecological communities are probably not bounded by patches, and bats move through the landscape searching for new habitat patches. So, landscapes with more available habitat would attract more bat individuals regardless habitat configuration in that landscape. This

1 mechanism could explain why natural vegetation cover explained bat total abundance. On the other  
2 hand, fragmentation *per se* reduced the number of different species present. The breaking apart of  
3 patches caused by fragmentation *per se* causes an increasing in the density of edges and a decrease in  
4 mean patch size in the landscape (Fahrig 2003). Both could increase the frequency with which bat  
5 individuals need to move between patches and cross vegetation edges. However, if bat abundance is  
6 strongly related to habitat amount but not to habitat configuration because bats are not bounded by  
7 patches, the only reason for a contrary response of species richness would be caused by differences  
8 in fragmentation *per se* sensitivity among species. Idiosyncrasies on bat dispersal capacity and edge  
9 sensitivity it is a possible cause for this results, for instance, a study showed that two species of the  
10 family Vespertilionidae have different abilities to cross a highway (Kerth & Melber 2009), also  
11 species or group-specific responses to edges have been shown for bats on Neotropics (Estrada-  
12 villegas *et al.* 2010; Gorresen *et al.* 2005; Meyer *et al.* 2008), such as forest insectivores species are  
13 more edge sensitives than open-space insectivores (Estrada-villegas *et al.* 2010).

14         There are few landscape-scale studies on bats to which we can compare our results. Most  
15 studies evaluate effects of patch scale variables, such as patch isolation, (Estrada-villegas *et al.* 2010;  
16 Meyer *et al.* 2009, 2008), which cannot be interpreted clearly as effects of composition or  
17 configuration (Fahrig 2003). Most landscape-scale studies did not aim to estimate the effects of  
18 fragmentation independent from habitat amount (Bernard & Fenton 2002; Cosson *et al.* 1999;  
19 Estrada & Coates-estrada 2002; Harvey & Villalobos 2007; Medellín *et al.* 2000; Mehr *et al.* 2011).  
20 Studies that did test the effects of habitat configuration independent of habitat amount on bat  
21 abundance or species richness found either no effects (Duchamp & Swihart 2008; Mendenhall *et al.*  
22 2014) or a positive effect of fragmentation *per se* (Ethier & Fahrig 2011). More research is needed to  
23 definitively explain the difference between these previous studies and our results.

24         The negative effect of fragmentation *per se* on species richness is likely related to our results  
25 on trait variance. Our second prediction was that the variance in species traits should decrease with

1 increasing landscape change. This prediction was supported for the effects of fragmentation *per se*  
2 on two of the four tested biological traits, body mass and number of guilds. Fragmented landscapes  
3 have lower variance in body mass and fewer guilds. This result is indicating a filtering process in  
4 which the probability of disappearance of a given species depends on its biological traits (Cardillo *et*  
5 *al.* 2006; Henle *et al.* 2004). Our results suggest that the largest and smallest species, particularly  
6 carnivores and aerial insectivores, disappeared from fragmented landscapes. Carnivores bats are in  
7 general large and forest dwellers (Kalko *et al.* 2008). They are possibly affected by fragmentation  
8 *per se* because they depend of a sort of different species to maintain stable population (MacArthur  
9 1955), also they have low mobility, they prefer to use forest to edge and they are edge sensitives  
10 (Kalko *et al.* 2008). All aerial insectivores in our study preferentially use background-cluttered  
11 spaces (Schnitzler & Kalko 2012). Their negative response to fragmentation *per se* seems initially  
12 intriguing because they use edges as hunting habitats. Such species have been shown to be negatively  
13 affected by island isolation and size, but this could vary accordingly to the matrix type (Estrada-  
14 villegas *et al.* 2010). A possible alternative explanation lies on the natural heterogeneity of Cerrado,  
15 which is a mosaic of grass-like, savanna-like and forest vegetation. The edges among these natural  
16 patches could be potential preferential hunting sites for background-cluttered insectivores. On the  
17 other hand, edges between natural vegetation and human-altered ones can be not as suitable for  
18 Cerrado background-cluttered insectivores.

19 Our results did not support our prediction that the scale of effect of landscape variables on  
20 abundance would be smaller than on species richness. One possible explanation is that the time scale,  
21 and therefore the spatial scale, over which the landscape affects abundance and richness are similar,  
22 and both relate to within-generation rather than between-generation movements (Jackson and Fahrig  
23 2014). This is supported by work suggesting that both bat richness and total abundance are more  
24 influenced by local scale variables than regional scale variables (Estrada-Villegas *et al.* 2012; López-  
25 González *et al.* 2014). Our results also did not support our fourth prediction, that animalivorous

would show smaller scales of effect than phytophagous. This prediction was based on the assumption that resources for animalivorous are less clumped in the landscape (O'Neill *et al.* 1988; Thies & Kalko 2004), and the scale of effect depends on the movement range of a species (Jackson & Fahrig 2012). Possibly, the differences in dispersal ability of phytophagous and animalivorous cannot suggest differences in the scale of effect related to landscape structure.

Our results suggest that the appropriate landscape size for evaluation of landscape structure effects on bats in our region is a landscape of radius 8 km. The use of an inappropriate scale in landscape studies can produce erroneous conclusions on effects of landscape structure on biodiversity (Wiens 1989). A relationship between biodiversity and landscape structure can even exhibit opposite results if landscape variables are measured at different scales (Smith *et al.* 2011). Several studies relating landscape structure to bat richness used landscapes at or less than 5km radius (Duchamp & Swihart 2008; Mendenhall *et al.* 2014, Ethier & Fahrig 2011; Gorresen *et al.* 2005). These studies may have inaccurately characterized the effects of landscape structure on bats, which may explain why our results are different from previous results, i.e. our negative effect of fragmentation *per se* on bat richness.

The major aim of this study was to identify the relative importance of natural vegetation cover and landscape configuration in influencing bat richness and abundance. Natural vegetation cover was a good predictor of the bat abundance, mostly for phytophagous (frugivores and nectarivores), which are important pollinators and seed dispersers at the Neotropical region (Muscarella & Fleming 2007). In contrast to our prediction, fragmentation *per se* was a good predictor of species richness, mostly for aerial insectivores and carnivores. These effect occurred at similar landscape extents (8 km radius), suggesting larger scales of effect of landscape structure than previously thought. We suggest that future studies that aim to relate landscape structure to bat responses should measure landscape structure at these larger scales to avoid misleading results.

## Acknowledgements

The field work was supported by International Foundation for Science (IFS), various CNPq grants, PELD, Anglo American Group and CAPES. P. Mendes receives a scholarship from CNPq and another one from the “sandwich doctorate program” CAPES. P. De Marco was funded by continuous productivity CNPq grants (305542/2010-9). We are grateful LAPIG-UFG laboratory for providing help with satellite images, and F.P. Peixoto and D.P. Silva for the helpful comments on the manuscript. We thank S. de Jesus, P.V.S. Bernardo, L.M. Camargos, P.H.P. Braga, B.C. Gomes, C. Sobral, P. Coelho, A. Bispo, landowners and all fieldwork assistants for helping in sampling design, field work and discussions. We also thank ICMBio for providing the licenses to sample bats, National Forest of Silvania and Emas National Park for permitting surveys at their conservation units. We thank Metaland laboratory, Universidade Federal de Goiás, Goiânia, Brazil and GLEL laboratory, Carleton University, Ottawa, Canada equip for suggestions that improved the work.

## References

- Aguiar LMS, Bernard E & Machado RB, 2014. Habitat use and movements of *Glossophaga soricina* and *Lonchophylla dekeyseri* ( Chiroptera : Phyllostomidae ) in a Neotropical savannah. *Zoologia (Curitiba, Impresso)*, 31(3):223–229.
- Aguirre LF, 2002. Structure of a netropical savanna bat community. *Journal of Mammalogy*, 83(3):775–784.
- Barnosky AD, Matzke N, Tomiya S, *et al.*, 2011. Has the Earth’s sixth mass extinction already arrived? *Nature*, 471:51–57.
- Barton K, 2014. MuMIn: Multi-model inference. r package version 1.10.5, (<http://cran.r-project.org/package=MuMIn>).
- Bernard E & Fenton MB, 2002. Species diversity of bats ( Mammalia : Chiroptera ) in forest fragments , primary forests , and savannas in central Amazonia , Brazil. *Methodology*, 1140:1124–1140.

- 1 Bernard E & Fenton MB, 2003. Bat Mobility and Roosts in a Fragmented Landscape in Central.  
2 *Current*, 35(2):262–277.
- 3 Buchmann CM, Schurr FM, Nathan R & Jeltsch F, 2013. Habitat loss and fragmentation affecting  
4 mammal and bird communities—The role of interspecific competition and individual space use.  
5 *Ecological Informatics*, 14:90–98.
- 6 Burnham KP & Anderson DR, 1998. *Model Selection and Multimodel Inference*. Second ed., New  
7 York: Springer.
- 8 Cardillo M, Mace GM, Gittleman JL & Purvis A, 2006. Latent extinction risk and the future  
9 battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the*  
10 *United States of America*, 103(11):4157–61.
- 11 Cisneros LM, Fagan ME & Willig MR, 2014. Effects of human-modified landscapes on taxonomic,  
12 functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*,  
13 21:523–533.
- 14 Cosson J-F, Pons J-M & Masson D, 1999. Effects of forest fragmentation on frugivorous and  
15 nectarivorous bats in French Guiana. *Journal of Tropical Ecology*, 15:515–534.
- 16 Den Boer PJ, 1968. Spreading of risk and stabilization of animal number. *Acta Biotheoretica*, 18(1-  
17 4):165–194.
- 18 Den Boer PJ, 1981. On the Survival of Populations in a Heterogeneous and Variable Environment.  
19 *Oecologia*, 50:39–53.
- 20 Denzinger A & Schnitzler H-U, 2013. Bat guilds, a concept to classify the highly diverse foraging  
21 and echolocation behaviors of microchiropteran bats. *Frontiers in physiology*, 4(July):164.
- 22 Dirzo R, Young HS, Galetti M, *et al.*, 2014. Defaunation in the Anthropocene. *Science*,  
23 345(6195):401–406.
- 24 Duchamp JE & Swihart RK, 2008. Shifts in bat community structure related to evolved traits and  
25 features of human-altered landscapes. *Landscape Ecology*, 23(7):849–860.
- 26 Estrada A & Coates-estrada R, 2002. Bats in continuous forest , forest fragments and in an  
27 agricultural mosaic habitat-island at Los Tuxtlas , Mexico. *Biological Conservation*, 103:237–  
28 245.
- 29 Estrada-Villegas S, McGill BJ & Kalko EK V, 2012. Climate, habitat, and species interactions at  
30 different scales determine the structure of a Neotropical bat community. *Ecology*, 93(5):1183–  
31 93.
- 32 Estrada-villegas S, Meyer CFJ & Kalko EK V, 2010. Effects of tropical forest fragmentation on  
33 aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, 143(3):597–  
34 608.
- 35 Ethier K & Fahrig L, 2011. Positive effects of forest fragmentation, independent of forest amount, on  
36 bat abundance in eastern Ontario, Canada. *Landscape Ecology*, 26(6):865–876.

- 1    Fahrig L, 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology,*  
2        *Evolution, and Systematics*, 34(1):487–515.
- 3    Fahrig L, 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of*  
4        *Biogeography*, 40(9):1649–1663.
- 5    Faria D, Laps RR, Baumgarten J & Cetra M, 2006. Bat and Bird Assemblages from Forests and  
6        Shade Cacao Plantations in Two Contrasting Landscapes in the Atlantic Forest of Southern  
7        Bahia, Brazil. *Biodiversity and Conservation*, 15(2):587–612.
- 8    Flynn DFB, Molinari N, Lin BB & Mayfield MM, 2008. Loss of functional diversity under land use  
9        intensification across multiple taxa. *Ecology Letters*, 12(1):22–33.
- 10   García-Morales R, Badano EI & Moreno CE, 2013. Response of Neotropical Bat Assemblages to  
11        Human Land Use. *Conservation biology : the journal of the Society for Conservation Biology*,  
12        00(0):1–11.
- 13   Gorresen PM, Willig MR & Strauss RE, 2005. Multivariate analysis of scale-dependent associations  
14        between bats and landscape structure. *Ecological applications*, 15(6):2126–2136.
- 15   Gregorin R, Gonçalves E, Aires CC & Carmignotto AP, 2011. Morcegos (Mammalia : Chiroptera)  
16        da Estação Ecológica Serra Geral do Tocantins : composição específica e considerações  
17        taxonômicas. *Biota*, 11(1):300–311.
- 18   Grueber CE, Nakagawa S, Laws RJ & Jamieson IG, 2011. Multimodel inference in ecology and  
19        evolution: challenges and solutions. *Journal of evolutionary biology*, 24(4):699–711.
- 20   Harvey CA & Villalobos JAG, 2007. Agroforestry systems conserve species-rich but modified  
21        assemblages of tropical birds and bats. *Biodiversity & Conservation*, 16:2257–2292.
- 22   Henle K, Davies KF, Kleyer M, Margules C & Settele J, 2004. Predictors of Species Sensitivity to  
23        Fragmentation. *Biodiversity and Conservation*, 13(1):207–251.
- 24   Henry M, Pons J-M & Cosson J-F, 2007. Foraging behaviour of a frugivorous bat helps bridge  
25        landscape connectivity and ecological processes in a fragmented rainforest. *The Journal of*  
26        *animal ecology*, 76(4):801–13.
- 27   Holdaway RJ & Sparrow AD, 2006. Assembly rules operating along a primary riverbed grassland  
28        successional sequence. *Journal of Ecology*, 94(6):1092–1102.
- 29   Jackson HB & Fahrig L, 2012. What size is a biologically relevant landscape? *Landscape Ecology*,  
30        27(7):929–941.
- 31   Jackson ND & Fahrig L, 2014. Landscape context affects genetic diversity at a much larger spatial  
32        extent than population abundance. *Ecology*, 95(4):871–81.
- 33   Jacomassa FAF & Pizo MA, 2010. Birds and bats diverge in the qualitative and quantitative  
34        components of seed dispersal of a pioneer tree. *Acta Oecologica*, 36(5):493–496.

- 1 Jones G, Jacobs D, Kunz T, Willig M & Racey P, 2009. Carpe noctem: the importance of bats as  
2 bioindicators. *Endangered Species Research*, 8(July):93–115.
- 3 Jones KE, Purvis A & Gittleman JL, 2003. Biological correlates of extinction risk in bats. *The*  
4 *American naturalist*, 161(4):601–14.
- 5 Jung K & Kalko EK V, 2010. Where forest meets urbanization : foraging plasticity of aerial  
6 insectivorous bats in an anthropogenically altered environment Where forest meets  
7 urbanization : foraging plasticity of aerial insectivorous bats in an anthropogenically altered  
8 environment. *Society*, 91(1):144–153.
- 9 Kalka MB, Smith AR & Kalko EK V, 2008. Bats Limit Arthropods and Herbivory in a Tropical  
10 Forest. *Science*, 320(April):2008–2008.
- 11 Kalko EK V, Estrada Villegas S, Schmidt M, Wegmann M & Meyer CFJ, 2008. Flying high--  
12 assessing the use of the aerosphere by bats. *Integrative and comparative biology*, 48(1):60–73.
- 13 Kerth G & Melber M, 2009. Species-specific barrier effects of a motorway on the habitat use of two  
14 threatened forest-living bat species. *Biological Conservation*, 142(2):270–279.
- 15 Klingbeil BT & Willig MR, 2010. Seasonal differences in population-, ensemble- and community-  
16 level responses of bats to landscape structure in Amazonia. *Oikos*, 119(10):1654–1664.
- 17 López-González C, Presley SJ, Lozano A, Stevens RD & Higgins CL, 2014. Ecological  
18 biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta  
19 diversity, and environmental gradients to species richness and composition patterns. *Ecography*,  
20 37:1–12.
- 21 MacArthur R, 1955. Fluctuations of Animal Populations and a Measure of Community Stability.  
22 *Ecology*, 36(3):533–536.
- 23 Martin AE & Fahrig L, 2012. Measuring and selecting scales of effect for landscape predictors in  
24 species – habitat models. *Ecological Applications*, 22(8):2277–2292.
- 25 Medellín RA, Equihua M & Amin MA, 2000. Bat Diversity and Abundance as Indicators of  
26 Disturbance in Neotropical Rainforests. *Conservation Biology*, 14(6):1666–1675.
- 27 Mehr M, Brandl R, Hothorn T, *et al.*, 2011. Land use is more important than climate for species  
28 richness and composition of bat assemblages on a regional scale. *Mammalian Biology -*  
29 *Zeitschrift für Säugetierkunde*, 76(4):451–460.
- 30 Mello MAR, Kalko EK V & Silva WR, 2013. Effects of moonlight on the capturability of  
31 frugivorous phyllostomid bats ( Chiroptera : Phyllostomidae ) at different time scales.  
32 30(4):397–402.
- 33 Mendenhall CD, Karp DS, Meyer CFJ, Hadly E a & Daily GC, 2014. Predicting biodiversity change  
34 and averting collapse in agricultural landscapes. *Nature*, 509(7499):213–7.
- 35 Meyer CFJ, Fründ J, Lizano WP & Kalko EKV, 2007. Ecological correlates of vulnerability to  
36 fragmentation in Neotropical bats. *Journal of Applied Ecology*, 45(1):381–391.

- 1 Meyer CFJ, Kalko EK V & Kerth G, 2009. Small-Scale Fragmentation Effects on Local Genetic  
2 Diversity in Two Phyllostomid Bats with Different Dispersal Abilities in Panama. *Nature*,  
3 41(1):95–102.
- 4 Meyer J, Fründ J, Lizano WP & Kalko EK V, 2008. Ecological correlates of vulnerability to  
5 fragmentation in Neotropical bats. *Journal of Applied Ecology*, 45:381–391.
- 6 Mickleburgh SP, Hutson AM & Racey PA, 2002. A review of the global conservation status of bats  
7 major threats. *Oryx*, 36(1):18–34.
- 8 Monadjem A & Reside A, 2008. The influence of riparian vegetation on the distribution and  
9 abundance of bats in an African savanna. *Acta Chiropterologica*, 10(2):339–348.
- 10 Muchhala N, 2002. Flower Visitation by Bats in Cloud Forests of Western Ecuador. *Biotropica*,  
11 34(3):387–395.
- 12 Murphy GEP & Romanuk TN, 2014. A meta-analysis of declines in local species richness from  
13 human disturbances. *Ecology and evolution*, 4(1):91–103.
- 14 Muscarella R & Fleming TH, 2007. The role of frugivorous bats in tropical forest succession.  
15 *Biological reviews of the Cambridge Philosophical Society*, 82(4):573–90.
- 16 Norberg UM & Rayner JM V, 1987. Ecological morphology and flight in bats (Mammalia;  
17 Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Society*,  
18 316(1179):335–427.
- 19 O'Neill R V., Milne BT, Turner MG & Gardner RH, 1988. Resource utilization scales and landscape  
20 pattern. *Landscape Ecology*, 2(1):63–69.
- 21 Ockinger E, Schweiger O, Crist TO, *et al.*, 2010. Life-history traits predict species responses to  
22 habitat area and isolation: a cross-continental synthesis. *Ecology letters*, 13(8):969–79.
- 23 Pardini R, 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape.  
24 *Biodiversity & Conservation*, 13:2567–2586.
- 25 Pardini R, Bueno ADA, Gardner T a, Prado PI & Metzger JP, 2010. Beyond the fragmentation  
26 threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PloS one*,  
27 5(10):e13666.
- 28 Pasher J, Mitchell SW, King DJ, *et al.*, 2013. Optimizing landscape selection for estimating relative  
29 effects of landscape variables on ecological responses. *Landscape Ecology*, 28:371–383.
- 30 Petchey OL, Evans KL, Fishburn IS & Gaston KJ, 2007. Low functional diversity and no  
31 redundancy in British avian assemblages. :977–985.
- 32 Poulin B, Wright SJ & Calder O, 1999. Interspecific synchrony and asynchrony in the fruiting  
33 phenologies of congeneric bird-dispersed plants in Panama. *Journal of Tropical Ecology*],  
34 15:213–227.

- 1 Prugh LR, Hodges KE, Sinclair ARE & Brashares JS, 2008. Effect of habitat area and isolation on  
2 fragmented animal populations. *Proceedings of the National Academy of Sciences of the United*  
3 *States of America*, 105(52):20770–5.
- 4 Quesnelle PE, Fahrig L & Lindsay KE, 2013. Effects of habitat loss, habitat configuration and matrix  
5 composition on declining wetland species. *Biological Conservation*, 160:200–208.
- 6 Rangel TFLVB, Diniz-Filho JAF & Bini LM, 2010. SAM: a comprehensive application for Spatial  
7 Analysis in Macroecology. *Ecography*, 33:46–50.
- 8 Rasband W., 2014. ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, USA,  
9 <http://imagej.nih.gov/ij/>, 1997–2014.
- 10 Rempel RS, Kaukinen D & Carr AP, 2012. Patch Analyst and Patch Grid. Ontario Ministry of  
11 Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.
- 12 Ricklefs RE, 2008. Disintegration of the ecological community. *The American naturalist*,  
13 172(6):741–50.
- 14 Ries L, Fletcher RJ, Battin J & Sisk TD, 2004. ECOLOGICAL RESPONSES TO HABITAT  
15 EDGES: Mechanisms, Models, and Variability Explained. *Annual Review of Ecology,*  
16 *Evolution, and Systematics*, 35(1):491–522.
- 17 Rollinson DP, Coleman JC & Downs CT, 2013. Seasonal Differences in Foraging Dynamics ,  
18 Habitat Use and Home Range Size of Wahlberg ’ s Epauletted Fruit Bat in an Urban  
19 Environment Seasonal differences in foraging dynamics , habitat use and home range size of  
20 Wahlberg ’ s epauletted fruit bat in an. 48(2):340–350.
- 21 Rueda M, Hawkins B a., Morales-Castilla I, *et al.*, 2013. Does fragmentation increase extinction  
22 thresholds? A European-wide test with seven forest birds. *Global Ecology and Biogeography*,  
23 22(12):1282–1292.
- 24 Sano EE, Rosa R, Brito JLS & Ferreira LG, 2010. Land cover mapping of the tropical savanna  
25 region in Brazil. :113–124.
- 26 Schnitzler H-U & Kalko EKV, 2012. Echolocation by Insect-Eating Bats. 51(7):557–569.
- 27 Silva DP & De Marco P, 2014. No Evidence of Habitat Loss Affecting the Orchid Bees *Eulaema*  
28 *nigrita* Lepeletier and *Eufriesea auriceps* Friese (Apidae: Euglossini) in the Brazilian Cerrado  
29 Savanna. *Neotropical Entomology*,
- 30 Smith AC, Fahrig L & Francis CM, 2011. Landscape size affects the relative importance of habitat  
31 amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, 34(1):103–113.
- 32 Smith AC, Koper ÆN, Francis CM & Fahrig ÆL, 2009. Confronting collinearity : comparing  
33 methods for disentangling the effects of habitat loss and fragmentation. :1271–1285.
- 34 Thies W & Kalko EK V, 2004. Phenology of neotropical pepper plants ( Piperaceae ) and their  
35 association with their main dispersers , two short-tailed fruit bats , *Carollia perspicillata* and *C .*  
36 *castanea* ( Phyllostomidae ). *Oikos*, 104:362–376.

- 1 Thomas J a, Bourn N a, Clarke RT, *et al.*, 2001. The quality and isolation of habitat patches both  
2 determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society*  
3 *of London B*, 268(1478):1791–6.
- 4 Thornton DH, Branch LC & Sunkist ME, 2011. The relative influence of habitat loss and  
5 fragmentation: do tropical mammals meet the temperate paradigm? *Ecological applications : a*  
6 *publication of the Ecological Society of America*, 21(6):2324–33.
- 7 Threlfall CG, Law B & Banks PB, 2012. Influence of landscape structure and human modifications  
8 on insect biomass and bat foraging activity in an urban landscape. *PloS one*, 7(6):e38800.
- 9 Trevelin LC, Silveira M, Port-Carvalho M, Homem DH & Cruz-Neto AP, 2013. Use of space by  
10 frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil.  
11 *Forest Ecology and Management*, 291:136–143.
- 12 Trzcinski MK, Fahrig L & Merriam G, 1999. Independent effects of forest cover and fragmentation  
13 in the distribution of forest breeding birds. *Ecological applications*, 9(2):586–593.
- 14 Uezu A & Metzger JP, 2011. Vanishing bird species in the Atlantic Forest: relative importance of  
15 landscape configuration, forest structure and species characteristics. *Biodiversity and*  
16 *Conservation*, 20(14):3627–3643.
- 17 Villard M-A & Metzger JP, 2014. REVIEW: Beyond the fragmentation debate: a conceptual model  
18 to predict when habitat configuration really matters. *Journal of Applied Ecology*, 51(2):309–  
19 318.
- 20 Wiens J a., 1989. Spatial Scaling in Ecology. *Functional Ecology*, 3(4):385–397.
- 21 Wiescher PT, Pearce-Duvet JMC & Feener DH, 2012. Assembling an ant community: species  
22 functional traits reflect environmental filtering. *Oecologia*, 169(4):1063–74.
- 23 Womack KM, Amelon SK & Thompson FR, 2013. Summer Home Range Size of Female Indiana  
24 Bats (*Myotis Sodalis*) in Missouri, USA. *Acta Chiropterologica*, 15(2):423–429.

25

26

## 1 **Appendix 1**

2 Geographic coordinates in decimal degrees and municipality of sample sites. 12 sample sites were  
 3 sampled twice, once in each season, and 8 were sample only during the wet season. All  
 4 municipalities are located at the state of Goiás, Brazil, and the predominant vegetation is Cerrado, a  
 5 savannic formation.

<b>Municipality</b>	<b>Latidute</b>	<b>Longitude</b>	<b>Season</b>
São Luís dos Montes			
Belos	-50.6519	-16.5132	Wet
Palmeiras de Goiás	-49.7887	-16.8216	Both
Silvânia	-48.6176	-16.6988	Both
Guapó	-49.5301	-16.9648	Both
Vianópolis	-48.2176	-16.5617	Wet
Catalão	-47.7214	-18.0477	Both
Catalão	-48.0163	-18.1316	Both
Catalão	-48.0449	-18.4163	Wet
Petrolina de Goiás	-49.3613	-16.1714	Both
Mozarlândia	-50.4543	-14.5594	Both
São Miguel do Araguaia	-50.0356	-13.3709	Wet
São Miguel do Araguaia	-50.2482	-13.4813	Wet
Barro Alto	-48.9780	-15.1017	Both
Mineiros	-52.9809	-17.9096	Both
Silvânia	-48.6667	-16.6330	Both
Aruanã	-50.8825	-14.5862	Both
Pirenópolis	-48.9416	-15.8909	Wet
Goianésia	-49.2237	-15.5455	Both

6

## 1 Appendix 2

2 Species captured and respective guild, family and number of captures during the wet and dry  
 3 seasons, 35 species were sampled during the field work. We sampled 18 patches during the wet  
 4 season and 12 during the dry one.

Species	Guild	Family	Wet season	Dry season
<i>Anoura caudifer</i>	Nectarivore	Phyllostomidae	3	2
<i>Artibeus cinereus</i>	Frugivore	Phyllostomidae	9	3
<i>Artibeus lituratus</i>	Frugivore	Phyllostomidae	49	14
<i>Artibeus obscurus</i>	Frugivore	Phyllostomidae	25	6
<i>Artibeus planirostris</i>	Frugivore	Phyllostomidae	69	22
<i>Carollia brevicauda</i>	Frugivore	Phyllostomidae	17	2
<i>Carollia perspicillata</i>	Frugivore	Phyllostomidae	350	129
<i>Chiroderma villosum</i>	Frugivore	Phyllostomidae	4	0
<i>Chrotopterus auritus</i>	Gleaning	Phyllostomidae	1	1
<i>Desmodus rotundus</i>	Hematophagous	Phyllostomidae	25	10
<i>Eptesicus brasiliensis</i>	Aerial insectivore	Vespertilionidae	3	2
<i>Eptesicus diminutus</i>	Aerial insectivore	Vespertilionidae	3	0
<i>Glossophaga soricina</i>	Nectarivore	Phyllostomidae	43	28
<i>Lophostoma brasiliense</i>	Gleaning	Phyllostomidae	2	3
<i>Lophostoma silvicola</i>	Gleaning	Phyllostomidae	8	0
<i>Macrophyllum macrophyllum</i>	Gleaning	Phyllostomidae	1	0
<i>Mesophylla maconellii</i>	Frugivore	Phyllostomidae	3	0
<i>Micronycteris cf. sanborni</i>	Gleaning	Phyllostomidae	1	0
<i>Micronycteris minuta</i>	Gleaning	Phyllostomidae	0	1
<i>Mimon crenulatum</i>	Gleaning	Phyllostomidae	0	1
<i>Molossops temminckii</i>	Aerial insectivore	Molossidae	1	0
<i>Myotis nigricans</i>	Aerial insectivore	Vespertilionidae	19	2
<i>Myotis sp.</i>	Aerial insectivore	Vespertilionidae	1	0
<i>Phyllostomus discolor</i>	Onivore	Phyllostomidae	5	0
<i>Phyllostomus elongatus</i>	Onivore	Phyllostomidae	1	0
<i>Phyllostomus hastatus</i>	Onivore	Phyllostomidae	12	1
<i>Platyrrhinus helleri</i>	Frugivore	Phyllostomidae	22	3
<i>Platyrrhinus lineatus</i>	Frugivore	Phyllostomidae	44	12
<i>Pteronotus gymnonotus</i>	Aerial insectivore	Mormoopidae	1	0
<i>Pteronotus parnellii</i>	Aerial insectivore	Mormoopidae	1	0
<i>Saccopteryx leptura</i>	Aerial insectivore	Emballunoridae	1	0
<i>Sturnira lilium</i>	Frugivore	Phyllostomidae	8	3
<i>Trachops cirrhosus</i>	Gleaning	Phyllostomidae	7	0
<i>Uroderma magnirostrum</i>	Frugivore	Phyllostomidae	2	0
<i>Vampyressa pusilla</i>	Frugivore	Phyllostomidae	3	0
<b>TOTAL</b>			744	245

### 1 Appendix 3

2 Moran I index and related p values showing the spatial autocorrelation for seven distance classes of  
 3 species richness and abundance. Data from wet and both seasons are shown in separated.

<b>Wet season</b>				
<b>Class (km)</b>	<b>Species richness</b>		<b>Total abundance</b>	
	<b>Moran I</b>	<b>P</b>	<b>Moran I</b>	<b>p</b>
53	0.091	0.643	0.234	0.256
134	-0.415	0.040	-0.081	0.623
192	-0.384	0.050	-0.155	0.392
243	0.556	0.025	0.043	0.809
310	0.011	0.955	-0.374	0.055
412	-0.377	0.095	-0.131	0.508
538	-0.024	0.849	-0.001	1
<b>Both seasons</b>				
<b>Class</b>	<b>Species richness</b>		<b>Total abundance</b>	
	<b>Moran I</b>	<b>P</b>	<b>Moran I</b>	<b>p</b>
49	-0.007	0.990	0.428	0.211
126	-0.155	0.613	0.033	0.894
184	-0.245	0.397	-0.39	0.151
233	0.086	0.784	-0.304	0.286
290	0.130	0.688	-0.73	0.010
393	-0.491	0.106	-0.332	0.296
515	-0.111	0.698	0.342	0.141

4

5

6

## 1 **Appendix 4**

2 Pearson correlation index for each local environmental variable with each predictor variable at  
 3 different landscape sizes, here radius of landscape. We did not find any strong correlation between  
 4 those pairs of variables. Inverse number of patches represents the habitat configuration in the  
 5 direction patchy to continuous landscapes.

Predictor	Radius of landscape	Rain	Wind	Understorey	Canopy	N. trees	Lianas
Natural vegetation cover	500m	-0.22	-0.08	0.17	-0.03	0.19	-0.20
	2km	-0.07	0.03	0.19	0.01	0.03	-0.02
	4km	-0.05	-0.03	0.10	-0.06	-0.24	-0.16
	6km	-0.01	0.06	0.09	-0.13	-0.22	-0.18
	8km	0.04	0.08	0.11	-0.14	-0.23	-0.20
	10km	0.06	-0.02	0.33	0.16	0.19	0.29
Inverse number of patches	500m	0.23	0.17	-0.03	-0.13	0.20	-0.35
	2km	-0.02	-0.13	0.36	0.15	0.19	-0.01
	4km	0.06	-0.15	0.10	0.10	0.08	-0.15
	6km	0.04	-0.07	0.08	0.06	0.09	-0.22
	8km	0.04	-0.08	0.13	0.07	0.12	-0.21
	10km	-0.03	-0.07	0.18	0.08	0.33	0.05

6

## 1 Appendix 5

2 Standardized partial coefficients for the most parsimonious model relating total abundance and  
 3 species richness sampled during the wet season to natural area and number of patches, measured at  
 4 six different landscape sizes (500m, 2km, 4km, 6km, 8km and 10km radius from sampling site).  
 5 Akaike information criterion corrected for small samples and weight of each model are also shown.  
 6 Predictor variables were standardized *a priori* for the analysis. Each line represents the best model  
 7 considering all competing models for that specific landscape size and response variable.

	Radius of landscape	Natural vegetation cover	Inverse Number of patches	AICc	Weight
Total abundance	500m			173.29	0.652
	2km			173.29	0.439
	4km	12.526		171.79	0.536
	6km	13.626		170.84	0.563
	8km	13.749		170.73	0.579
	10km			173.29	0.591
Species Richness	500m			101.03	0.478
	2km			101.03	0.429
	4km		1.453	100.55	0.411
	6km		1.479	100.45	0.427
	8km		1.516	100.28	0.447
	10km			101.03	0.516

## 1    **Appendix 6**

2    Importance of each predictor variable for each landscape size, for data collected during both seasons.  
3    Importance is the sum of weights of all models containing that variable. The same analysis was  
4    repeated for two response variables total bat abundance and observed species richness sampled  
5    during wet season. \* indicates that the confidence interval of the weighted partial regression  
6    coefficient does not span to zero.

7    Standardized partial coefficients for the most parsimonious model for two response variables, total  
8    abundance and species richness sampled for data collected during both seasons. Analyses were  
9    performed for landscape variables, natural vegetation cover and inverse number of patches, measured  
10    at six different landscape sizes (500m, 2km, 4km, 6km, 8km and 10km of radius from sampling site).  
11    Akaike information criterion corrected for small samples and weight of each model are also shown.  
12    Predictor variables were standardized *a priori* for the analysis. Each table line represents the best  
13    model considering all competing ones for that specific landscape size and response variable.

Radius	Total abundance		Species richness	
	Natural vegetation cover	Inverse number of patches	Natural vegetation cover	Inverse number of patches
500m	0.135	0.135	0.38	0.16
2km	0.27	0.154	0.68	0.19
4km	0.296	0.14	0.4	0.22
6km	0.43	0.19	0.37	0.23
8km	0.51	0.2	0.39	0.3
10km	0.177	0.159	0.203	0.143

## 1 **Appendix 7**

2 Standardized partial coefficients for the most parsimonious model for two response variables, total  
 3 abundance and species richness sampled for data collected during both seasons. Analyses were  
 4 performed for landscape variables, natural vegetation cover and inverse number of patches, measured  
 5 at six different landscape sizes (500m, 2km, 4km, 6km, 8km and 10km of radius from sampling site).  
 6 Akaike information criterion corrected for small samples and weight of each model are also shown.  
 7 Predictor variables were standardized *a priori* for the analysis. Each table line represents the best  
 8 model considering all competing ones for that specific landscape size and response variable.

9

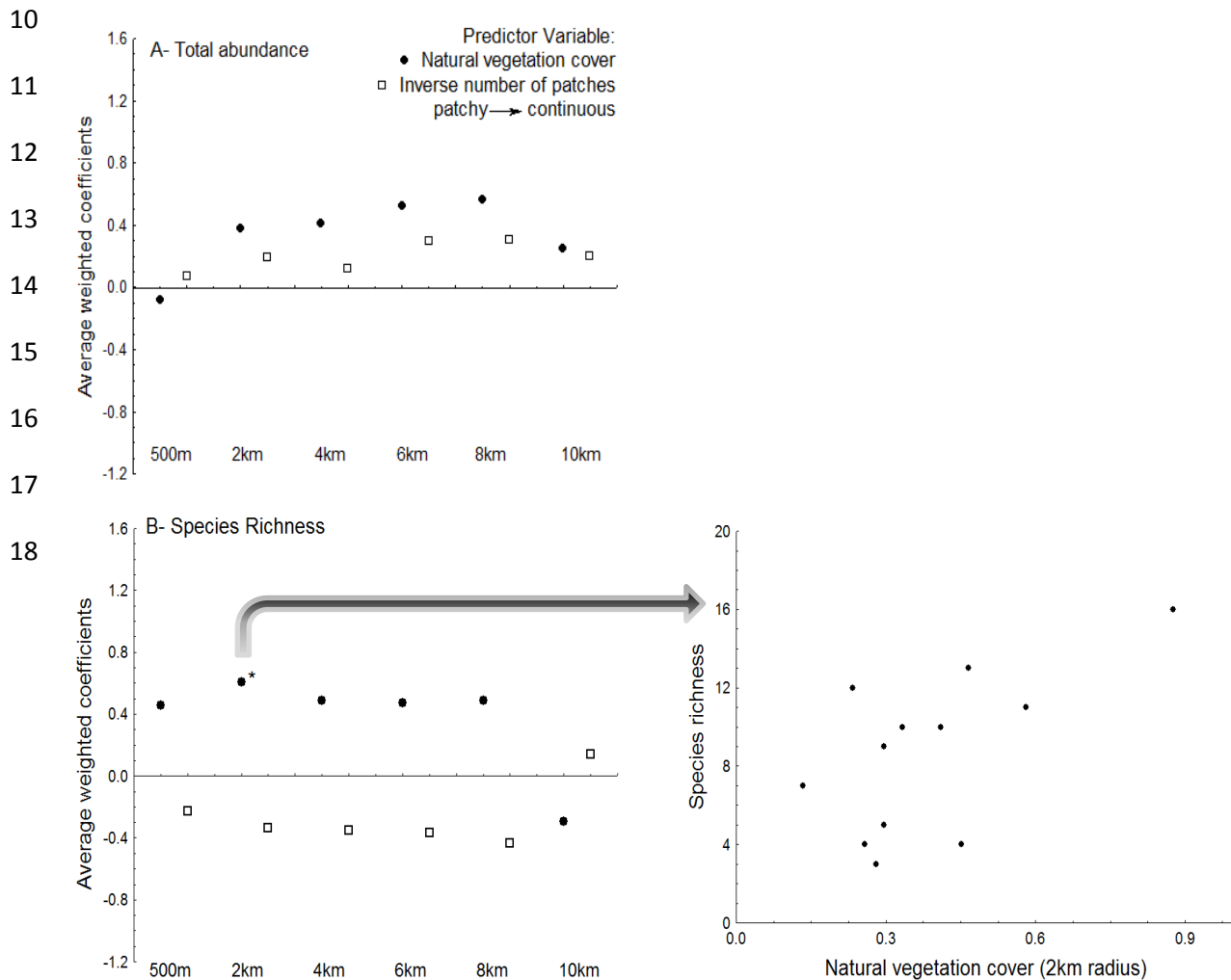
	<b>Radius</b>	<b>Amount of natural area</b>	<b>Inverse number of patches</b>	<b>AICc</b>	<b>Weight</b>
Abundance	500m			128.99	0.74
	2km			128.99	0.62
	4km			128.99	0.61
	6km			128.99	0.49
	8km			128.99	0.43
	10km			128.99	0.69
Species richness	500m			72.19	0.50
	2km			70.08	0.60
	4km			72.19	0.42
	6km			72.19	0.43
	8km			72.19	0.36
	10km			72.19	0.67

10

11

## 1 Appendix 8

2 Average of the weighted standardized partial coefficients of predictors for each landscape size  
 3 obtained using a multi-model inference approach. Data collected during both seasons. Solid circles  
 4 are the weighted standardized coefficients for natural vegetation cover. Open squares are the same  
 5 coefficient for inverse number of patches. Asterisks are confidence intervals of 95% that does not  
 6 span zero and are considered significant. A- weighted standardized coefficients for total abundance,  
 7 number of bats captured; and B- for species richness; C- dispersion of sample units at the best scale  
 8 of effect (2km, where the coefficient was larger) between bat species richness and natural vegetation  
 9 cover.



## 1 Appendix 9

2 Standardized partial coefficients for the most parsimonious models relating four response variables,  
 3 variance in body size, wingspan to wing width ratio, ear size to body mass ratio, and number of  
 4 feeding habits to natural vegetation cover and number of patches, measured at six landscape sizes  
 5 (500m, 2km, 4km, 6km, 8km and 10km radius from sampling site). Akaike information criterion  
 6 corrected for small samples and the weight of each model are also shown. Predictor variables were  
 7 standardized *a priori* for the analysis. Each line represents the best model considering all competing  
 8 models for that specific landscape size and response variable.

	Radius of landscape	Natural vegetation cover	Inverse number of patches	AICc	Weight
Body Mass	500m			239.28	0.560
	2km	66.320		239.14	0.380
	4km		68.630	238.90	0.320
	6km		79.400	237.60	0.452
	8km		88.950	236.30	0.552
	10km			239.30	0.538
Wing Shape	500m			-83.50	0.568
	2km			-83.50	0.560
	4km			-83.50	0.441
	6km			-83.50	0.461
	8km			-83.50	0.468
	10km			-83.50	0.50
Ear	500m			-12.20	0.645
	2km			-12.20	0.624
	4km			-12.20	0.555
	6km			-12.20	0.539
	8km			-12.20	0.548
	10km			-12.20	0.442
Guilds	500m			26.00	0.607
	2km		0.199	25.00	0.490
	4km		0.183	25.70	0.418
	6km		0.192	25.30	0.430
	8km		0.201	24.90	0.446
	10km	-0.201	0.319	22.20	0.568

1 **Appendix 10-** Standardized partial coefficients for the most parsimonious models relating  
2 phytophagous and animalivorous abundances to natural cover and number of patches at six different  
3 landscape sizes (500m, 2km, 4km, 6km, 8km and 10km radius from sampling site). Akaike  
4 information criterion corrected for small samples and the weight of each model are also shown.  
5 Predictor variables were standardized *a priori*. Each line represents the best model considering all  
6 competing models for that landscape size and response variable.

	Radius of landscape	Natural vegetation cover	Inverse number of patches	AICc	Weight
Phytophagous	500m			178.32	0.64
	2km			178.32	0.64
	4km			178.32	0.33
	6km	19.21	15.18	177.01	0.45
	8km	18.49	13.88	177.81	0.35
	10km			178.32	0.40
Animalivorous	500m			97.44	0.61
	2km			97.44	0.52
	4km			97.44	0.41
	6km			97.44	0.35
	8km			97.44	0.35
	10km			97.44	0.47

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22

**CHAPTER 2: The relative importance of local and landscape variables on bat occupancy**

**Student: Poliana Mendes**  
Programa de Pós-Graduação em Ecologia e Evolução  
Universidade Federal de Goiás  
**Advisor: Dr. Paulo De Marco Júnior**  
Universidade Federal de Goiás  
**Collaborators: Luciana Signorelli Faria Lima & Kimberly A. With**  
Kansas State University

## Abstract

Landscape and local variables are measured at different scales, but both can affect species occupancy. Landscape variables would be more important if occupancy is affected by composition or configuration of the landscape. Local variables would be more important if species are sensitive to slight differences on vegetation structure, such as habitat quality. We tested if local or landscape variables would be more important to explain eight bat species occupancy, using data from 16 sampled forest areas in the Brazilian Cerrado. Landscape variables were measures for two landscape sizes, 2km and 8km of radius; they were natural vegetation amount and number of patches in the landscape. Local variables were measured in three quadrants of 10X10m, they were canopy cover, understory height, number of trees and number of Lianas. For *Sturnira lilium* and *Myotis nigricans* landscape variables were more important, while for *Desmodus rotundus* local variables were more important. For the other five species, *Artibeus cinereus*, *Artibeus lituratus*, *Glossophaga soricina*, *Platyrrhinus incarum*, and *Platyrrhinus lineatus*, local and landscape variables per performed as well as models only considering a constant as intercept. This result is suggesting idiosyncratic results depending of species, both local and landscape variables can be important to explain bat occupancy in forest patches.

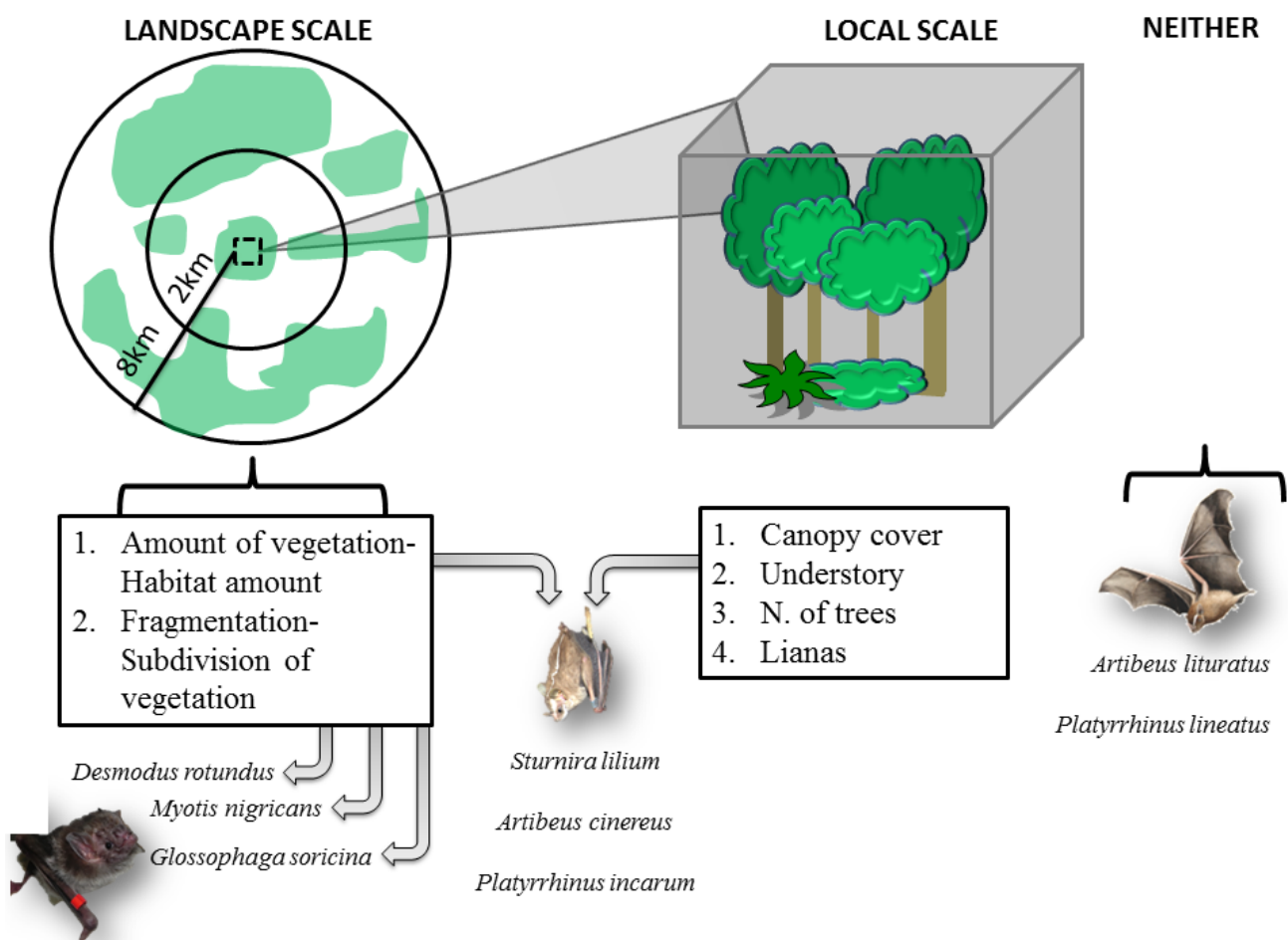
**Keywords** Detectability, Chiroptera, fragmentation, habitat quality and habitat loss.

## 1    **Introduction**

2  
3        Many environmental variables could potentially influence species incidence, either because  
4 they are related with conditions, either with resources that allow populations to persist. The influence  
5 of those environmental variables in species incidence is one of the most common research subjects in  
6 ecology. However, this issue is strongly influenced by the studied scale (Wiens 1989). At a broader  
7 scale, mostly climate variables have been related to species distribution ranges and species richness  
8 (Brown 1984; Soberón & Nakamura 2009). At an intermediate and finer scale, respectively,  
9 landscape and local variables have been related to occupancy and species richness (e.g. Estrada-  
10 Villegas *et al.* 2012; López-González *et al.* 2014; Mendenhall *et al.* 2014). Occupancy accounts for  
11 the probability of a site to be occupied by a taxon given its detectability (Mackenzie *et al.* 2006), so  
12 it is an interesting response variable to understand how environmental changes in finer scales may  
13 affect species incidence.

14        Despite the vagueness of “intermediate and finer scale” expression in the previous paragraph,  
15 occupancy analyses are usually dealing with the landscape or local spatial scales (Blevins & With  
16 2011; Mortelliti *et al.* 2012), which are mostly defined upon the grain size used to measure the  
17 environmental variables (Figure 1). Usually we expect that an acceptable grain-size for landscape  
18 variables should be related to species biology, such as home-range sizes (Jackson & Fahrig 2012).  
19 Landscape variables are taken from a classification of an “aerial view” of the landscape, separating  
20 each vegetation type in that landscape according with expected perception of the studied species.  
21 Examples of landscape scale variables are forest amount, edge density or number of forest patches in  
22 a landscape. On the other hand, local variables are taken from a “ground view”, where local details  
23 are collected of a sampling site, and are in general connected with habitat quality (Mortelliti *et al.*  
24 2010). Examples of local variables could be vegetation structure, such as mean of tree height, density  
25 of trees or litter height; or stream structure, such as stream width or floating velocity. Both types of

variables may affect species occupancy (Blevins & With 2011; Mortelliti *et al.* 2012), but the relative importance of each one depends on the studied species. The search for a predictive view of individual species responses is related to how species perceive habitat differences or, as stated by Macarthur & Levins (1964), “the grain-size of response to environmental variables”. If species choose sites to forage and roost based on slight distinctions on vegetation, they would respond to local level variables; but if they only differentiate sites based on broad vegetation types, they would respond to landscape structure. Some biomic differences among species, such as body size and dispersal capacity may direct affect how those species are expected to perceive environmental differences (With 1994).



10

11 **Figure 1-** Conceptual model and expected responses of bats to environmental variables taken in  
 12 different grain sizes. While landscape variables are taken from an aerial view of the landscape, local

variables are taken from a ground view. Our three competitive hypotheses are that landscape scale, local scale or none of these would be more important to explain bat occupancy for eight bat species. We expect that importance of each type of variable depends of species habitat perception. We have particular predictions for each species depending of its dispersal ability; forage behavior and reported occurrence in human-altered areas (see Introduction for specific predictions). © *A. lituratus* illustration- Leandro Lopes de Souza. © *D. rotundus* photo- Poliana Mendes. © *P. incarum* photo Pedro Henrique Pereira Braga.

Bat diversity, abundance and composition are strongly correlated with both local (habitat quality) and landscape (surrounding vegetation) variables (Estrada-Villegas *et al.* 2012; López-González *et al.* 2014; Mehr *et al.* 2011). Nevertheless, effects of human landscape alteration in bats seem to be idiosyncratic, and different species may exhibit distinct responses to these changes (Harvey & Villalobos 2007; Medellín *et al.* 2000; Mendenhall *et al.* 2014). Phyllostomidae bats, for example, are benefitted by agroforest systems (Faria *et al.* 2006), but they avoid sites where the understory or canopy was removed (García-Morales *et al.* 2013). The predicted importance of vegetation characteristics for bats may highlight the impact of current land use changes in bat assemblages, but also how those effects are amplified due to important ecosystem services performed by bats, such as pollination, insect control and seed dispersal ecological functions (Fleming *et al.* 2009; Jacomassa & Pizo 2010; Kalka *et al.* 2008; Muscarella & Fleming 2007; Quesada *et al.* 2004).

Landscapes have experienced enormous changes in the past decades in a worldwide scale, mostly due to conversion to agriculture (Murphy & Romanuk 2014). Tropical savannas are among the most harvested areas in the world (Hoekstra *et al.* 2004). The Cerrado, a savanna in Brazil, is considered a biodiversity hotspot (Myers *et al.* 2000), being the most threatened and richest tropical savanna in the world (Da Silva & Bates 2002). The exploitation of this biome is still increasing,

1 because it is located in a major agricultural frontier in Brazil and, most impacted by pasturelands  
2 (Sano *et al.* 2010). Our aim is to investigate the relative importance of local and multi-grained  
3 landscape vegetation variables in the occupancy of eight bats in the Brazilian Cerrado. We used  
4 multi-grained landscape variables, because landscape structure and composition may affect species at  
5 different grain-sizes (Wiens 1989). For each of the eight species we tested three competitive set of  
6 models: (1) occupancy is better explained by landscape level variables; (2) local variables or (3) for  
7 none of both variables. To test it, we sampled bats in 16 forest patches in Cerrado, collecting  
8 landscape (natural vegetation amount and number of patches) and local (canopy cover, understory  
9 height, tree density and lianas density) variables from sampling sites.

10 Local and landscape variables were chosen because of their potential correlation with bat  
11 occupancy. Natural vegetation amount in a landscape could be important if it is a good predictor of  
12 habitat amount for a species (Fahrig 2003). Landscape configuration, or subdivision of habitats,  
13 would be important because some bats are edge-sensitive (Kerth & Melber 2009; Meyer *et al.* 2007)  
14 and because it increases the number of times that an individual needs to cross the matrix (Pe'er *et al.*  
15 2011). Canopy cover could be related to protection against predators, wind and rain (Fenton *et al.*  
16 1998). Understory could be related to food resources amount available for some bat species (Thies &  
17 Kalko 2004; Trevelin *et al.* 2013). Tree density is related to roost and food availability (Evelyn &  
18 Stiles 2003). Liana quantity could be a predictor of obstacles (Tabanez & Viana 2000), that bats  
19 would encounter during flight.

20 We predict responses for both local and landscape variables depending of food and flight  
21 habits of each analyzed species (Figure 1). Hematophagous species, *Desmodus rotundus*, may be  
22 beneficiated by land-use intensification at landscape scale (García-Morales *et al.* 2013; Harvey &  
23 Villalobos 2007; Medellín *et al.* 2000), because they could use cattle as a food resource.  
24 Background-cluttered space aerial insectivore, *Myotis nigricans*, is expected to respond positively to  
25 fragmentation *per se* because they use edges to forage, at landscape scale (Denzinger & Schnitzler

2013; Estrada-villegas *et al.* 2010). Nectarivores bats, *Glossophaga soricina*, have high dispersal ability (Aguiar *et al.* 2014), and are expected to be affected by landscape scale variables. Understory frugivores, *Sturnira lilium*, should be dependent of understory height and benefit by edges, where understory vegetation is more abundant (Tabanez & Viana 2000), but are still positively related to amount of natural vegetation (Muscarella & Fleming 2007), at both local and landscape scale. Small canopy fruit-bats, *Artibeus cinereus* and *Platyrrhinus incarum*, should be affected by local variables, such as canopy density, and also for landscape variables, because they may wander in the landscape in search of mature fruits, at both local and landscape scale. Large canopy fruit-bats, *Platyrrhinus lineatus* and *Artibeus lituratus*, should not be sensitive to both landscape and local environmental variables, because they have a high dispersal capacity (Bianconi *et al.* 2006); movements of 70km have been found for *A. lituratus* (Menezes Jr. *et al.* 2008), and they use to occupy even highly human altered areas (Oprea *et al.* 2009).

## Methods

### Overview

We evaluated relative importance of landscape and local variables using bat incidence data on forest remnants that were sampled with mist nets during four nights. Landscape structure variables were measured for two landscape sizes, both at a 2km and 8km radius from sample site. They were natural vegetation cover and number of patches in the landscape. Local variables were sampled in quadrants close to the mist nets, for each quadrant we measured understory height, canopy cover, number of trees and number of Lianas. Competing models considering landscape or local variables were compared using a multi-model approach.

## 1    *Study area*

2            The study was developed in 16 landscapes in the state of Goiás, central Brazil. The  
3    predominant vegetation is a savannic formation called Cerrado. This biome has a mosaic of natural  
4    vegetation formations, such as dry forests, gallery forests, grasslands and wetlands (Sano *et al.*  
5    2010). The Cerrado biome has two distinct seasons per year, dry and wet, with different rainfall  
6    patterns. We selected 16 sampling sites with similar characteristics to avoid potential confounding  
7    variables. All sampling sites were forest patches, with similar size (90 to 400 ha) and shape (shape  
8    index < 2). Spatial data was obtained from the Ministry of Environment of Brazil  
9    (<http://siscom.ibama.gov.br/monitorabiomas>) for the year 2010. Forest vegetation was chosen  
10   because it has higher species richness compared to other savannic formations (Gregorin *et al.* 2011;  
11   Monadjem & Reside 2008). We found 209 forest patches in the state of Goiás following those  
12   criteria. Patches were selected in order to avoid correlations between the two measured landscape  
13   variables: natural vegetation amount and number of patches for the scale of 5km of radius. This scale  
14   was chosen because it was previously shown that this is the best scale to predict bat relative  
15   abundance and species richness (Gorresen *et al.* 2005). For site selection we calculated natural  
16   vegetation cover and number of natural patches within a buffer of 5km around the centroid of each  
17   one of the 209 forest patches following the previous criteria.

18

## 19   *Bat sampling and species selected*

20            Bats were sampled using 20 mist nets (10 X 2.5m), placed from the edge through the core of  
21   each forest patch, in groups of five nets, during four consecutive days (six hours each, starting at  
22   sunset). Nets stayed at the first place until the end of the four days. We sampled 16 forest patches,  
23   one patch at a time. Sampling occurred between March 2012 and March 2014. All bats were  
24   identified to species level.

We selected eight bats, among bats that were captured in more than 20% and less than 80% of sampling sites; one hematophague *Desmodus rotundus*, one background-cluttered areas aerial insectivore *Myotis nigricans*, one nectarivore *Glossophaga soricina*, one understory frugivore *Sturnira lilium*, two small canopy frugivores *Artibeus cinereus* and *Platyrrhinus incarum*, and two big canopy frugivores *Artibeus lituratus* and *Platyrrhinus lineatus*. Naïve occupancy varied from 0.25 to 0.75 among species.

### *Predictor variables*

We have two groups of competing predictor variables, local environmental variables and landscape variables. Landscape metrics were obtained of satellite images from LANDSAT ETM+ from August 2013, 30m resolution, compositional bands 5, 4 and 3. We used a different landscape data source than for site selection to improve the quality of the landscape classification, since we would use this data to relate bat occupancy with landscape metrics. We have used images from dry season to avoid clouds that could hamper classification. A supervised classification was performed to separate savanna+forest (natural vegetation) from all other land covers (matrix). We joined savanna and forest in the classification because many bat species use both savanna and forest to forage, roost or move (Aguirre 2002; Bernard & Fenton 2003), despite forest vegetation having more species (Gregorin *et al.* 2011; Monadjem & Reside 2008). Two landscape metrics representing landscape composition and configuration were measured: natural vegetation area and number of patches (Table 1). Natural vegetation area represents the amount of habitat in a landscape. Number of patches represents how subdivided is that vegetation, more subdivision means more small patches, higher edge density and more times crossing non-habitat areas. Patchy landscapes can have fewer individuals of edge-sensitive or matrix-avoiding species. We used the inverse of number of patches in analyses to keep the direction patchy to continuous landscapes. Both metrics were measured for two landscape sizes; with a radius of 2km and 8km, because we did not know at which scale bat

species would respond to landscape variables. We decided to choose two landscape sizes that would include even large daily movements (Aguiar *et al.* 2014; Trevelin *et al.* 2013; Womack *et al.* 2013).

We also sampled local variables at the same forest patches as bats were sampled. We sampled three quadrants of 10X10m, the first was placed at the beginning of the mist nets, the second at the middle, and the third at the end. At each quadrant we quantified the number of trees (with more than 5cm of branch diameter), height of understory, canopy density and presence of Lianas (Table 1). Number of trees in the quadrant was chosen because it represents an indirectly measurement of the amount of resources for bats, such as food and shelter. Understory height was chosen because some bat species preferentially use this part of vegetation. We measured understory height with a 2m pole divided into 10 equal parts; we counted for each corner of the quadrant, how many parts of the pole were covered by understory. Canopy density was chosen because canopy offers protection for some bats against predators, wind or rain. Canopy density was measured with a convex spherical densitometer measured in each corner and the center part of each quadrant. Number of Lianas was chosen because they are obstacles for bats during flight. All variables were standardized prior to the analysis. We also calculated correlations among variables to delete correlated variables avoiding collinearity problems in the following analyses (Table 2).

### *Detection bias*

Species may not be detected in all patches that they inhabit, so false absences are common in ecological studies. This detection bias can lead to an underestimation of occupancy (Kellner & Swihart 2014; Mackenzie *et al.* 2002). In way to reduce effects of false absences we took some cautions: 1) we avoided sampling bats on full moon nights, because of reduced sampling success (Mello *et al.* 2013); 2) samplings occurred only during wet season to avoid seasonality bias on detection; 3) sampling always started at sunset and lasted six hours to avoid bias caused by different time activity among bat species. Despite all these cautions, detection probability among sites can still

1 occur due a many and varied factors site specific. Considering this, we selected some environmental  
2 variables that could influence in bat activity and can influence the detection capability (Barros *et al.*  
3 2014; Mello *et al.* 2008a), such as air temperature, observer, wind and rain (Table 1). Temperature  
4 was measured during sampling surveys with an air thermometer. In this study two different people  
5 performed the sampling, and are included as observers in the analysis. Data for wind velocity and  
6 rain was obtained from the Brazilian meteorology institute (<http://inmet.gov.br>) for the closest  
7 meteorological station from sampling sites, when the velocity was larger than 4m/s it was considered  
8 as 1, and when the velocity was smaller, as 0. Precipitation larger than 1mm was considered as 1 for  
9 presence of rain. To confirm data about wind and rain, at each sampling night, the observer took note  
10 of the presence of rain and wind.

11 Detectability was accessed by calculating the probability of detecting a species since it is  
12 present. Detection probability is calculated using detection history in each one of the four nights  
13 sampled for each site. We used a multi-model approach, having models with each one of the  
14 detectability variables competing, as well as, a model having only a constant as a parameter (Table  
15 1). When the model having only a constant performed as good as a detection model ( $\Delta AIC < 2$ ), we  
16 did not consider that detection variable as important for occupancy models, avoiding unnecessary  
17 over parametrization. When a variable performed better than the model with only a constant, we  
18 consider that one or more variables in the occupancy models.

19

20

**Table 1-** Covariates used in detectability and occupancy models with respective descriptions.

Occupancy covariates include landscape and local variables. Landscape variables are natural vegetation amount and number of patches that were collected for two landscape sizes, radius of 2km and 8km from sampling site. Local variables are understory height, canopy cover, number of trees and number of Lianas. Local variables were collected in three quadrats (10X10m) located at the same place as mist nets were.

7

Covariates	Variable	Variable Type	Description
<b>Detection</b>			
Constant	.	None	Detection assumed to be constant
Temperature	Temp	Continuous	Mean temperature measured during bat survey (Celsius degrees)
Observer	Obse	Categorical	Observer that performed the survey, two observers
Wind	Wind	Categorical	Presence of wind during the survey (speed > 4m/s)
Rain	Rain	Categorical	Presence of rain during the survey
<b>Occupancy</b>			
Natural vegetation amount (2km radius)	Nat2	Continuous	Natural vegetation amount in a landscape of 2km of radius from the sampling site
Number of patches (2km radius)	NP2	Continuous	Number of patches in a landscape of 2km of radius from the sampling site
Natural vegetation amount (8km radius)	Nat8	Continuous	Natural vegetation amount in a landscape of 8km of radius from the sampling site
Number of patches (8km radius)	NP8	Continuous	Number of patches in a landscape of 8km of radius from the sampling site
Understory	Under	Continuous	Understory height measured in 12 spots in the area of sampling site
Canopy cover	Cano	Continuous	Canopy density measured with a densitometer in 15 spots in the area of sampling site
Number of trees	Tree	Continuous	Number of trees counted in 3 quadrats of 10X10m
Lianas	Lian	Continuous	Number of Lianas counted in 3 quadrats of 10X10m

8

9

**Table 2-** Pearson correlation coefficients for pairs of occupancy variables, four landscape variables and four habitat variables. Landscape variables included natural vegetation cover and number of patches for two different landscape sizes, radius of 2km and 8km. There were some missing values for habitat variables, correlations were made for the number of sampling units that were sampled for each habitat variable. Number of sampling units showed in parenthesis. Bold values are significant,  $p < 0.05$ . Because number of lianas and understory height are correlated we used only lianas in occupancy models, because lianas have less missing values. Landscape variables in different landscape sizes were not compared because they are not in competing models. Relative importance of different landscape sizes were tested in distinct analyses, because they are not independent.

Variables	Nat2	INP2	Nat8	INP8	Under	Cano	Tree
<b>Nat2</b>							
<b>INP2</b>	0.37 (18)						
<b>Nat8</b>							
<b>INP8</b>			0.46 (18)				
<b>Under</b>	0.19 (15)	0.43 (15)	0.11 (15)	0.17 (15)			
<b>Cano</b>	0.01 (17)	-0.16 (17)	-0.14 (17)	0.07 (17)	0.03 (15)		
<b>Tree</b>	0.03 (17)	0.20 (17)	-0.23 (17)	0.13 (17)	0.38 (15)	-0.24 (17)	
<b>Lian</b>	-0.02 (16)	-0.01 (16)	-0.20 (16)	-0.21 (16)	<b>0.55 (14)</b>	0.19 (16)	0.34 (16)

## 1 *Occupancy models*

2 Naïve occupancy rate is the proportion of sites at which the target species was detected.

3 Given problems with detectability and insufficient sampling effort, the naïve occupancy rate is

4 probably underestimated. Occupancy estimate, accounting for detectability, is modeled as a logistic  
5 function of predictor variables. We constructed nine types of models that could explain bat

6 occupancy in sampled sites according with our hypotheses (Table 3). We constructed models in that

7 only local variables were predictors, only landscape, or only each one of measured variables, besides  
8 a global model and constant model (only with a intercept). The same models were repeated for radii

9 of 2km and 8km. We used for discussion only the radius in that landscape variables performed better  
10 (smaller AIC).

11 We used single species, single season occupancy models, according to Mackenzie *et al.* 2006.

12 Akaike information criterion (AICc) corrected for small samples was calculated for all models

13 (Burnham & Anderson 1998). Also the importance of each variable that was the sum of weights of

14 all models in which that variable was in. It was possible to compare the importance of different

15 variables since each variable was used in the same number of models. Pearson Chi-square statistic

16 and a bootstrap procedure (10000 times) were used to define whether the data dispersion to the

17 model was unusually large in the global model. The bootstrap procedure calculates the

18 overdispersion parameter ( $\hat{c}$ ). When  $\hat{c} > 1$ , we used the square root of overdispersion parameter

19 multiplied by standard errors, calculating a Quasi-Akaike information criterion (QAICc). Occupancy

20 models have some assumption such as, occupancy status at each site does not change in different

21 surveys (nights sampled) over the season; probability of occupancy is constant across sites, unless it

22 is affected by covariates; and detection of species and detection histories are independent.

23 Detectability and occupancy analyses were performed using the software Presence (Hines 2006). In

24 some cases, numerical convergence in the models was not reached, so parameters estimation was not

25 reliable. In these cases, we changed the optimization method for simulated annealing that is a

stochastic model for optimization. Simulated annealing optimizations were performed using the package “unmarked” for software r (Fiske & Chandler 2011; R Core Team 2008).

**Table 3-** Competing models for explaining bat occupancy. Nine models competed for each landscape size, with a radius of 2km and 8km from sampling sites. The Global model included all local and landscape variables. Competing hypotheses were that only landscape variables would be more important to explain bat occupancy, only local variables or neither of them. Models that considered that only landscape variables would be important were constructed including or both landscape variables, only natural vegetation cover or only number of patches. Models that considered that only local variables would be important considered all local variables, only canopy cover, only number of trees or only number of lianas.

Competing models		Models	
Landscape size	2km radius	8km radius	
<i>Landscape variables hypothesis</i>	Nat2+Nup2	Nat8+Nup8	
Habitat amount	Nat2	Nat8	
Configuration	NP2	NP8	
<i>Local variables hypothesis</i>	Cano+Tree+Lian	Cano+Tree+Lian	
Canopy cover	Cano	Cano	
Number of trees	Tree	Tree	
Lianas	Lian	Lian	
<i>Global model</i>	Nat2+NP2+Can+Tree+Lian	Nat2+NP2+Can+Tree+Lian	
<i>Constant model</i>	Constant	Constant	

## Results

Models considering detectability were better to explain the data than other models (detectability equal to one) for two of the eight species: *Artibeus cinereus* and *Glossophaga soricina* (Table 4). For *A. cinereus*, temperature was an important variable to determine detectability, but for

*G. soricina* it was the presence of the observer. For these two species, occupancy models considered detectability variables. For other species, the model only considering a constant, performed as well as models with detectability covariates. For *Desmodus rotundus* and *Artibeus lituratus* temperature was as good as the model with constant detectability. For *Desmodus rotundus*, *Myotis nigricans*, *Sturnira lilium* and *Artibeus lituratus* wind was as good as the model with constant detectability.

**Table 4-** Detectability models for each species, covariates were temperature (Temp), observer (Obse), presence of wind (Wind) and presence of rain (Rain) during field works. Only models with  $\Delta AICc < 2$  are being showed. L is the model likelihood and k the number of parameters of a model.

Espécie	Model	AICc	$\Delta AICc$	Weight	L	k	Partial coefficients
<i>Desmodus rotundus</i>							
	psi(.),p(.)	47.68	0	0.43	0.02	2	
	psi(.),p(Wind)	48.56	0.88	0.28	0.02	3	Wind=-8.01
	psi(.),p(Temp)	49.14	1.46	0.21	0.02	3	Temp=-0.25
<i>Myotis nigricans</i>							
	psi(.),p(.)	44.39	0	0.43	0.01	2	
	psi(.),p(Wind)	45.54	1.147	0.24	0.01	3	Wind=-6.00
<i>Glossophaga soricina</i>							
	psi(.),p(Obse)	74.36	0	0.43	0.10	3	Obse=2.26
<i>Sturnira lilium</i>							
	psi(.),p(.)	42.15	0	0.43	0.05	2	
	psi(.),p(Wind)	43.71	1.56	0.20	0.04	3	Wind=-12.35
<i>Artibeus cinereus</i>							
	psi(.),p(Temp)	50.34	0	0.43	0.07	3	Temp=0.47
<i>Platyrrhinus incarum</i>							
	psi(.),p(.)	76.32	0	0.43	0.38	2	
<i>Artibeus lituratus</i>							
	psi(.),p(Temp)	78.17	0	0.43	0.01	3	Temp=2.37
	psi(.),p(.)	78.86	0.69	0.31	0.004	2	
<i>Platyrrhinus lineatus</i>							
	psi(.),p(.)	49.60	0	0.43	0.29	2	

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21

Global models had distinct fit to data, *Desmodus rotundus* (2km landscape;  $\chi^2=18.116$ ;  $p=0.445$  and 8km landscape;  $\chi^2=18.116$ ;  $p=0.453$ ), *Myotis nigricans* (2km landscape;  $\chi^2=12.607$ ;  $p=0.719$  and 8km landscape;  $\chi^2=12.621$ ;  $p=0.814$ ), *Glossophaga soricina* (2km landscape;  $\chi^2=30.704$ ;  $p=0.045$  and 8km landscape;  $\chi^2=30.177$ ;  $p=0.051$ ), *Sturnira lilium* (2km landscape;  $\chi^2=16.660$ ;  $p=0.200$  and 8km landscape;  $\chi^2=16.660$ ;  $p=0.206$ ), *Artibeus cinereus* (2km landscape;  $\chi^2=20.721$ ;  $p=0.236$  and 8km landscape;  $\chi^2=20.721$ ;  $p=0.230$ ), *Platyrrhinus incarum* (2km landscape;  $\chi^2=15.915$ ;  $p=0.718$  and 8km landscape;  $\chi^2=15.915$ ;  $p=0.718$ ), *Artibeus lituratus* (2km landscape;  $\chi^2=29.105$ ;  $p=0.059$  and 8km landscape;  $\chi^2=29.105$ ;  $p=0.060$ ) and *Platyrrhinus lineatus* (2km landscape;  $\chi^2=24.829$ ;  $p=0.150$  and 8km landscape;  $\chi^2=25.107$ ;  $p=0.136$ ). Overdispersion coefficient of global model varies from 0.68 to 1.50, and for five species overdispersion was larger than 1 (Table 5). In these cases QAICc was used instead of AICc.

We considered for interpretation only the scale (2km or 8km) in that landscape variables performed better (smaller AIC). For two species, models with landscape variables explained better data than any other models ( $\Delta AICc$  or  $\Delta QAICc < 2$ ), *Sturnira lilium* and *Myotis nigricans* (both at 8km scale). For one species only local variables were among best models, *Desmodus rotundus*. For the five last species, models only considering a constant performed as well as local or landscape variables. For three species models, local variables models were among best models, *Platyrrhinus incarum*, *Artibeus cinereus* and *Glossophaga soricina*. For two both landscape and local variables were among best models, *Artibeus lituratus* and *Platyrrhinus lineatus* (Table 5).

**Table 5-** Best models explaining bat occupancy. Only models with  $\Delta AICc$  or  $\Delta QAICc < 2$  are being shown. Local predictors are canopy cover (Cano), number of trees (Tree) and number of Lianas (Lian) collected in three quadrants (10X10m) at the same location as bats were sampled. Landscape variables included natural vegetation cover (Nat2 or Nat8, for radii of 2km or 8km scale) and inverse number of patches (INP2 or INP8) measured in two different landscape sizes, with a radius of 2km and 8km. When global models had overdispersion coefficients ( $\hat{c}$ )  $> 1$ , all the competing models were corrected by this overdispersion factor and QAICc was showed instead AICc. Number of parameters per model is k.  $\hat{\psi}$  is the naïve occupancy estimator, number of sampling sites that a species was detected divided by the number of landscapes sampled. \* are models that did not converged and we used a simulated annealing optimization approach to find partial coefficient values. Bold values represent the scale of effect (2km or 8km) in which results were interpreted, the scale of effect was chosen by the smaller values of AIC for models including landscape scale variables.

		Models	QAIC or AICc	$\Delta QAICc$ or $\Delta AICc$	w	k	Partial coefficients
<i>Desmodus rotundus</i>		( $\hat{\psi}=0.32$ )					
2km	$\hat{c}= 0.95$	psi(Cano),p(.)	41.12	0.00	0.88	3	Cano=-13.78
<b>8km</b>	<b><math>\hat{c}= 0.94</math></b>	<b>psi(Cano),p(.)</b>	<b>41.12</b>	<b>0.00</b>	<b>0.88</b>	<b>3</b>	<b>Cano= -13.78</b>
<i>Myotis nigricans</i>		( $\hat{\psi}=0.32$ )					
2km	$\hat{c}= 0.69$	psi(INP2),p(.)	42.73	0.00	0.38	3	INP2=3.47
		psi(.),p(.)	44.39	1.66	0.17	2	
		psi(Tree),p(.)	44.53	1.80	0.16	3	Tree= 1.54
<b>8km</b>	<b><math>\hat{c}= 0.68</math></b>	<b>psi(INP8),p(.)</b>	<b>36.60</b>	<b>0.00</b>	<b>0.65</b>	<b>3</b>	<b>*INP8= 18.51</b>
		<b>psi(Nat8+INP8),p(.)</b>	<b>38.04</b>	<b>1.44</b>	<b>0.31</b>	<b>4</b>	<b>*Nat8= 1.46, INP8=-23.74</b>

**Table 5-** Continuation

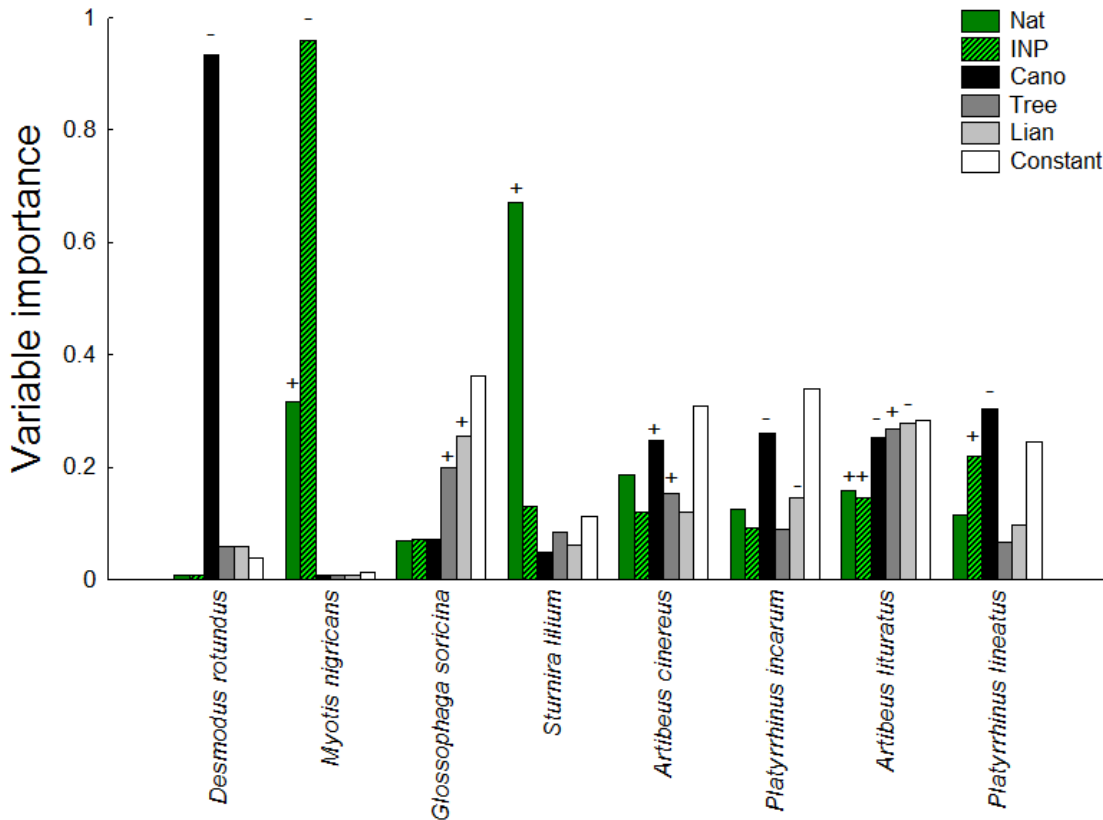
<i>Glossophaga soricina</i>		$(\hat{\psi}=0.63)$				
<b>2km</b>	<b><math>\hat{c}= 1.50</math></b>	<b>psi(.),p(Obse)</b>	<b>52.24</b>	<b>0.00</b>	<b>0.36</b>	<b>3 Obse=2.26</b>
		<b>psi(Liana),p(Obse)</b>	<b>53.04</b>	<b>0.80</b>	<b>0.24</b>	<b>4 Lian= 9.18;Obse=1.85</b>
		<b>psi(Tree),p(Obse)</b>	<b>53.55</b>	<b>1.31</b>	<b>0.19</b>	<b>4 Tree= 4.21 ; Obse= 1.82</b>
8km	$\hat{c}= 1.47$	psi(.),p(Obse)	53.13	0.00	0.36	3 Obse=2.26
		psi(Lian),p(Obse)	53.87	0.74	0.25	4 Lian= 9.18;Obse=1.85
		psi(Tree),p(Obse)	54.39	1.26	0.19	4 Tree= 4.21 ; Obse= 1.82
<i>Sturnira lilium</i>		$\hat{\psi}= 0.25$				
2km	$\hat{c}= 1.29$	psi(.),p(.)	33.72	0.00	0.32	2
		psi(Tree),p(.)	34.49	0.77	0.22	3 Tree=-1.72
		psi(Lian),p(.)	35.12	1.40	0.16	3 Lian= -1.33
		psi(Cano),p(.)	35.70	1.98	0.12	3 Cano=-0.978
<b>8km</b>	<b><math>\hat{c}= 1.28</math></b>	<b>psi(Nat8),p(.)</b>	<b>30.69</b>	<b>0.00</b>	<b>0.58</b>	<b>3 *Nat8=12.51</b>
<i>Platyrrhinus incarum</i>		$\hat{\psi}=0.75$				
2km	$\hat{c}= 0.78$	psi(.),p(.)	76.32	0.00	0.34	2
		psi(Cano),p(.)	76.99	0.66	0.24	3 *Cano=-10.87
		psi(Lian),p(.)	78.25	1.92	0.13	3 *Lian=-2.55
<b>8km</b>	<b><math>\hat{c}= 0.78</math></b>	<b>psi(.),p(.)</b>	<b>76.32</b>	<b>0.00</b>	<b>0.35</b>	<b>3</b>
		<b>psi(Cano),p(.)</b>	<b>76.99</b>	<b>0.66</b>	<b>0.25</b>	<b>3 *Cano=-10.87</b>
		<b>psi(Lian),p(.)</b>	<b>78.25</b>	<b>1.92</b>	<b>0.13</b>	<b>4 *Lian=-2.55</b>
<i>Artibeus cinereus</i>		$\hat{\psi}=0.38$				
2km	$\hat{c}= 1.20$	psi(.),p(Temp)	43.44	0.00	0.31	3 Temp= 0.47

**Table 5-** Continuation

		psi(Cano),p(Temp)	44.08	0.64	0.22	4 Cano=1.53; Temp= 0.47
		psi(Tree),p(Temp)	45.25	1.81	0.12	4 Tree=0.92; Temp=0.49
<b>8km</b>	<b><math>\hat{c}= 1.22</math></b>	<b>psi(.),p(Temp)</b>	<b>42.84</b>	<b>0.00</b>	<b>0.31</b>	<b>3 Temp= 0.47</b>
		<b>psi(Cano),p(Temp)</b>	<b>43.53</b>	<b>0.69</b>	<b>0.22</b>	<b>4 Cano=1.53; Temp= 0.47</b>
		<b>psi(Tree),p(Temp)</b>	<b>44.69</b>	<b>1.85</b>	<b>0.12</b>	<b>4 Tree=0.92; Temp=0.49</b>
<i>Artibeus lituratus</i>						
		$\hat{\psi}=0.63$				
<b>2km</b>	<b><math>\hat{c}= 1.42</math></b>	<b>psi(.),p(.)</b>	<b>57.17</b>	<b>0.00</b>	<b>0.28</b>	<b>2</b>
		<b>psi(Cano+Tree+Lian),p(.)</b>	<b>58.11</b>	<b>0.94</b>	<b>0.18</b>	<b>5 Cano= -9.12; Tree=8.78; Lian=-5.44</b>
		<b>psi(Nat2),p(.)</b>	<b>58.77</b>	<b>1.60</b>	<b>0.13</b>	<b>3 Nat2= 1.06</b>
		<b>psi(INP2),p(.)</b>	<b>58.95</b>	<b>1.78</b>	<b>0.12</b>	<b>3 INP2= 0.79</b>
<b>8km</b>	<b><math>\hat{c}= 1.41</math></b>	psi(.),p(.)	57.22	0.00	0.31	2
		psi(Cano+Tree+Lian),p(.)	58.15	0.93	0.19	5 Cano= -9.12; Tree=8.78; Lian=-5.44
<i>Platyrrhinus lineatus</i>						
		$\hat{\psi}=0.32$				
<b>2km</b>	<b><math>\hat{c}= 1.28</math></b>	psi(Cano),p(.)	39.43	0.00	0.34	3 Cano= -1.98
		psi(.),p(.)	39.86	0.43	0.27	2
<b>8km</b>	<b><math>\hat{c}= 1.31</math></b>	<b>psi(Cano),p(.)</b>	<b>38.77</b>	<b>0.00</b>	<b>0.29</b>	<b>3 Cano= -1.98</b>
		<b>psi(.),p(.)</b>	<b>39.13</b>	<b>0.36</b>	<b>0.25</b>	<b>2</b>
		<b>psi(INP8),p(.)</b>	<b>39.67</b>	<b>0.90</b>	<b>0.19</b>	<b>3 INP8=1.20</b>

1           Natural vegetation amount was the most important variable for *Sturnira lilium*, being  
2 positively related with occupancy of this species (Table 5). This variable was also incorporated in  
3 one of best models for *Artibeus lituratus* and *Myotis nigricans*, showing a positive relationship with  
4 occupancy. Inverse number of patches was the most important variable for *M. nigricans*, being  
5 positively related to occupancy, meaning that patchy landscapes are less probably to be occupied by  
6 *M. nigricans*. Inverse number of patches also occurred in one of the best models for *A. lituratus* and  
7 *P. lineatus*, being positively related to occupancy (Figure 2). Only for *A. lituratus*, the best scale of  
8 effect was for landscape variables with a 2km radius. In all the other cases when landscape variables  
9 were among the best models, landscape size was 8km. In the particular case of *M. nigricans* inverse  
10 number of patches was the best variable for both 2km and 8km landscape sizes.

11           Canopy cover was the most important variable and the only one among best models for  
12 *Desmodus rotundus*, being negatively related with occupancy, meaning that locals with more closed  
13 canopy, occupancy of *D. rotundus* is less probably. Canopy cover also was among best models for *A.*  
14 *lituratus*, *P. lineatus*, *P. incarum* and *A. cinereus*, being negatively related with occupancy for the  
15 first three; and positively for *A. cinereus*. Number of trees in the sampled quadrants was present in  
16 best models for *A. lituratus*, *A. cinereus* and *G. soricina*, being positively related with occupancy.  
17 Number of Lianas was present in best models for *A. lituratus*, *P. incarum* and *G. soricina*, being  
18 negatively related to the first two species, and positively to *Glossophaga soricina*. Predictions  
19 regarding if landscape, local or constant models would be better to explain species occupancy were  
20 corroborated for four species, although specific predictions, about positive or negative relations with  
21 variables not being correspondent in all cases (Table 6).



**Figure 2-** Importance of each predictor for each analyzed species. Local predictors are canopy cover (Cano), number of trees (Tree), number of Lianas (Lian). Landscape predictors are natural vegetation cover (Nat) and inverse number of patches (INP). Importance of predictors was taken only for the best scale of effect for landscape variables. So, landscape variables had smaller  $\Delta AICc$  for the landscape size of 2km, only landscape predictors at this scale were considered. For *A. lituratus*, *P. helleri* and *G. soricina* a landscape size with a 2km radius was used. For *D. rotundus*, *P. lineatus*, *S. lilium*, and *M. nigricans* the size of 8km. Importance of the model only with a constant occupancy is also being shown. Positive and negative signs above bars represent positive or negative relationships with occupancy for models that were among best models ( $\Delta AICc < 2$ ).

**Table 6-** Review of predictions and results obtained. Feeding habits, body mass and maximum dispersion were shown, because they are biological traits that could be related to species response to local and landscape variables. Maximum dispersion is according with literature. Bold models included the variable with most importance (sum of weights) in the analysis.

Species	Feeding habits	Body Mass	Max. Dispersion <sup>1</sup>	Prediction	Best models
<i>Desmodus rotundus</i>	Hematophague	35.00	5.5 km	Landscape	<b>Local</b>
<i>Myotis nigricans</i>	Insectivore	7.19	13 km	Landscape	<b>Landscape</b> (8km or 2km)
<i>Glossophaga soricina</i>	Nectarivore	11.33	6 km	Landscape	<b>Constant</b> or local
<i>Sturnira lilium</i>	Frugivore	18.81	5 km	Landscape and Local	<b>Landscape</b> (8km)
<i>Platyrrhinus incarum</i>	Frugivore	14.40		Landscape and Local	<b>Constant</b> or local
<i>Artibeus cinereus</i>	Frugivore	13.34	2 km	Landscape and Local	<b>Constant</b> or local
<i>Artibeus lituratus</i>	Frugivore	67.25	70 km	Constant	<b>Constant</b> , local or landscape (2km)
<i>Platyrrhinus lineatus</i>	Frugivore	23.60	9 km	Constant	<b>Local</b> , constant or landscape (8km)

<sup>1</sup> (Lourengo & Esbérard 2011; Wilson & La Val 1974)

## Discussion

Our results showed specific responses to landscape or local variables among species, which are not predictable by our original framework based on biological traits, such as diet, dispersal ability and body mass. We predicted that *Desmodus rotundus*, *Myotis nigricans* and *Glossophaga soricina* would be affected only by landscape variables, *Sturnira lilium* and *Artibeus cinereus* would be affected by both landscape and local variables and *Artibeus lituratus* and *Platyrrhinus lineatus* would not be affected by any of that variables. A clear relation between occupancy and one type of variable (at local or landscape scale) was observed only for three of the eight analyzed species. Landscape variables explained *Myotis nigricans* and *Sturnira lilium* occupancy, corroborating our predictions. However, local variables explained *Desmodus rotundus*, not corroborating our predictions. For all other species, the constant model explained as well as models including local or landscape variables.

The hypothesis that landscape variables would be important to explain bat occupancy was corroborated for *M. nigricans* and *S. lilium* (Figure 2), and at a less extent for *Artibeus lituratus* and

1 *Platyrrhinus lineatus*. For the last two species results needed to be interpreted with some caution  
2 because that the model with occupancy being constant performed as well as models with landscape  
3 variables (Mackenzie *et al.* 2006). Species that responded to landscape variables are probably being  
4 affected by changes in the surrounding areas, not mattering peculiarities of vegetation on sampled  
5 site. There are evidence in the literature that abundance or presence of different animals, including  
6 bats, can be affected by landscape variables (e.g. Duchamp & Swihart 2008; Smith *et al.* 2011;  
7 Thornton *et al.* 2011; Trzcinski *et al.* 1999). These changes can be related to the availability of  
8 habitat or/and configuration of habitat patches in the landscape.

9 *M. nigricans* occupancy was positively related to landscape continuity or in other words  
10 negatively related to fragmentation, contrary of expectation that this species would be positively  
11 related to fragmentation since it is an edge space aerial insectivore (Denzinger & Schnitzler 2013). A  
12 previous study with the relation of size and isolation of islands found no effect on *M. nigricans*  
13 presence (Estrada-villegas *et al.* 2010). Other species of *Myotis* have been positively related to forest  
14 patches aggregation and tree corridors in landscapes (Duchamp & Swihart 2008), and also positively  
15 related to fragmentation (Ethier & Fahrig 2011). Negative effects of fragmentation could be  
16 generally interpreted as indicative of edge-sensitivity, matrix effects or dependence on larger  
17 patches. Edge-sensitivity does not seem to be an explanation for *M. nigricans*, which is specialized in  
18 hunting insects in edge spaces (Kalko *et al.* 2008). However, *M. nigricans* would use edges among  
19 different types of vegetation in natural areas, for example, edges between forest and savannic  
20 vegetation, but it does not mean that *M. nigricans* is adapted to use edges with agricultural areas.

21 *S. lilium* was positively related to amount of natural areas. We predicted that *S. lilium*, an  
22 understory frugivore, would be affected by both landscape and local variables. Nevertheless local  
23 variables, including understory height were not important explaining its occupancy. *S. lilium* use to  
24 eat Solanaceae fruits and roost in foliages and tree cavities (Evelyn & Stiles 2003; Mello *et al.*  
25 2008a). This species uses large areas and different night roosts (Mello *et al.* 2008b), exploiting the

1 landscape and being likely to respond to landscape variables. The amount of natural vegetation in a  
2 landscape can be related to amount of habitat for this species. Results in which habitat amount is  
3 more important than other variables are relatively common in literature (Smith *et al.* 2011; Trzcinski  
4 *et al.* 1999; With & Pavuk 2011). Also they are intuitive since landscape with larger habitat amount  
5 would have more places for foraging, roosting, reproduction and movements.

6 The hypothesis that local variables would be important for explaining bat occupancy was  
7 corroborated to *D. rotundus*, and with some cautions to *G. soricina*, *P. incarum* and *A. cinereus*. For  
8 the last three species results needed to be interpreted with caution, because the constant model  
9 performed as well as model with local variables (Mackenzie *et al.* 2006). The importance of local  
10 variables can mean that individuals choose areas to use based on local characteristics, or based on  
11 habitat quality (Mortelliti *et al.* 2010). It has been shown for different animal species, cases when  
12 local variables are more important than landscape ones (e.g. Jellinek *et al.* 2004; Nessimian *et al.*  
13 2008; Thomas *et al.* 2001; Vieira *et al.* 2014). In general, these results are interpreted with specific  
14 relations between measured local variables and the biology of studied species.

15 Canopy cover was negatively related to *D. rotundus* occupancy (Figure 2). Canopy cover is  
16 associated with how much the sampling site was covered with leaves at the canopy. More covered  
17 places would offer to bats protection against predators, wind and rain (Fenton *et al.* 1998), so these  
18 variables was thought in first place being positively related to bat occupancy. However, in the  
19 particular case of *D. rotundus*, the use of cattle as a food resource makes them resistant, and maybe  
20 beneficiate, to human changes. This species is constantly associated to cattle rabies, and considered  
21 as a plague, although *D. rotundus* inappropriate control (without an effective species level  
22 identification of individuals) could result in serious threat to other endangered bat species (Aguiar *et*  
23 *al.* 2010). Livestock kept in a forest can damage the trees and open drains (Adams 1975) decreasing  
24 canopy cover. This relation opens the possibility to interpret the negative association of *D. rotundus*  
25 occupancy with canopy cover as a result of the impact caused by cattle in those areas.

1           Some relationships between landscape and local variables and occupancy need to be  
2 discussed with some caution, since they were as good as constant models to explain species  
3 occupancy. Tree density, for example, was positively related to *G. soricina* and *A. cinereus*  
4 occupancy. Tree density was thought as being associated to local resources, such as food and shelter  
5 in sampling site (Evelyn & Stiles 2003), trees can offer food resources to frugivores and nectarivores  
6 and resting sites between flights. We did not measure actual food resources for these bats, so if food  
7 resources are the reason for this result, it is not possible to know. However, it is known that some  
8 bats, for example, *G. soricina*, have high flight activity with short periods of resting. Liana quantity  
9 was positively related to *G. soricina* occupancy, and negatively to *P. incarum*. Liana are more  
10 common in degraded sites and forest edges (Tabanez & Viana 2000). They represent obstacles to  
11 flight of animals, and this could be the reason for the negative response of *P. incarum*. The positive  
12 response of *G. soricina*, concomitantly with the positive response to tree density, can be related to its  
13 high maneuverability during flight (Kalko *et al.* 2008), or use of flower resources.

14           Finally, the hypothesis that neither local and landscape variables determine occupancy  
15 patterns was constructed based on biology of two species, *A. lituratus* and *P. lineatus*. Both are large  
16 frugivores that have been encountered in a range of environmental, from intact forest to urban areas  
17 (Menezes Jr. *et al.* 2008; Trevelin *et al.* 2013). Surprising, both species had in the best models, local  
18 and landscape variables, as with the model with constant occupancy. *A. lituratus* was negatively  
19 related to Canopy cover and Lianas, and positively related to tree density, amount of natural  
20 vegetation and inverse number of patches. *P. lineatus* is negatively related with Canopy cover and  
21 positively related with inverse number of patches. Both are large species that possibly need some  
22 obstacle-free space to fly. Relation with landscape variables are possibly related to sensitivity to  
23 landscapes changes. Both local and landscape variables have been showing influencing species  
24 occupancy (Blevins & With 2011; Mortelliti *et al.* 2012), this result can be related to a concomitantly

1 process of sensitivity to habitat quality and surrounding composition and configuration of habitat  
2 patches.

3 Bat occupancy of different species could respond to landscape variable in different scales of  
4 effect, landscape sizes. To avoid false results, we used landscape variables measured in two distinct  
5 landscape sizes, circular landscapes with a radius of 2km and 8km from the sampling site. Four  
6 species were related with landscape variables in best models, the best scale of effect was with an  
7 8km radius for three species (*Myotis nigricans*, *Sturnira lilium* and *Platyrrhinus lineatus*) and 2km  
8 radius for one species (*A. lituratus*). The best scale of effect for *A. lituratus* was intriguing, since this  
9 species has high dispersal ability (Mendes *et al.* 2009; Menezes Jr. *et al.* 2008), and dispersal ability  
10 is related to scale of effect (Jackson & Fahrig 2012). The concern about this result is that the model  
11 where occupancy was kept constant was as good as models with landscape variables for *A. lituratus*  
12 and *P. lineatus*. *A. lituratus* and has been related with landscape variables in a scale of effect with  
13 1km and 5km radii in a previous multiple scale approach (Gorresen *et al.* 2005).

14 The majority of studies that account for detectability find a probability of detection smaller  
15 than one (Kellner & Swihart 2014), suggesting that considering detectability is important to avoid  
16 uncorrected ecological results. Bats have taxon-specific detection probabilities (Meyer *et al.* 2011).  
17 Seasonality, sampling method and moon phase, for example, seem to be important factors  
18 determining detection (Esbérard 2007; Meyer *et al.* 2011), our sampling design controlled for these  
19 issues. However air temperature, observer, presence of wind, and rain, were tested if they were  
20 affecting bat detectability. Temperature was among the best models to predict *D. rotundus*,  
21 *A. cinereus* and *A. lituratus* presence. It is known that some species are better in regulating body  
22 temperature with changes in air temperature than others; and some bats can have events of  
23 hypothermia when submitted to lower temperature than they are used to (Mcnab 1969). Small  
24 stenodermatines, for example *A. cinereus*, are example of bats that decrease body temperature when  
25 aerial temperature is low (Mcnab 1969). *A. cinereus* had more probability of detection in warmer

1 nights (see Table 4), and the only best model for explaining *A. cinereus* detection was the one  
2 considering temperature. Wind was among best models explaining detection of *D. rotundus*, *M.*  
3 *nigricans* and *S. lilium*. Wind has the property of change flight pattern of bats (Sapir *et al.* 2014),  
4 what could affect their probability of being detected. However, a study with Neotropical insectivores  
5 did not find any relation between wind speed and insectivores activity (Barros *et al.* 2014). Observer  
6 was important only for detection of *G. soricina*, despite this species is not hard to identify (Gardner  
7 *et al.* 2007), remaining not clear why observer was an important factor.

8         We aimed to identify if landscape or local variables were more important to explain bat  
9 occupancy. Both local and landscape variables can be important to predict bat occupancy depending  
10 of the species, and both positive and negative relationships with occupancy could be found for the  
11 same variable, highlighting an idiosyncratic pattern of responses. It is important to note that  
12 measuring landscape variables in more than one scale can reduce the chances of finding a false  
13 absence of relation with landscape variables, since different species had different best scale of  
14 effects. Despite idiosyncratic patterns indirectly suggest that single conservation management  
15 decisions are hard to be taken, results can be interpreted in a general form that both local and  
16 landscape scales are important to be consider when the aim is keeping bat occupancy probability.  
17 Otherwise, it is easy to incorporate landscape variables such as habitat amount and isolation on the  
18 current approaches for conservation spatial prioritization such as the Zonation or other frameworks  
19 (Grantham *et al.* 2009; Moilanen *et al.* 2008). These variables could be readily spatialized and an  
20 estimated effect of them on species occupancy could be also mapped and interpreted into a broader  
21 scope. This is not true for local environmental variables that usually reflect subtle variations on  
22 habitat quality (Mortelliti *et al.* 2010). For instance, some of them, such as understory cover, are not  
23 easily estimated using satellite data, and may be difficult to include into those frameworks based on  
24 large-scale spatial prioritization. Currently, the use of vegetation indexes such as NDVI is our best  
25 guess to provide useful habitat quality surrogates (Cumming 2000). Nevertheless, it remain to be

1 better evaluated the degree of association to these integrative measures with some more finer-scale  
2 variables measure here that have been useful to predict bat occupancy in our models. At landscape  
3 scales, conservation management would focus in land use, and accessed using aerial images of  
4 landscapes. At local scales, conservation management approach need to be more detailed, identifying  
5 not only the habitat amount, as well as habitat quality.

## 7 **Acknowledges**

9 The field work was supported by International Foundation for Science (IFS), various CNPq grants,  
10 PELD, Anglo American Group and CAPES. P. Mendes receives a scholarship from CNPq and  
11 another one from the “sandwich doctorate program” CAPES. P. De Marco was funded by continuous  
12 productivity CNPq grants (305542/2010-9). We are grateful LAPIG-UFG laboratory for providing  
13 help with satellite images, and L. Sales for the helpful comments on the manuscript. We thank S. de  
14 Jesus, P.V.S. Bernardo, L.M. Camargos, P.H.P. Braga, B.C. Gomes, C. Sobral, P. Coelho, A. Bispo,  
15 landowners and all fieldwork assistants for helping in sampling design and field work. We also thank  
16 ICMBio for providing the licenses to sample bats, National Forest of Sylvania and Emas National  
17 Park for permitting surveys at their conservation units. We also thank L.L. Souza for a illustration  
18 and P.H.P. Braga for a photo.

## 20 **References**

- 21 Adams SN, 1975. Sheep and cattle grazing in forest: A review. *Journal of Applied Ecology*,  
22 12(1):143–152.
- 23 Aguiar LMS, Bernard E & Machado RB, 2014. Habitat use and movements of *Glossophaga soricina*  
24 and *Lonchophylla dekeyseri* ( Chiroptera : Phyllostomidae ) in a Neotropical savannah.  
25 *Zoologia (Curitiba, Impresso)*, 31(3):223–229.

- 1 Aguiar LMS, Brito D & Machado RB, 2010. Do Current Vampire Bat ( *Desmodus rotundus* )  
2 Population Control Practices Pose a Threat to Dekeyser's Nectar Bat's ( *Lonchophylla dekeyseri*  
3 ) Long-Term Persistence in the Cerrado? *Acta Chiropterologica*, 12(2):275–282.
- 4 Aguirre LF, 2002. Structure of a neotropical savanna bat community. *Journal of Mammalogy*,  
5 83(3):775–784.
- 6 Barros MAS, Pessoa DMA & Rui AM, 2014. Habitat use and seasonal activity of insectivorous bats  
7 ( Mammalia : Chiroptera ) in the grasslands of southern Brazil. *Revista Brasileira de Zoologia*,  
8 31(2):153–161.
- 9 Bernard E & Fenton MB, 2003. Bat Mobility and Roosts in a Fragmented Landscape in Central.  
10 *Current*, 35(2):262–277.
- 11 Bianconi GV, Mikich SB & Pedro WA, 2006. Movements of bats (Mammalia, Chiroptera) in  
12 Atlantic Forest remnants in southern Brazil. *Revista Brasileira de Zoologia*, 23(4):1199–1206.
- 13 Blevins E & With K a., 2011. Landscape context matters: local habitat and landscape effects on the  
14 abundance and patch occupancy of collared lizards in managed grasslands. *Landscape Ecology*,  
15 26(6):837–850.
- 16 Brown JH, 1984. On the Relationship between Abundance and Distribution of Species. *The*  
17 *American Naturalist*, 124(2):255.
- 18 Burnham KP & Anderson DR, 1998. *Model Selection and Multimodel Inference*. Second ed., New  
19 York: Springer.
- 20 Cumming GS, 2000. Using habitat models to map diversity : pan-African species richness of ticks ( *Acari* : *Ixodida* ). *Journal of Biogeography*, 27:425–440.
- 22 Da Silva JMC & Bates JM, 2002. Biogeographic Patterns and Conservation in the South American  
23 Cerrado : A Tropical Savanna Hotspot. *BioScience*, 52(3):225–234.
- 24 Denzinger A & Schnitzler H-U, 2013. Bat guilds, a concept to classify the highly diverse foraging  
25 and echolocation behaviors of microchiropteran bats. *Frontiers in physiology*, 4(July):164.
- 26 Duchamp JE & Swihart RK, 2008. Shifts in bat community structure related to evolved traits and  
27 features of human-altered landscapes. *Landscape Ecology*, 23(7):849–860.
- 28 Esbérard CEL, 2007. Influência do ciclo lunar na captura de morcegos Phyllostomidae. 97(1):81–85.
- 29 Estrada-Villegas S, McGill BJ & Kalko EK V, 2012. Climate, habitat, and species interactions at  
30 different scales determine the structure of a Neotropical bat community. *Ecology*, 93(5):1183–  
31 93.
- 32 Estrada-villegas S, Meyer CFJ & Kalko EK V, 2010. Effects of tropical forest fragmentation on  
33 aerial insectivorous bats in a land-bridge island system. *Biological Conservation*, 143(3):597–  
34 608.

- 1 Ethier K & Fahrig L, 2011. Positive effects of forest fragmentation, independent of forest amount, on  
2 bat abundance in eastern Ontario, Canada. *Landscape Ecology*, 26(6):865–876.
- 3 Evelyn MJ & Stiles DA, 2003. Roosting Requirements of Two Frugivorous Bats (*Sturnira lilium* and  
4 *Arbiteus intermedius*) in Fragmented Neotropical Forest. *Biotropica*, 35(3):405–418.
- 5 Fahrig L, 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology,*  
6 *Evolution, and Systematics*, 34(1):487–515.
- 7 Faria D, Laps RR, Baumgarten J & Cetra M, 2006. Bat and Bird Assemblages from Forests and  
8 Shade Cacao Plantations in Two Contrasting Landscapes in the Atlantic Forest of Southern  
9 Bahia, Brazil. *Biodiversity and Conservation*, 15(2):587–612.
- 10 Fenton MB, Cumming DHM, Rautenbach ILN, *et al.*, 1998. Bats and the Loss of Tree Canopy in  
11 African Woodlands. *Conservation Biology*, 12(2):399–407.
- 12 Fiske IJ & Chandler RB, 2011. unmarked : An R Package for Fitting Hierarchical Models of Wildlife  
13 Occurrence and Abundance. *Journal of Statistical software*, 43(10):1–23.
- 14 Fleming TH, Geiselman C & Kress WJ, 2009. The evolution of bat pollination: a phylogenetic  
15 perspective. *Annals of botany*, 104(6):1017–43.
- 16 García-Morales R, Badano EI & Moreno CE, 2013. Response of Neotropical Bat Assemblages to  
17 Human Land Use. *Conservation biology : the journal of the Society for Conservation Biology*,  
18 00(0):1–11.
- 19 Gorresen PM, Willig MR & Strauss RE, 2005. Multivariate analysis of scale-dependent associations  
20 between bats and landscape structure. *Ecological applications*, 15(6):2126–2136.
- 21 Grantham HS, Wilson K a, Moilanen A, Rebelo T & Possingham HP, 2009. Delaying conservation  
22 actions for improved knowledge: how long should we wait? *Ecology letters*, 12(4):293–301.
- 23 Gregorin R, Gonçalves E, Aires CC & Carmignotto AP, 2011. Morcegos (Mammalia : Chiroptera)  
24 da Estação Ecológica Serra Geral do Tocantins : composição específica e considerações  
25 taxonômicas. *Biota*, 11(1):300–311.
- 26 Harvey CA & Villalobos JAG, 2007. Agroforestry systems conserve species-rich but modified  
27 assemblages of tropical birds and bats. *Biodiversity & Conservation*, 16:2257–2292.
- 28 Hines JE, 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-  
29 PWRC.
- 30 Hoekstra JM, Boucher TM, Ricketts TH & Roberts C, 2004. Confronting a biome crisis: global  
31 disparities of habitat loss and protection. *Ecology Letters*, 8(1):23–29.
- 32 Jackson HB & Fahrig L, 2012. What size is a biologically relevant landscape? *Landscape Ecology*,  
33 27(7):929–941.
- 34 Jacomassa FAF & Pizo MA, 2010. Birds and bats diverge in the qualitative and quantitative  
35 components of seed dispersal of a pioneer tree. *Acta Oecologica*, 36(5):493–496.

- 1 Jellinek S, Driscoll D a. & Kirkpatrick JB, 2004. Environmental and vegetation variables have a  
2 greater influence than habitat fragmentation in structuring lizard communities in remnant urban  
3 bushland. *Austral Ecology*, 29(3):294–304.
- 4 Kalka MB, Smith AR & Kalko EK V, 2008. Bats Limit Arthropods and Herbivory in a Tropical  
5 Forest. *Science*, 320(April):2008–2008.
- 6 Kalko EK V, Estrada Villegas S, Schmidt M, Wegmann M & Meyer CFJ, 2008. Flying high--  
7 assessing the use of the aerosphere by bats. *Integrative and comparative biology*, 48(1):60–73.
- 8 Kellner KF & Swihart RK, 2014. Accounting for imperfect detection in ecology: a quantitative  
9 review. *PloS one*, 9(10):1–8.
- 10 Kerth G & Melber M, 2009. Species-specific barrier effects of a motorway on the habitat use of two  
11 threatened forest-living bat species. *Biological Conservation*, 142(2):270–279.
- 12 López-González C, Presley SJ, Lozano A, Stevens RD & Higgins CL, 2014. Ecological  
13 biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta  
14 diversity, and environmental gradients to species richness and composition patterns. *Ecography*,  
15 37:1–12.
- 16 Lourenço EC & Esbérard CEL, 2011. Marcação-recaptura de morcegos : Relevância e exemplos de  
17 estudos ecológicos.
- 18 Macarthur R & Levins R, 1964. Competition, Habitat Selection, and Character displacement in a  
19 patchy environment. *Zoology (Jena, Germany)*, 51:1207–1210.
- 20 Mackenzie DI, Nichols JD, Lachman GB, *et al.*, 2002. Estimating site occupancy rates when  
21 detection probabilities are less than one. *Ecology*, 83(8):2248–2255.
- 22 Mackenzie DI, Nichols JD, Royle JA, *et al.*, 2006. *Occupancy estimation and modeling: inferring*  
23 *patterns and dynamics of species occurrence*. 1<sup>o</sup> ed., Burlington.
- 24 McNab BK, 1969. The economics of temperature regulation in Neotropical bats. *Comparative*  
25 *Biochemistry and Physiology*, 31:227–268.
- 26 Medellín RA, Equihua M & Amin MA, 2000. Bat Diversity and Abundance as Indicators of  
27 Disturbance in Neotropical Rainforests. 14(6):1666–1675.
- 28 Mehr M, Brandl R, Hothorn T, *et al.*, 2011. Land use is more important than climate for species  
29 richness and composition of bat assemblages on a regional scale. *Mammalian Biology -*  
30 *Zeitschrift für Säugetierkunde*, 76(4):451–460.
- 31 Mello MAR, Kalko EKV & Silva WR, 2008a. Diet and abundance of the bat *Sturnira lilium*  
32 (Chiroptera) in a Brazilian montane Atlantic forest. *Journal of Mammalogy*, 89(2):485–492.
- 33 Mello MAR, Kalko EKV & Silva WR, 2008b. Movements of the bat *Sturnira lilium* and its role as a  
34 seed disperser of Solanaceae in the Brazilian Atlantic forest. *Journal of Tropical Ecology*,  
35 24(02):225–228.

- 1 Mello MAR, Kalko EK V & Silva WR, 2013. Effects of moonlight on the capturability of  
2 frugivorous phyllostomid bats ( Chiroptera : Phyllostomidae ) at different time scales.  
3 30(4):397–402.
- 4 Mendenhall CD, Karp DS, Meyer CFJ, Hadly E a & Daily GC, 2014. Predicting biodiversity change  
5 and averting collapse in agricultural landscapes. *Nature*, 509(7499):213–7.
- 6 Mendes P, Vieira TB, Oprea M & Ditchfield AD, 2009. Long-distance movement of *Artibeus*  
7 *lituratus* (Chiroptera: Phyllostomidae) in the state of Espírito Santo, Brazil. *Ecotropica*,  
8 15(i):43–46.
- 9 Menezes Jr. LF, Duarte AC, Novaes RLM, *et al.*, 2008. Deslocamento de *Artibeus lituratus* (Olfers ,  
10 1818) (Mammalia , Chiroptera) entre ilha e continente no Estado do Rio de Janeiro , Brasil.  
11 *Biota Neotropica*, 8(2):243–245.
- 12 Meyer CFJ, Aguiar LMS, Aguirre LF, *et al.*, 2011. Accounting for detectability improves estimates  
13 of species richness in tropical bat surveys. *Journal of Applied Ecology*, 48(3):777–787.
- 14 Meyer CFJ, Fründ J, Lizano WP & Kalko EKV, 2007. Ecological correlates of vulnerability to  
15 fragmentation in Neotropical bats. *Journal of Applied Ecology*, 45(1):381–391.
- 16 Moilanen A, Arponen A, Stokland JN & Cabeza M, 2008. Assessing replacement cost of  
17 conservation areas : How does habitat loss influence priorities ? *Biological Conservation*,  
18 142(3):575–585.
- 19 Monadjem A & Reside A, 2008. The influence of riparian vegetation on the distribution and  
20 abundance of bats in an African savanna. *Acta Chiropterologica*, 10(2):339–348.
- 21 Mortelliti A, Amori G & Boitani L, 2010. The role of habitat quality in fragmented landscapes: A  
22 conceptual overview and prospectus for future research. *Oecologia*, 163(2):535–547.
- 23 Mortelliti A, Sozio G, Boccacci F, *et al.*, 2012. Effect of habitat amount, configuration and quality in  
24 fragmented landscapes. *Acta Oecologica*, 45:1–7.
- 25 Murphy GEP & Romanuk TN, 2014. A meta-analysis of declines in local species richness from  
26 human disturbances. *Ecology and evolution*, 4(1):91–103.
- 27 Muscarella R & Fleming TH, 2007. The role of frugivorous bats in tropical forest succession.  
28 *Biological reviews of the Cambridge Philosophical Society*, 82(4):573–90.
- 29 Myers N, Mittermeier R a, Mittermeier CG, Da Fonseca G a & Kent J, 2000. Biodiversity hotspots  
30 for conservation priorities. *Nature*, 403(6772):853–8.
- 31 Nessimian JL, Venticinque EM, Zuanon J, *et al.*, 2008. Land use, habitat integrity, and aquatic insect  
32 assemblages in Central Amazonian streams. *Hydrobiologia*, 614(1):117–131.
- 33 Oprea M, Mendes P, Vieira TB & Ditchfield AD, 2009. Do wooded streets provide connectivity for  
34 bats in an urban landscape? *Biodiversity and Conservation*, 18(9):2361–2371.

- 1 Pe'er G, Henle K, Dislich C & Frank K, 2011. Breaking functional connectivity into components: a  
2 novel approach using an individual-based model, and first outcomes. *PloS one*, 6(8):e22355.
- 3 Quesada M, Stoner KE, Lobo J a., *et al.*, 2004. Effects of Forest Fragmentation on Pollinator  
4 Activity and Consequences for Plant Reproductive Success and Mating Patterns in Bat-  
5 pollinated Bombacaceous Trees. *Biotropica*, 36(2):131.
- 6 R Core Team, 2008. R: A language and environment for statistical computing. Vienna, Austria.:  
7 Foundation for Statistical Computing, (<http://www.r-project.org>).
- 8 Sano EE, Rosa R, Brito JLS & Ferreira LG, 2010. Land cover mapping of the tropical savanna  
9 region in Brazil. :113–124.
- 10 Sapir N, Horvitz N, Dechmann DKN, Fahr J & Wikelski M, 2014. Commuting fruit bats beneficially  
11 modulate their flight in relation to wind. *Proceedings. Biological sciences / The Royal Society*,  
12 281:1–8.
- 13 Smith AC, Fahrig L & Francis CM, 2011. Landscape size affects the relative importance of habitat  
14 amount, habitat fragmentation, and matrix quality on forest birds. *Ecography*, 34(1):103–113.
- 15 Soberón J & Nakamura M, 2009. Niches and distributional areas : Concepts , methods , *PNAS*,  
16 106(2):19644–19650.
- 17 Tabanez AAJ & Viana VM, 2000. Patch Structure within Brazilian Atlantic Forest Fragments and  
18 Implications for Conservation. *Biotropica*, 32(4b):925–933.
- 19 Thies W & Kalko EK V, 2004. Phenology of neotropical pepper plants ( Piperaceae ) and their  
20 association with their main dispersers , two short-tailed fruit bats , *Carollia perspicillata* and *C .*  
21 *castanea* ( Phyllostomidae ). *Oikos*, 104:362–376.
- 22 Thomas J a, Bourn N a, Clarke RT, *et al.*, 2001. The quality and isolation of habitat patches both  
23 determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society*  
24 *of London B*, 268(1478):1791–6.
- 25 Thornton DH, Branch LC & Sunquist ME, 2011. The relative influence of habitat loss and  
26 fragmentation: do tropical mammals meet the temperate paradigm? *Ecological applications : a*  
27 *publication of the Ecological Society of America*, 21(6):2324–33.
- 28 Trevelin LC, Silveira M, Port-Carvalho M, Homem DH & Cruz-Neto AP, 2013. Use of space by  
29 frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil.  
30 *Forest Ecology and Management*, 291:136–143.
- 31 Trzcinski MK, Fahrig L & Merriam G, 1999. Independent effects of forest cover and fragmentation  
32 on the distribution of forest breeding birds. *Ecological applications*, 9(2):586–593.
- 33 Vieira TB, Dias-Silva K & Pacífico E, 2014. Effects of riparian vegetation integrity on fish and  
34 heteroptera communities. *Applied Ecology and environmental research*, 13(1):53–65.
- 35 Wiens J a., 1989. Spatial Scaling in Ecology. *Functional Ecology*, 3(4):385–397.

- 1 Wilson DE & La Val RK, 1974. *Myotis nigricans*. *Mammalian Species*, 39:1–3.
- 2 With K a., 1994. Using fractal analysis to assess how species perceive landscape structure.  
3 *Landscape Ecology*, 9(1):25–36.
- 4 With K a. & Pavuk DM, 2011. Habitat area trumps fragmentation effects on arthropods in an  
5 experimental landscape system. *Landscape Ecology*, 26(7):1035–1048.
- 6 Womack KM, Amelon SK & Thompson FR, 2013. Summer Home Range Size of Female Indiana  
7 Bats (*Myotis Sodalis*) in Missouri, USA. *Acta Chiropterologica*, 15(2):423–429.
- 8

# Appendix 1

Models explaining bat occupancy. Only models with  $\Delta AICc < 2$  are being showed. Local predictors are canopy cover, number of trees and number of Lianas collected in three quadrants (10X10m) at the same location as bats were sampled. Landscape variables included natural vegetation cover and inverse number of patches measured in two different landscape sizes, 2km and 8km of radius. When global models had overdispersion coefficients ( $\hat{c}$ )  $> 1$ , all the competing models were corrected by this overdispersion factor and QAICc was showed instead AICc. Number of parameters per model is k.  $\hat{\psi}$  is the naïve occupancy estimator, number of sampling sites that a species was detected divided by the number of landscapes sampled. \* are species that global models had overdispersion coefficients ( $\hat{c}$ )  $> 1$ .

11

Species	Model	QAICc/AICc	$\Delta QAICc/\Delta AICc$	w	k
<i>Desmodus rotundus</i>					
2km	psi(Cano),p(.)	41.12	0.00	0.88	3
	psi(Cano+Tree+Lian),p(.)	46.90	5.78	0.05	5
	psi(.),p(.)	47.68	6.56	0.03	2
	psi(Tree),p(.)	50.27	9.15	0.01	3
	psi(Lian),p(.)	50.44	9.32	0.01	3
	psi(INP2),p(.)	50.66	9.54	0.01	3
	psi(Nat2),p(.)	50.68	9.56	0.01	3
	psi(Nat2+INP2),p(.)	54.25	13.13	0.00	4
	psi(Nat2+INP2+Cano+Tree+Lian),p(.)	58.90	17.78	0.00	7
8km	psi(Cano),p(.)	41.12	0.00	0.88	3
	psi(Cano+Tree+Lian),p(.)	46.90	5.78	0.05	5
	psi(.),p(.)	47.68	6.56	0.03	2
	psi(Tree),p(.)	50.27	9.15	0.01	3
	psi(Lian),p(.)	50.44	9.32	0.01	3
	psi(INP8),p(.)	50.64	9.52	0.01	3
	psi(Nat8),p(.)	50.76	9.64	0.01	3
	psi(Nat8+INP8),p(.)	54.27	13.15	0.00	4
	psi(Nat8+INP8+Cano+Tree+Lian),p(.)	58.90	17.78	0.00	7
<i>Myotis nigricans</i>					
2km	psi(INP2),p(.)	42.73	0.00	1.00	3
	psi(.),p(.)	44.39	1.66	0.44	2
	psi(Tree),p(.)	44.53	1.80	0.41	3

Appendix 1- Continuation					
	psi(Nat2+INP2),p(.)	45.13	2.40	0.30	4
	psi(Cano+Tree+Lian),p(.)	46.46	3.73	0.15	5
	psi(Nat2),p(.)	47.11	4.38	0.11	3
	psi(Cano),p(.)	47.14	4.41	0.11	3
	psi(Lian),p(.)	47.38	4.65	0.10	3
	psi(Nat2+INP2+Cano+Tree+Lian),p(.)	56.60	13.87	0.00	7
8km	psi(INP8),p(.)	36.60	0.00	1.00	3
	psi(Nat8+INP8),p(.)	38.04	1.44	0.49	4
	psi(.),p(.)	44.39	7.79	0.02	2
	psi(Tree),p(.)	44.53	7.93	0.02	3
	psi(Cano+Tree+Lian),p(.)	46.46	9.86	0.01	5
	psi(Cano),p(.)	47.14	10.54	0.01	3
	psi(Nat8),p(.)	47.26	10.66	0.00	3
	psi(Lian),p(.)	47.38	10.78	0.00	3
	psi(Nat8+INP8+Cano+Tree+Lian),p(.)	54.40	17.80	0.00	7
<i>Glossophaga soricina</i> *					
2km	psi(.),p(Obse)	52.24	0.00	1.00	3
	psi(Lian),p(Obse)	53.04	0.80	0.67	4
	psi(Tree),p(Obse)	53.55	1.31	0.52	4
	psi(INP2),p(Obse)	55.67	3.43	0.18	4
	psi(Nat2),p(Obse)	55.80	3.56	0.17	4
	psi(Tree),p(Obse)	55.85	3.61	0.16	4
	psi(Cano+Tree+Lian),p(Obse)	59.15	6.91	0.03	6
	psi(Nat2+INP2),p(Obse)	60.01	7.77	0.02	5
	psi(Nat2+INP2+Cano+Tree+Lian),p(Obse)	78.15	25.91	0.00	8
8km	psi(.),p(Obse)	53.13	0.00	1.00	3
	psi(Lian),p(Obse)	53.87	0.74	0.69	4
	psi(Tree),p(Obse)	54.39	1.26	0.53	4
	psi(INP8),p(Obse)	56.59	3.46	0.18	3
	psi(Nat8),p(Obse)	56.70	3.57	0.17	3
	psi(Cano),p(Obse)	56.74	3.61	0.16	4
	psi(Cano+Tree+Lian),p(Obse)	59.91	6.78	0.03	6
	psi(Nat8+INP8),p(Obse)	60.42	7.29	0.03	5
	psi(Nat8+INP8+Cano+Tree+Lian),p(Obse)	78.87	25.74	0.00	8
<i>Sturnira lilium</i> *					
2km	psi(.),p(.)	33.72	0.00	1.00	2
	psi(Tree),p(.)	34.49	0.77	0.68	3
	psi(Lian),p(.)	35.12	1.40	0.50	3
	psi(Cano),p(.)	35.70	1.98	0.37	3
	psi(Nat2),p(.)	35.98	2.26	0.32	3
	psi(INP2),p(.)	36.79	3.07	0.22	3
	psi(Nat2+INP2),p(.)	39.45	5.73	0.06	4
	psi(Nat2+INP2+Cano+Tree+Lian),p(.)	44.37	10.65	0.00	7

**Appendix 1- Continuation**

8km	psi(Nat8),p(.)	30.69	0.00	1.00	3
	psi(.),p(.)	33.95	3.26	0.20	2
	psi(Nat8+INP8),p(.)	34.33	3.64	0.16	4
	psi(Tree),p(.)	34.71	4.02	0.13	3
	psi(Lian),p(.)	35.34	4.65	0.10	3
	psi(Cano),p(.)	35.93	5.24	0.07	3
	psi(INP8),p(.)	36.27	5.58	0.06	3
	psi(Cano+Tree+Lian),p(.)	39.91	9.22	0.01	5
	psi(Nat8+INP8+cano+Tree+Lian),p(.)	44.51	13.82	0.00	7
<i>Artibeus cinereus</i> *					
2km	psi(.),p(Temp)	43.44	0.00	1.00	3
	psi(Cano),p(Temp)	44.08	0.64	0.73	4
	psi(Tree),p(Temp)	45.25	1.81	0.40	4
	psi(Lian),p(Temp)	45.88	2.44	0.30	4
	psi(Nat2+INP2),p(Temp)	46.17	2.73	0.26	5
	psi(INP2),p(Temp)	46.26	2.82	0.24	4
	psi(Nat2),p(Temp)	46.59	3.15	0.21	4
	psi(Cano+Tree+Lian),p(Temp)	47.91	4.47	0.11	6
	psi(Nat2+INP2+Cano+Tree+Lian),p(Temp)	59.07	15.63	0.00	8
8km	psi(.),p(Temp)	42.84	0.00	1.00	3
	psi(Cano),p(Temp)	43.53	0.69	0.71	4
	psi(Tree),p(Temp)	44.69	1.85	0.40	4
	psi(Cano),p(Temp)	44.88	2.04	0.36	4
	psi(Lian),p(Temp)	45.30	2.46	0.29	4
	psi(Nat8+INP8+Cano+Tree+Lian),p(Temp)	45.66	2.82	0.24	5
	psi(INP8),p(Temp)	46.67	3.83	0.15	4
	psi(Cano+Tree+Lian),p(Temp)	47.46	4.62	0.10	6
	psi(Nat8+INP8+Cano+Tree+Lian),p(Temp)	58.69	15.85	0.00	8
<i>Platyrrhinus incarum</i>					
2km	psi(.),p(.)	76.32	0.00	0.34	2
	psi(Cano),p(.)	76.99	0.66	0.24	3
	psi(Lian),p(.)	78.25	1.92	0.13	3
	psi(Nat2),p(.)	78.64	2.32	0.11	3
	psi(Tree),p(.)	79.40	3.08	0.07	3
	psi(INP2),p(.)	79.40	3.08	0.07	3
	psi(Nat2+INP2),p(.)	82.10	5.78	0.02	4
	psi(Cano+Tree+Lian),p(.)	82.36	6.03	0.02	5
	psi(Nat2+INP2+Cano+Tree+Lian),p(.)	94.33	18.01	0.00	7
8km	psi(.),p(.)	76.32	0.00	0.35	3
	psi(Cano),p(.)	76.99	0.66	0.25	3
	psi(Lian),p(.)	78.25	1.92	0.13	4
	psi(Nat8),p(.)	79.23	2.91	0.08	7
	psi(INP8),p(.)	79.40	3.08	0.08	5

Appendix 1- Continuation					
	psi(Tree),p(.)	79.40	3.08	0.08	3
	psi(Cano+Tree+Lian),p(.)	82.36	6.03	0.02	3
	psi(Nat8+INP8),p(.)	82.92	6.60	0.01	3
	psi(Nat8+INP8+cano+Tree+Lian),p(.)	91.45	15.13	0.00	2
<i>Artibeus lituratus</i> *					
2km	psi(.),p(.)	57.17	0.00	1.00	2
	psi(Cano+Tree+Lian),p(.)	58.11	0.94	0.63	5
	psi(Nat2),p(.)	58.77	1.60	0.45	3
	psi(INP2),p(.)	58.95	1.78	0.41	3
	psi(Lian),p(.)	59.26	2.09	0.35	3
	psi(Tree),p(.)	59.48	2.31	0.32	3
	psi(Cano),p(.)	59.85	2.68	0.26	3
	psi(Nat2+INP2),p(.)	61.69	4.52	0.10	4
	psi(Nat2+INP2+Cano+Tree+Lian),p(.)	70.11	12.94	0.00	7
8km	psi(.),p(.)	57.22	0.00	1.00	2
	psi(Cano+Tree+Lian),p(.)	58.15	0.93	0.63	5
	psi(Lian),p(.)	59.31	2.09	0.35	3
	psi(INP8),p(.)	59.31	2.09	0.35	3
	psi(Tree),p(.)	59.53	2.31	0.32	3
	psi(Nat8),p(.)	59.78	2.56	0.28	3
	psi(Cano),p(.)	59.90	2.68	0.26	3
	psi(Nat8+INP8),p(.)	62.85	5.63	0.06	4
	psi(Nat8+INP8+cano+Tree+Lian),p(.)	70.15	12.93	0.00	7
<i>Platyrrhinus lineatus</i> *					
2km	psi(Cano),p(.)	39.43	0.00	1.00	3
	psi(.),p(.)	39.86	0.43	0.81	2
	psi(INP2),p(.)	41.84	2.41	0.30	3
	psi(Lian),p(.)	41.90	2.47	0.29	3
	psi(Nat2),p(.)	42.13	2.70	0.26	3
	psi(Tree),p(.)	42.72	3.29	0.19	3
	psi(Nat2+INP2),p(.)	45.19	5.76	0.06	4
	psi(Cano+Tree+Lian),p(.)	46.49	7.06	0.03	5
	psi(Nat2+INP2+Cano+Tree+Lian),p(.)	55.58	16.15	0.00	7
8km	psi(Cano),p(.)	38.77	0.00	1.00	3
	psi(.),p(.)	39.13	0.36	0.84	2
	psi(INP8),p(.)	39.67	0.90	0.64	3
	psi(Lian),p(.)	41.19	2.42	0.30	3
	psi(Nat8),p(.)	41.27	2.50	0.29	3
	psi(Tree),p(.)	41.99	3.22	0.20	3
	psi(Nat8+INP8),p(.)	43.24	4.47	0.11	4
	psi(Cano+Tree+Lian),p(.)	45.85	7.08	0.03	5
	psi(Nat8+INP8+cano+Tree+Lian),p(.)	55.20	16.43	0.00	7

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22

**CHAPTER 3: Bat species vulnerability to land-use changes in Cerrado: integrating climatic suitable areas with deforestation data at the landscape scale**

**Student: Poliana Mendes**  
Programa de Pós-Graduação em Ecologia e Evolução  
Universidade Federal de Goiás  
**Advisor: Dr. Paulo De Marco Júnior**  
Universidade Federal de Goiás  
**Collaborator: Pedro Henrique Coelho Ramos**  
Universidade Federal de Goiás

## Abstract

Climatic variables are commonly used to predict suitable areas for species occurrence. However, local processes such as landscape changes may affect habitat suitability. In this sense, we propose to identify species climatic suitable areas deforestation exposure for eight bat species in Cerrado. In addition, we looked at the landscape scale to explore how bat sensitivity to land-use change could reduce bat persistence in the landscape, since this landscape lies within a climatic suitable area. We used scenarios of sensitivity to habitat loss (deforestation amount) and fragmentation (landscape shape index). We used the median of landscape metrics as thresholds to determine species persistence in a landscape. For two species, *Myotis nigricans* and *Sturnira lilium*, we compared the scenarios described above with empirical-derived scenarios, in which thresholds were obtained empirically from a previous occupation study. Changes in land-use affected more the suitable areas of *Artibeus cinereus*, *Myotis nigricans* and *Platyrrhinus lineatus*. These species had also those a lower number of sites with suitable areas in the Cerrado. Overall, species were more exposed to land-use changes in southern Cerrado, a region more affected by humans due to the proximity to major urban centers. Sensitivity to fragmentation would affect specie's suitable areas in the north slightly more than sensitivity to habitat loss. Empirical-derived scenarios for *Sturnira lilium* were more optimistic than scenarios using the variable median, while empirical-derived scenarios for *Myotis nigricans* were more pessimistic. Considering that deforestation has already reached 50% of the Cerrado, if we examine suitable areas of *Sturnira lilium* and *Myotis nigricans*, 54% and 65% of climatically-suitable areas would be lost, respectively. Furthermore, considering sensitivity to land-use changes at landscape scale such values increase to 65% and 80% of suitable area, respectively. Such a pessimistic scenario highlights that even with small losses to distributional area, suitable areas that may be important to maintain large bat populations could be more threatened than previously estimated.

**Keywords:** Chiroptera, sensitivity, exposure, habitat loss, fragmentation, landscape shape index and ecological niche modeling.

## 1 **Introduction**

2  
3 The well-accepted concept of ecological niche states that the set of conditions and resources  
4 allowing the persistence of a given population consists of an existing hyper-volume of an  
5 environmental variable space (Hutchinson 1957). In geographic terms, this hyper-volume can be  
6 expressed as the biotope, i.e. localities with environmental characteristics suitable for specie's  
7 occurrence (Colwell *et al.* 2009). Climatic variables such as temperature and humidity could directly  
8 affect species occurrence at a local scale (Guisan & Thuiller 2005; Thomas 2010). Due to such  
9 influence, climatic variables have been extensively used as predictors of local suitability within an  
10 ecological niche modelling (ENM) approach (Soberon 2007). ENM is usually developed at the  
11 regional scale, comprising all the geographic range of a species or large areas within its geographic  
12 distribution. However, ENM based on climatic variables does not account for how much  
13 distributional areas are being affected by local processes (e.g. landscape changes). Landscape  
14 change, in turn, is a major factor reducing natural populations worldwide (Foley *et al.* 2005; Haddad  
15 *et al.* 2015), affecting vulnerability of those species.

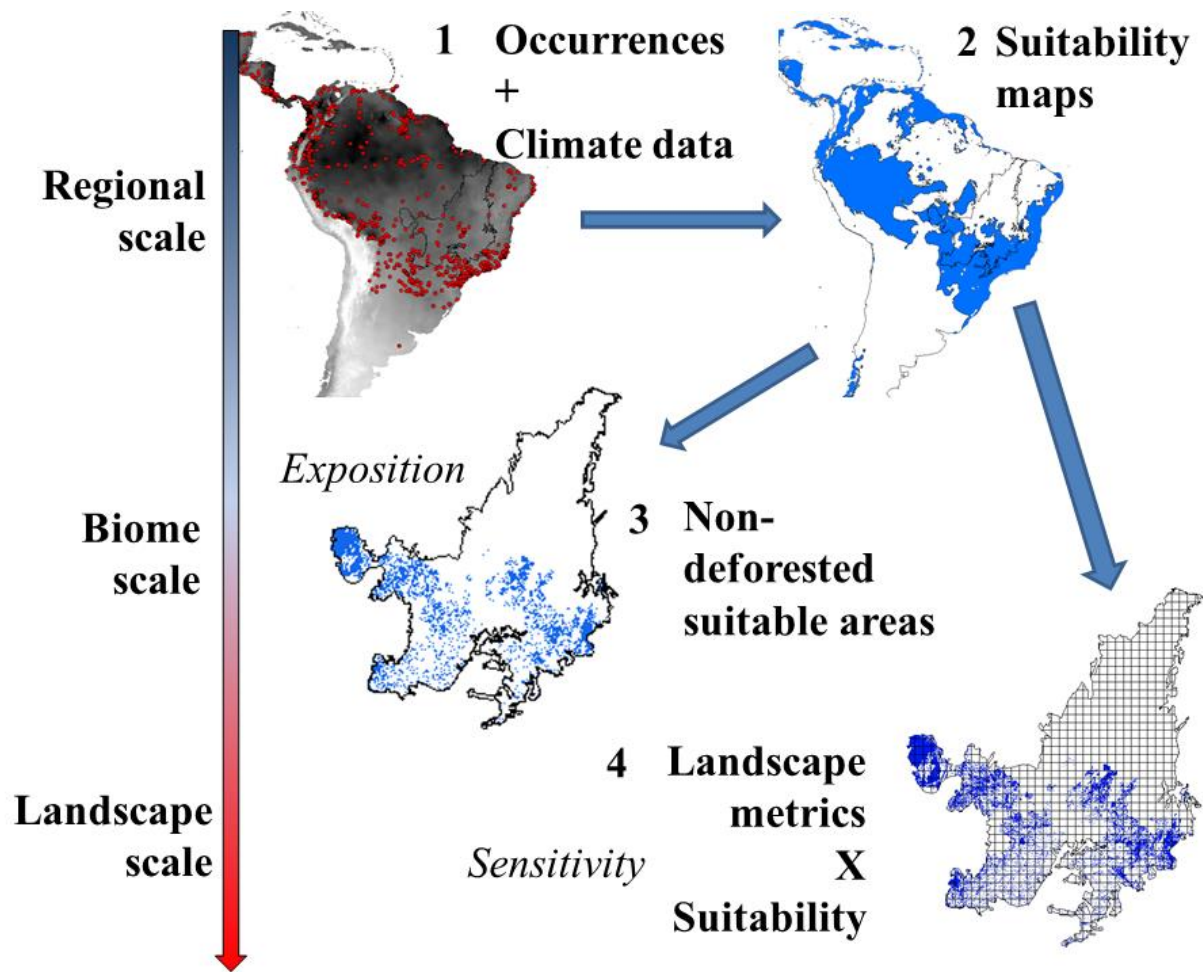
16 Vulnerability is a term that denotes how threatened a species is in a relation to both natural  
17 and anthropogenic environmental changes (Dawson *et al.* 2011). In this sense, vulnerability to land-  
18 use changes could be assessed exploring how climate-suitable areas for species occurrences are  
19 under pressure due to land-use changes. This approach considers that an area may have suitable  
20 conditions for specie's persistence, but such suitability might not guarantee specie's survival owing  
21 land-use pressures happening in the area. Therefore, the disturbance on specie's suitable areas due to  
22 changes in the landscape structure can be considered as an exposure metric for assessing  
23 vulnerability of those species. However, some species could be more affected by this exposure than  
24 others (Betts *et al.* 2014). Differences in sensitivity, i.e. the likelihood of a species being affected by  
25 exposure to stressor agents, is probably related to particular ecological traits of each species, which

1 may be difficult to predict (Henle *et al.* 2004). Both the level of exposure and the degree of  
2 sensitivity of a particular species may determine how conservation actions should be taken to  
3 mitigate in this threatening process (Dawson *et al.* 2011).

4         Several species, including bats (Jones *et al.* 2009), are exposed to a range of human-induced  
5 environmental changes such as climate change, land-use changes, biological invasions, pollution,  
6 and water contamination (Dirzo *et al.* 2014; Murphy & Romanuk 2014). Despite that climate  
7 variables affect bat species richness and composition (Estrada-Villegas *et al.* 2012; Stevens 2013),  
8 landscape variables tend to have a larger predictive power (López-González *et al.* 2014; Mehr *et al.*  
9 2011). Furthermore, bats are vagile animals that use diverse components of a landscape within their  
10 home-range (Aguiar *et al.* 2014; Trevelin *et al.* 2013). Bat populations are being negatively affected  
11 by the conversion of natural into agricultural areas, and some bat species are more sensitive to  
12 specific landscape metrics than others (Duchamp & Swihart 2008; García-Morales *et al.* 2013;  
13 Gorresen & Willig 2004; Medellín *et al.* 2000; Mehr *et al.* 2011). Due to such differences in  
14 sensitivity a lot of effort in scientific research has been applied to identify these species and  
15 landscape metrics (García-Morales *et al.* 2013; Jones *et al.* 2009). It is reasonable that for exploring  
16 bat's vulnerability it is important to consider changes at the landscape scale, such as changes in  
17 landscape composition or configuration. Additionally, species might respond to a different land-use  
18 changes (e.g. the maximum value of habitat loss beyond which populations would be considerably  
19 reduced) (Swift & Hannon 2010). One way to evaluate species thresholds to land-use changes is  
20 through occupancy models. Detailed occupancy analyses are welcomed to a better evaluation of  
21 species individual response to landscape changes that could represent an empirical basis for a  
22 complete vulnerability analysis (Mackenzie *et al.* 2006).

23         The Cerrado biome, a Brazilian savanna, has been highly impacted by land-use changes  
24 (Klink & Machado 2005; Sano *et al.* 2010), and bats in Cerrado are possibly exposed to those  
25 changes. However, considering the differences in suitability caused by different responses to climatic

1 variables, we expect that the level of exposure is widely variable among bat species. Nevertheless, at  
2 the landscape scale bats could be sensitive to a certain threshold of land-use changes level (e.g. 30%  
3 of remaining natural vegetation). Here we propose to bring the regional concept of sensitivity to a  
4 landscape scale, assessing the exposure of climate suitable areas in Cerrado to habitat loss and  
5 fragmentation, as well as the effect of possible thresholds of land-use changes affecting specie's  
6 persistence in landscapes (Figure 1). Considering that bats could be sensitive to landscape structure,  
7 we created scenarios in which species would be sensitive to a certain level of habitat loss or  
8 fragmentation in a landscape. For example, species responding to a certain level of fragmentation  
9 would not occur in a fragmented landscape even if the amount of suitable habitat was as high as in  
10 other landscapes. Sensitivity thresholds were delimited by two different ways: using a scenario,  
11 and using an empirical-derived threshold extracted from occupancy models. Overall, the aim of this  
12 approach was: (1) to determine which species have more climatically-suitable areas exposed to  
13 deforestation, (2) where these species are being exposed to habitat loss and fragmentation, and (3)  
14 where they would disappear first if they were sensitive to a particular threshold of habitat loss or  
15 fragmentation.



**Figure 1-** A conceptual model for relating species's vulnerability to land-use changes using ecological niche modeling. Changes in scale are represented by an arrow at the left side. At the continental scale, species occurrence data and bioclimatic data were used to build ecological niche models (1), representing the suitable areas for that species (2). At the regional scale, these suitable areas can be overlapped to non-deforested areas to evaluate specie's exposure to deforestation (3). At the landscape scale, the biome is subdivided into landscapes, and landscape metrics are calculated for each grid cell (4). Species could have a threshold of landscape metrics (e.g. habitat loss) to persist in a landscape.

## 1 **Methods**

### 3 *Overview*

4       We divided our methods in three steps: (1) species distribution modeling, (2) specie's exposure  
5 to deforestation, and (3) scenarios of species sensitivity to habitat loss and fragmentation at a  
6 landscape scale. Environmental suitability was calculated using Maxent (Elith *et al.* 2006). Exposure  
7 was obtained by subtracting deforested areas from climatically suitable areas. We developed  
8 sensitivity scenarios using each suitable cell as an individual landscape, calculating the percentage of  
9 natural vegetation loss (representing habitat loss) and the landscape shape index for each landscape  
10 (representing fragmentation). We created thresholds of sensitivity to habitat loss and fragmentation  
11 using the median of both variables and using empirical-derived data for two species.

### 13 *Occurrence data*

14       Based on the availability of occurrence records and on the representation of the feeding habit  
15 spectrum in the Cerrado, we selected eight bat species occurring on the biome: *Artibeus cinereus*,  
16 *Artibeus lituratus*, *Desmodus rotundus*, *Glossophaga soricina*, *Myotis nigricans*, *Platyrrhinus*  
17 *incarnum*, *Platyrrhinus lineatus* and *Sturnira lilium* (Table 1). Occurrence data were obtained through  
18 museums databases (for all Neotropical region), data from collaborating researchers (M. Oprea and  
19 T. B. Vieira, comprising four locations only for Brazil), data collected first-hand (see Chapter 2) and  
20 scientific articles (only for Brazil). Databases used are from the Smithsonian Museum, GBIF (Global  
21 Biodiversity Information Facility), MANIS (Mammal Networked Information System), and CRIA  
22 Species Link (<http://splink.cria.org.br/>). We searched for scientific articles in “Web of Science”  
23 using the keywords “Chiroptera and Brazil”; and in Scielo (Scientific Electronic Library Online)  
24 using the keywords “Chiroptera, morcegos, Brazil and Brasil”. Whenever geographic coordinates  
25 were not available in scientific articles or in the databases we used the Google Earth software

(Google Inc. 2009) to identify the most approximate coordinates from informed landmarks (only for occurrences from Brazil).

We compared occurrence data with geographic distributions of species from International Union for Conservation of Nature and Natural Resources (IUCN) to avoid errors of false occurrences. We had a case of a taxonomic change in an analyzed species, *Platyrrhinus incarum* was synonym of *Platyrrhinus helleri* until 2010 (Velazco *et al.* 2010). Therefore, occurrences of *P. helleri* registered before 2010 and overlapping *P. incarum* distribution were considered as *P. incarum* occurrences. We found a total of 62,235 occurrences (Table 1), but only one occurrence per cell (9.25 X 9.25 km) was considered for species distribution modelling. We did it to avoid results being affected by sampling bias (Kadmon *et al.* 2004).

**Table 1-** Bat species considered in this study, its habits, number of occurrences found and unique occurrences. Unique occurrences are the amount of occurrences in different cells (9.25 X 9.25 km). SCF = small canopy frugivore, LCF = large canopy frugivore, HE = hematofague, NE = nectarivore, BCAI = background-cluttered aerial insectivore and UF = understory frugivore.

Species	Habits	Occurrences	Unique occurrences
<i>Artibeus cinereus</i>	SCF	1,841	324
<i>Artibeus lituratus</i>	LCF	11,927	1,810
<i>Desmodus rotundus</i>	HE	10,429	1,636
<i>Glossophaga soricina</i>	NE	16,298	1,925
<i>Myotis nigricans</i>	BCAI	7,102	820
<i>Platyrrhinus incarum</i>	SCF	158	78
<i>Platyrrhinus lineatus</i>	LCF	1,368	374
<i>Sturnira lilium</i>	UF	13,102	1,779
<b>TOTAL</b>		62,235	8,743

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24

*Ecological niche modeling*

We developed ecological niche models using data from climatic variables provided by the WorldClim (available at <http://www.worldclim.org/>) at a resolution of 9.24 X 9.24 km grid cells. A total of 19 bioclimatic variables derived from monthly temperature and rainfall were used. However, the strong collinearity among variables may be a problem in modelling procedures (Jiménez-Valverde *et al.* 2011). In this sense, we followed other recent applications (e.g. Silva *et al.* 2014) aiming to circumvent this problem. We ran a principal component analysis with bioclimatic variables and used the six principal component axes (with a total explanation power of 95%) to perform species distribution modeling (Appendix 1). Previous studies have shown that climatic variables may affect bat distribution, abundance and species richness (Estrada-Villegas *et al.* 2012; Stevens 2013), suggesting therefore that the use of climatic variables as a predictor of suitable sites for bats is coherent.

We built the ecological niche models using Maximum Entropy (Maxent), software Maxent version 3.3.3 (Phillips *et al.* 2004). Maxent calculates a function of bioclimatic variables that minimize the distance between the prediction of suitability and actual occurrences (Elith *et al.* 2011). This method allows for the use of presence only data; and some random background units would be considered in the model to improve suitability estimation (Elith *et al.* 2011). Maxent is a method in species distribution modelling with high predictive power, in part due to its complexity (Elith *et al.* 2006; Hernandez *et al.* 2006; Rangel & Loyola 2012). We converted suitability maps derived from Maxent into binary maps using the balance threshold obtained from Receiver Operating Characteristic curves (ROC) (Pearce *et al.* 2000). This threshold is a balance between omission and commission errors. We evaluated the models using the area under the curve ROC (AUC) and true skilled statistics (TSS) (Allouche *et al.* 2006; Liu *et al.* 2011).

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22

*Deforestation data*

We quantified species exposure to deforestation using two land cover data sources. We used a land cover data of 2010 from the Instituto Brasileiro de Meio Ambiente (IBAMA, <http://siscom.ibama.gov.br/monitorabiomas/cerrado/index.htm>). IBAMA used a previous land use data from PROBIO project (“Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira”), year of 2002, and added deforestation data collected using the satellite LANDSAT from 2002 to 2010. Deforestation data from 2011 until 2014 was obtained from Laboratório de Processamento de Imagens e Geoprocessamento (LAPIG, <http://www.lapig.iesa.ufg.br/>). LAPIG used data from the satellite MODIS (MOD13Q1), and validated using data from satellites LANDSAT and CBERS to monitor deforestation yearly. Despite differences on the methods for evaluating deforestation, we considered that joining both datasets would provide a more realistic and updated scene of deforestation in Cerrado. We transformed deforestation data into a grid a hundred times smaller than the suitability data (0.0925 X 0.0925 km grid cells).

*Exposure and Sensitivity scenarios*

We evaluated exposure to deforestation of an individual species by subtracting the deforested pixels from the species suitable area. Therefore, exposure was the sum of deforested areas in each suitable cell divided by the sum of suitable cells area:

$$EXPO = \frac{\sum_{i=1}^n (DA)}{\sum_{i=1}^n (SA)}$$

where *EXPO* is the exposure to deforestation of a species, *i* is each suitable cell (i.e. 9.24 x 9.24 km), *n* is the number of cells, *DA* is the deforested area in each suitable cell and *SA* is the suitable cell size.

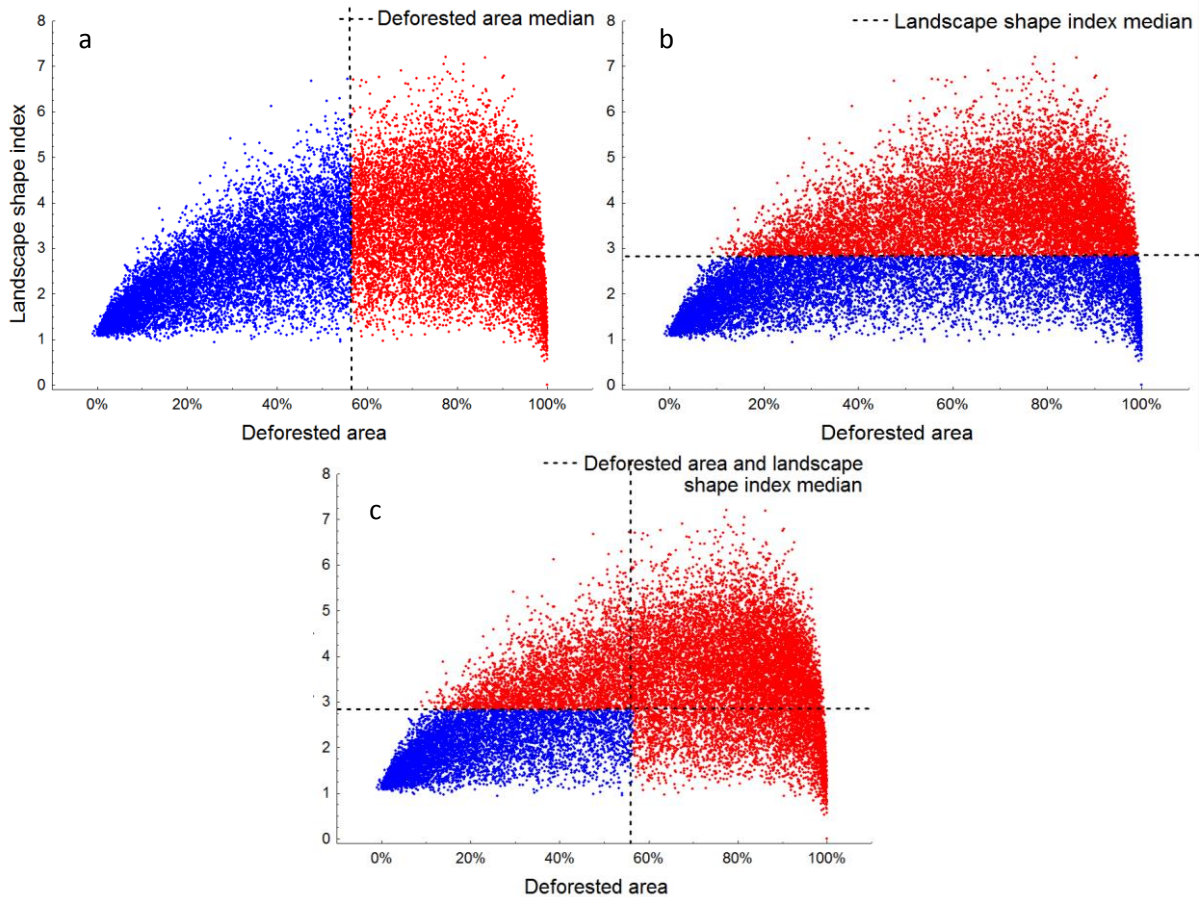
1 We considered that a given species could be sensitive to two factors at the landscape scale:

2 habitat amount and fragmentation. We considered each 9.24 x 9.24 km cell of the modelling  
3 procedures as an individual landscape. Our design allowed us to evaluate both habitat amount and  
4 fragmentation metrics for each landscape unit. Habitat loss, calculated for each landscape, was the  
5 sum of non-forested pixels and the landscape shape index (LSI) representing fragmentation. LSI is  
6 the total edge perimeter divided by the edge perimeter if all natural vegetation was one circle:

$$LSI = \frac{TE}{2\pi \times \sqrt{A/\pi}}$$

7 where, *TE* is the total of edge and *A* is the natural vegetation area in a landscape. Large values of LSI  
8 mean that the landscape have more edges, if all vegetation was within one circular patch, LSI would  
9 be equal to 1. Total edge was the sum of the size of pixel's edges adjacent to a non-forested pixel or  
10 a border of the landscape.

11 We separated landscapes into four categories: (1) landscapes where species sensitive to  
12 habitat loss would disappear (Figure 2a, red circles), (2) landscapes where species sensitive to  
13 fragmentation would disappear (Figure 2b, red circles), (3) landscapes where species sensitive to  
14 habitat loss or fragmentation would disappear (Figure 2c, red circles), and (4) landscapes where no  
15 species would disappear (Figure 2c, blue circles). The threshold for separating these groups was the  
16 median of deforestation (0.56) and landscape shape index (2.81).



**Figure 2-** Scenarios of species sensitivity to landscape changes. Each unit is a cell (9.24 X 9.24km) in the biome Cerrado. Landscape changes were habitat loss in each cell (the sum of non-forested pixels) and fragmentation (measured with the landscape shape index). Cells were separated by the median of each variable (habitat loss median = 0.56; landscape shape index median = 2.81). *a*) red circles are cells with high habitat loss where sensitive species would disappear; *b*) red circles are cells with high landscape shape index where sensitive species would disappear; *c*) red circles are cells with high habitat loss or landscape shape index where sensitive species would disappear, and blue cells are those with low deforestation and landscape shape index.

## 1 *Empirical-derived sensitivity scenario*

2 We used empirical-derived sensitivity data for *Myotis nigricans* and *Sturnira lilium*.

3 Occupancy probability of these species is correlated to landscape variables (see Chapter 2). We

4 considered the landscape metric value in which the probability of occupancy changes from zero to

5 one as a threshold for sensitivity. To obtain each threshold value we performed occupancy models

6 using incidence data of *M. nigricans* and *S. lilium* from 16 sampling sites. Samples were made using

7 20 mist nets positioned from the edge towards the core of the patch, six hours after sunset, during

8 four nights. All patches were located in Goiás State, in a savanna-like vegetation type within

9 Cerrado. All sampling sites were positioned in a forest patch. Despite having different sizes (from 90

10 to 400 ha), all sites had a circle similar shape (Shape index < 2).

11 We performed occupancy models using the software PRESENCE (Hines 2006). Predictors

12 were natural vegetation amount and number of patches taken in a landscape size of 8 km of radius

13 from the sampling site. *M. nigricans* was related to fragmentation (number of patches), while *S.*

14 *lilium* was related to natural vegetation amount. We extracted the last predictor value before

15 occupation probability changed from zero to one (Figure 3). To transform natural vegetation amount

16 into deforested area we subtracted natural vegetation amount (that was relative to landscape size)

17 from 1. To transform the number of patches into landscape shape index we extracted the identity of

18 the landscape where occupation probability changed from zero to one and calculated the landscape

19 shape index using the same land cover data cited above. Threshold for *Sturnira lilium* was 0.28 of

20 natural vegetation amount that means 0.72 of deforestation. Threshold for *Myotis nigricans* was 194

21 patches (considering a circular landscape with 8km of radius). For this landscape the shape index

22 was 2.14. All transformations in data before the extraction of real sensitivity thresholds imply in

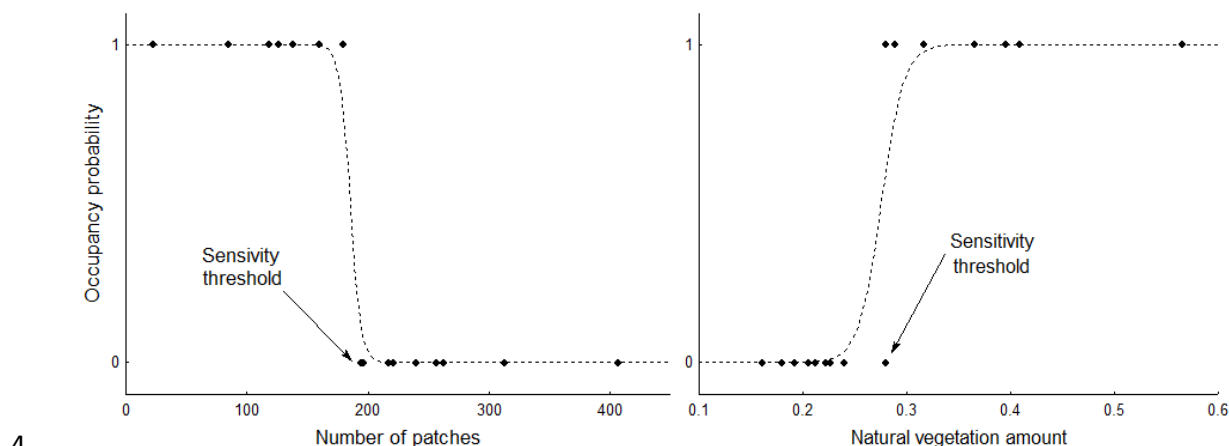
23 some caveats on the interpretation of the results. However, such datasets are the most realistic

24 surrogates of sensitivity that we dispose heretofore. Moreover, surrogated variables are measuring

25 similar characteristics of landscape measured by other variables at occupancy models. For example,

1 landscape shape index and the number of patches are expected to be positively correlated because  
2 they measure a similar characteristic of landscape.

3



4

5 **Figure 3-** Results used to define a realistic sensitivity threshold to landscape changes.  
6 Sensitivity thresholds were defined as the last point with occupancy probability zero, just  
7 before occupancy probability changes to one. (a) *Myotis nigricans* was related to  
8 fragmentation (number of patches) and (b) *Sturnira lilium* to habitat loss (natural vegetation  
9 amount).

10

## 11 Results

12

13 AUC values of ecological niche models ranged from 0.73 to 0.86, and TSS values ranged  
14 from 0.36 to 0.61 (Table 2), both indicating that the Maximum Entropy (Maxent) had an acceptable  
15 performance predicting suitable areas for bats. Suitable areas (i.e. cells with suitability above the  
16 balanced threshold) ranged from 409,300 km<sup>2</sup> to approximately 2,000,000 km<sup>2</sup>, the last one being all  
17 Cerrado territory (Table 2). *Artibeus cinereus* had the smallest suitable area in Cerrado, while  
18 *Glossophaga soricina* had the largest one (Table 2). Species exposure to deforestation (i.e. amount of

suitable area lost by deforestation) varied from 50% to 70%. *Desmodus rotundus* and *Glossophaga soricina* were the species with less suitable area loss, while *Platyrrhinus lineatus* and *Myotis nigricans* were the species with more suitable area loss due current deforestation (Table 2).

**Table 2-** Ecological niche modeling results showing AUC and TSS values that allow a modelling evaluation. Distribution size represents the Cerrado area in which environmental suitability was larger than the balanced threshold. Lost area after deforestation was calculated subtracting suitable areas by current deforestation on each location. Loss considering deforestation is the percentage of suitable area that was lost due to Cerrado deforestation.

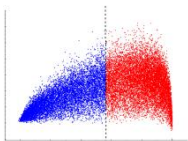
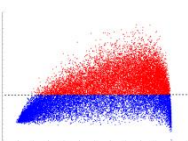
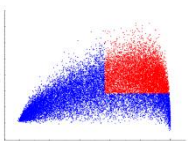
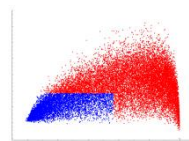
Species	AUC	TSS (ROC)	Distribution size (km <sup>2</sup> X1000)	Lost area after deforestation (km <sup>2</sup> X1000)	Loss considering deforestation (%)
<i>Artibeus cinereus</i>	0.818	0.538	409.30	239.30	58.5
<i>Artibeus lituratus</i>	0.743	0.398	1,799.24	1,003.98	55.8
<i>Desmodus rotundus</i>	0.730	0.362	2,104.75	1,083.95	51.5
<i>Glossophaga soricina</i>	0.751	0.400	2,038.79	1,029.59	50.5
<i>Myotis nigricans</i>	0.750	0.371	928.79	612.07	65.9
<i>Platyrrhinus incarum</i>	0.843	0.610	1,396.18	748.35	53.6
<i>Platyrrhinus lineatus</i>	0.862	0.591	792.25	548.34	69.2
<i>Sturnira lilium</i>	0.753	0.415	1,872.21	1,016.61	54.3

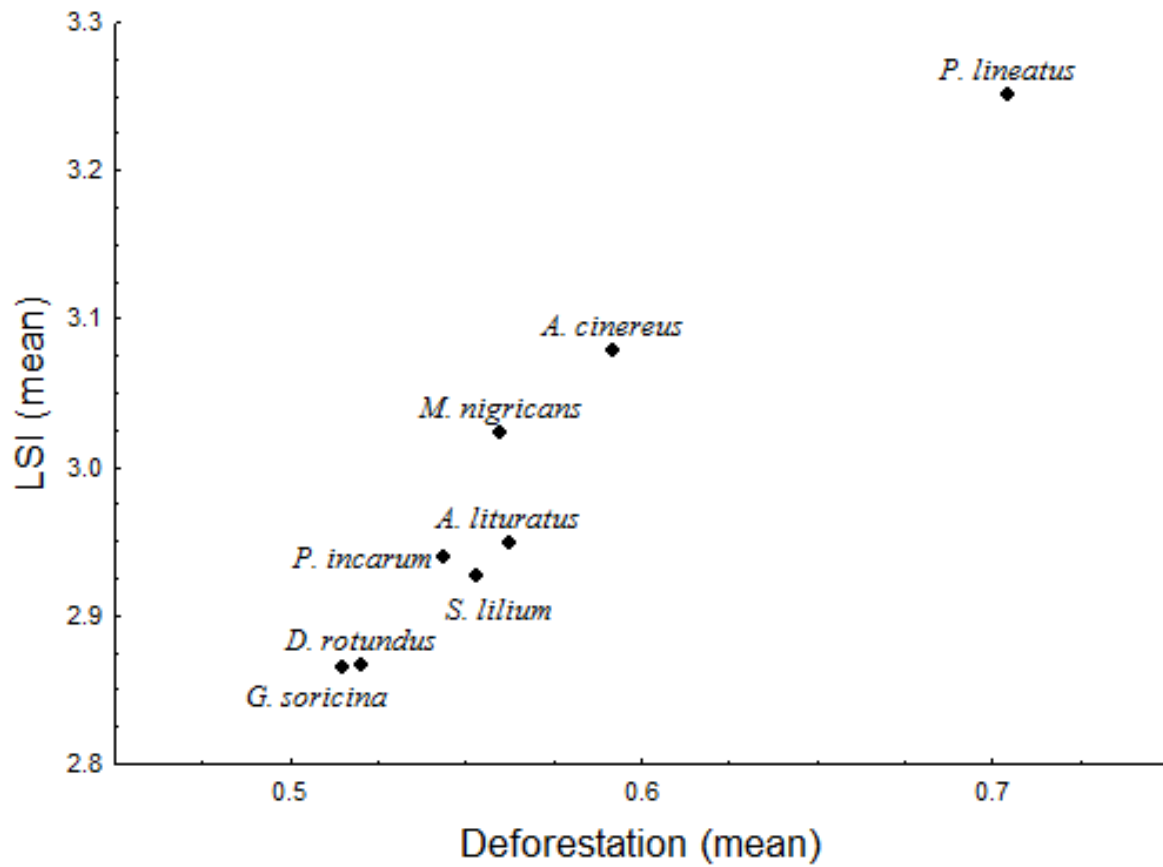
1 According to our findings, *Platyrrhinus lineatus* and *Myotis nigricans* are expected to lose a  
2 larger percentage of suitable areas due to their sensitivity to landscape changes (Table 3). *Desmodus*  
3 *rotundus* and *Glossophaga soricina*, in turn, would be less affected if they were sensitive (Table 3).  
4 Species with a large proportion of suitable area affected by deforestation are also affected by  
5 fragmentation (Figure 4). However, species would lose slightly more suitable areas if they were  
6 sensitive to fragmentation than to deforestation, but these differences were always smaller than 6%  
7 (Table 3). Small differences in the loss of suitable area in scenarios with sensitivity to different  
8 variables indicate that both variables are not independent (see Figure 2). Despite the small  
9 differences in the loss of suitable areas, it was possible to observe differences in the locations where  
10 those losses would happen (Figure 5). Species with suitable areas at southern Cerrado would be more  
11 affected by landscape changes than species with suitable areas at northern Cerrado (Figure 5),  
12 despite some high fragmentation level cells being located in the north (See *Desmodus rotundus* in  
13 Figure 5 for an example). Nonetheless, sensitivity to fragmentation would occur northern than  
14 sensitivity to habitat loss (Figure 5). Almost for all analyzed species, high suitability areas were  
15 located in southern Cerrado, with high levels of loss of predicted suitable areas due to landscape  
16 changes (Figure 5).

17

18

1 **Table 3-** Loss estimates of suitable areas at landscape scale under sensitivity scenarios. Suitable area  
2 loss with habitat loss sensitivity is the percentage of area that would be lost if a species does not  
3 occur in cells (landscapes) with high deforestation levels. Suitable area loss with fragmentation  
4 sensitivity is the percentage of lost area if a species does not occur in cells with high fragmentation  
5 levels. All percentages are relative to species suitable area size. Blue cells = landscapes that would  
6 not be lost in a scenario; red cells = landscapes that would be lost in a scenario; Horizontal axis in  
7 graphs are the percentage deforested area (DA); and vertical axes the landscape shape index (LSI).

Species	Suitable cells with high deforestation level (%)	Suitable cells with high fragmentation level (%)	Suitable cells with high deforestation and fragmentation level (%)	Suitable cells with high deforestation or fragmentation level (%)
				
<i>Artibeus cinereus</i>	68.3	74.8	66.4	76.7
<i>Artibeus lituratus</i>	66.3	71.4	64.0	73.7
<i>Desmodus rotundus</i>	61.1	67.4	58.9	69.5
<i>Glossophaga soricina</i>	60.5	66.9	58.4	69.0
<i>Myotis nigricans</i>	68.3	74.0	66.3	76.0
<i>Platyrrhinus incarum</i>	64.2	70.0	62.1	72.2
<i>Platyrrhinus lineatus</i>	81.8	85.5	79.5	87.8
<i>Sturnira lilium</i>	65.1	70.5	62.8	72.7



**Figure**

4- Mean deforestation for each suitable cell of a species and mean of landscape shape index (LSI).

Mean values were calculated for all suitable cells of each species.

Suitable cells with:



High fragmentation



High deforestation



High fragmentation and deforestation



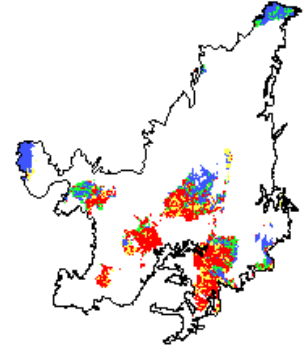
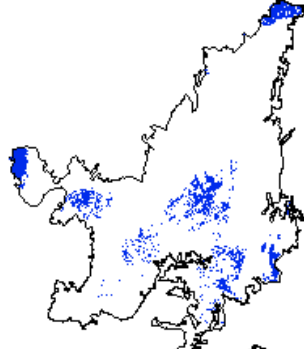
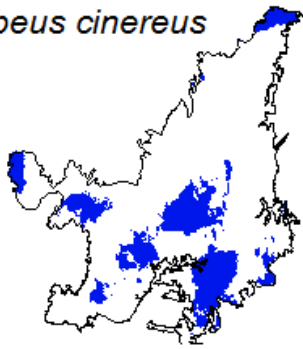
Low deforestation and fragmentation

Suitable areas

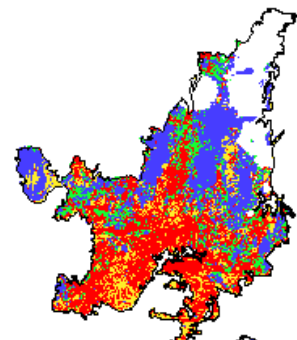
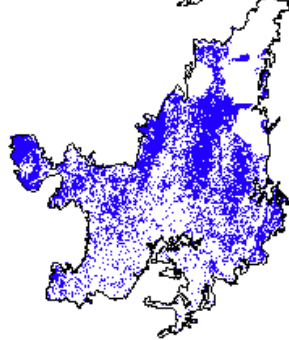
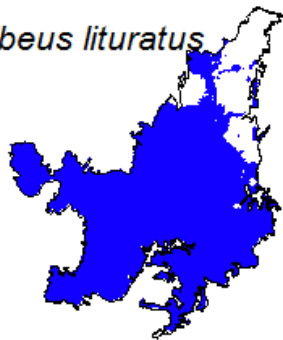
Non-deforested suitable areas

Sensitivity scenarios

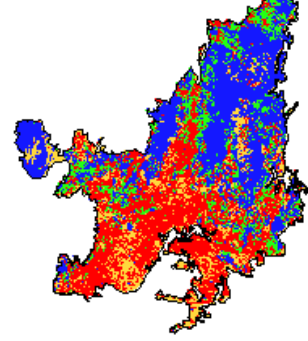
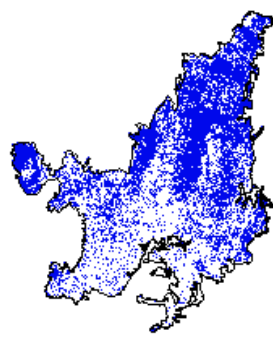
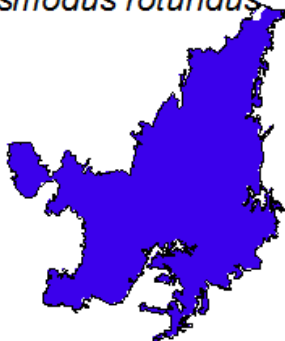
*Artibeus cinereus*



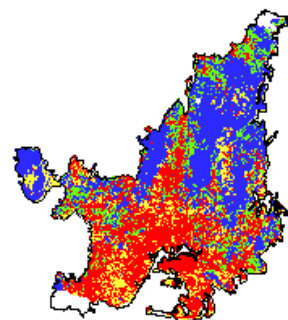
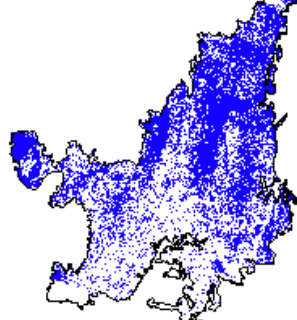
*Artibeus lituratus*

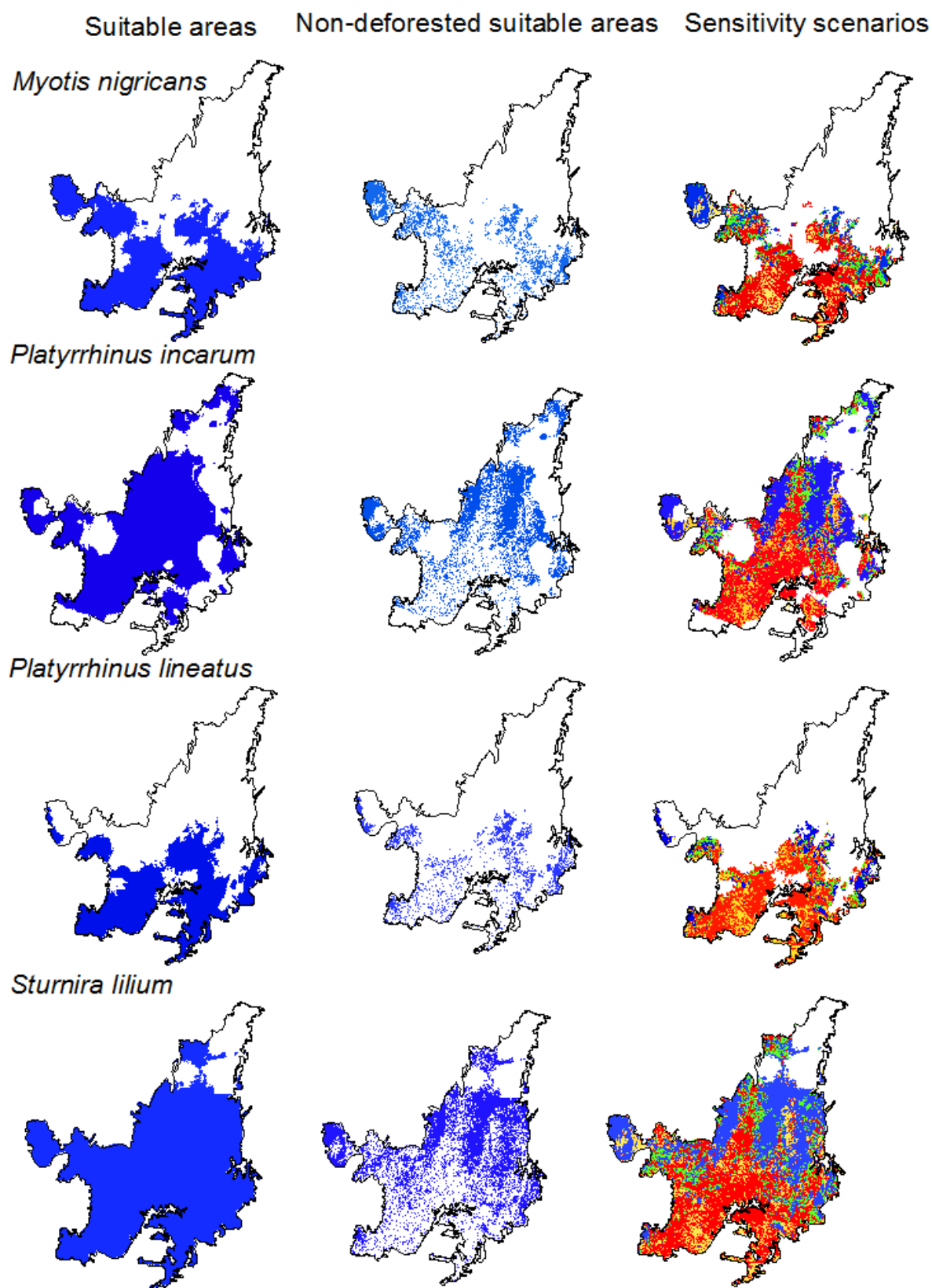


*Desmodus rotundus*



*Glossophaga soricina*





1  
2 **Figure 5-** Spatial distribution of suitable cells and effects of land-use changes on bat species in

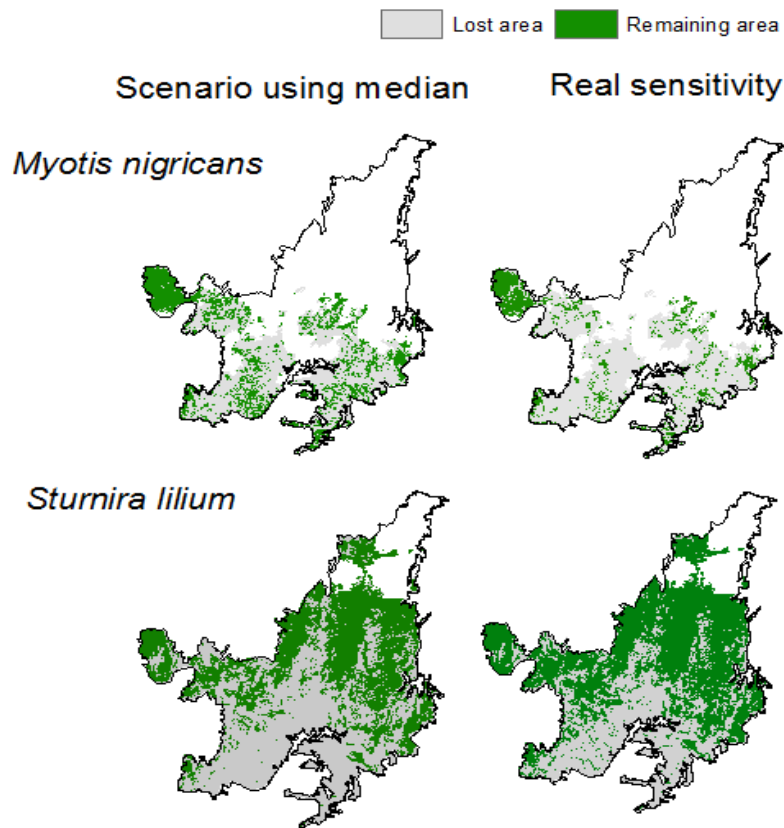
1 Cerrado. In the left side suitable areas for each species, suitable areas were defined as the areas  
2 above a balance threshold of suitability (see Methods). Non-deforested suitable areas represent the  
3 remaining suitable areas considering current deforestation. In the right side, suitable cells with high  
4 levels of habitat loss (deforested pixels) and/or fragmentation (measured with landscape shape  
5 index). Blue area in the right side is composed by suitable cells with low deforestation and  
6 fragmentation. Different colors in the right maps can be interpreted as different sensitivity scenarios  
7 to land-use changes.

8  
9 Considering the empirical-derived sensitivity scenarios performed for *Myotis nigricans* and  
10 *Sturnira lilium* using occupancy curves related to habitat loss and fragmentation, we found that  
11 previous scenarios (variable median as a threshold) were pessimistic for *Sturnira lilium* and  
12 optimistic for *Myotis nigricans* (Figure 6). In empirical-derived scenarios the loss of suitable areas  
13 for *Myotis nigricans* using fragmentation as a predictor was of 81%, while in the scenario using the  
14 median was of 74% (Table 4). For *Sturnira lilium*, the loss of suitable areas using habitat loss as a  
15 predictor was of 60% in the empirical-derived scenario and of 65% in the scenario using the median  
16 (Table 4).

1 **Table 4-** Comparison between sensitivity scenarios and empirical-derived sensitivity scenarios for  
2 predicting effects of land-use changes over suitable areas for *Myotis nigricans* and *Sturnira lilium*.  
3 Empirical threshold values were obtained from occupancy models that suggested that *M. nigricans*  
4 was affected by fragmentation and *S. lilium* by habitat loss (See chapter 2). Sensitivity scenarios  
5 thresholds were the variable median. Fragmentation was measured using the landscape shape index  
6 (LSI) and habitat loss quantifying deforested area. Each species was evaluated only for this related  
7 variable. Loss of suitable areas for *Myotis nigricans* was larger than in the scenario using the median,  
8 whereas for *Sturnira lilium* loss of suitable areas was smaller than in the scenario using the median.

	<b>Landscape metric</b>	<b>Median (Scenario)</b>	<b>Threshold (Occupancy)</b>	<b>Loss (Scenario)</b>	<b>Loss (Realistic)</b>
<i>Myotis nigricans</i>	LSI	2.81	2.14	73.96	81.20
<i>Sturnira lilium</i>	Deforested	0.56	0.72	65.07	60.16

9



**Figure 6-** Differences of remaining suitable areas under different scenarios: using the median (sensitivity scenario) and using a threshold from occupancy model (empirical-derived sensitivity scenario). For *Myotis nigricans* both scenarios shown used only sensitivity to fragmentation (landscape shape index), while for *Sturnira lilium* only sensitivity to habitat loss was used.

## Discussion

Patterns of exposure to land-use changes among species may be explained by the marginality of Cerrado on species distribution and the greater suitability of areas under human pressure. Among the analyzed species, *Platyrrhinus lineatus*, *Myotis nigricans* and *Artibeus cinereus* were the most exposed to deforestation in suitable areas of Cerrado. These species were also those with the smallest

1 suitable areas in Cerrado. At first sight, such results may be not relevant for bat specialists, since  
2 these species are widely distributed in a range of vegetation types (e.g. Fischer & Grande ; Oprea *et*  
3 *al.* 2009; Talamoni *et al.* 2013; Zortéa & Alho 2008). However, Cerrado represents a marginal  
4 distribution area for *Platyrrhinus lineatus* and *Artibeus cinereus* (Gardner 2007). While *P. lineatus*  
5 does not occur in the northwest of Cerrado, *A. cinereus* does not occur in the west of Cerrado, except  
6 for few occurrences in Bolivia. At the marginal areas of a species distribution habitat is usually less  
7 suitable, with smaller and more fluctuating populations (Brown 1984; Cuervo & Møller 2013). In  
8 this sense, the small suitable areas in Cerrado for *P. lineatus* and *A. cinereus* may be a result of their  
9 marginal distribution. Additionally, for both *P. lineatus* and *A. cinereus* suitable areas were located  
10 in south Cerrado, the most affected area by deforestation in this biome (Klink & Machado 2005;  
11 Sano *et al.* 2010). Despite the distribution of *M. nigricans* not having marginal areas in Cerrado  
12 (Gardner 2007), most of the suitable areas for this species were also located in south Cerrado, with a  
13 lack of occurrences in northern Cerrado.

14 All analyzed bat species had higher suitability areas in southern Cerrado, but only few of  
15 them had also high suitability areas in northern Cerrado. Southern areas of Cerrado are the most  
16 impacted by pastures and croplands due to the occupation history of this biome that began in the  
17 south, closer to major urban areas (Klink & Machado 2005; Sano *et al.* 2010). Croplands, the major  
18 driver of fragmentation, are more concentrated in southern Cerrado, whereas pasturelands are  
19 distributed throughout the biome (Carvalho *et al.* 2009). Southern Cerrado areas have also more  
20 species richness (Blamires *et al.* 2008; Diniz-filho *et al.* 2008; Rangel *et al.* 2007). Nevertheless, the  
21 lower species richness of northern areas may be related to the disproportionally less bat biological  
22 surveys performed in this region (Bernard *et al.* 2011). In situations where a species has large  
23 suitable areas, exposure to impacts in one part of its geographic range would buffer the effects of that  
24 impact (Dawson *et al.* 2011). Therefore, species with high suitability cells through all Cerrado would  
25 be less affected by the impact biased to latitude. For example, *Desmodus rotundus* and *Glossophaga*

1 *soricina*, both species proportionally less affected by the exposure to deforestation at suitable areas,  
2 are species with suitable areas occurring through all Cerrado. Furthermore, the higher exposure of  
3 bat species to deforestation in southern Cerrado highlights the importance of attention over these  
4 areas, however the actual impact of this exposure on species would depend of their sensitivity.

5         Sensitivity is the degree on which the persistence of a species would be affected by an  
6 environmental change (Dawson *et al.* 2011). Therefore, sensitive species would be more affected,  
7 while non-sensitive would less affected. We created scenarios to simulate two types of sensitivity  
8 among species at a landscape scale and their effects on suitable areas: habitat loss and fragmentation  
9 sensitivity. We used an approach that considers species-specific thresholds on landscape structure  
10 predicting species persistence in its home-range, mixing the sensitivity concept at a regional scale  
11 with landscape context logic (Turner 2005). In this case, sensitivity was taken at the landscape scale,  
12 representing a threshold of habitat loss and fragmentation in a landscape where species would not  
13 persist. Our results showed that sensitivity to fragmentation would cause a slightly larger loss of  
14 suitable landscapes than sensitivity to habitat loss for all species. Both sensitivities would cause a  
15 major loss at southern Cerrado, but landscapes that would be affected only by fragmentation are  
16 northern than landscapes that would be affected only by habitat loss sensitivity. We argue that  
17 mapping sensitivity effects on distribution is a complementary approach to the exposure analysis,  
18 indicating specific areas which populations could be at endangered if they were sensitive to different  
19 environmental factors. A different approach to access sensitivity is the detecting biological traits that  
20 mediate species responses to land-use changes (Henle *et al.* 2004), and generalize it through the  
21 ranking of species based on their sensitivity. However, identifying these traits may represent an  
22 onerous work since intuitive predictions about how biological traits mediate sensitivity to landscape  
23 changes are usually not corroborated (Cagnolo *et al.* 2009; Comont *et al.* 2012; Meyer *et al.* 2007;  
24 Zimbres *et al.* 2012). Creating scenarios of sensitivity may be a solution to theoretical access effects  
25 of sensitivity on biodiversity.

1           Scenarios are useful tools to assess biological patterns or processes when realistic data is not  
2 available (Peterson *et al.* 2003). Nevertheless, they always need to be treated with caution since they  
3 may be a blurry and malformed mirror image of reality. Some species may not be sensitive to land-  
4 use changes because they are deflected to these changes, finding resources such as food and roost in  
5 highly modified landscapes (García-Morales *et al.* 2013). Another possibility is that bat species are  
6 sensitive to other environmental factors not explored here, for example, pesticide use, climate  
7 change, wind turbines or lighting (Jones *et al.* 2009). The most realistic form to assess species  
8 sensitivity to land-use changes is relating species' persistence, incidence or abundance to those  
9 changes, being thereby possible to find a land-use threshold for the species. Among the analyzed  
10 species, *Artibeus lituratus* was pointed as edge density sensitive (Gorresen *et al.* 2005; Klingbeil &  
11 Willig 2010), *Glossophaga soricina* as patch size and patch isolation sensitive, *Myotis nigricans* as  
12 fragmentation sensitive and *Sturnira lilium* as forest cover, edge density sensitive and patch isolation  
13 (Gorresen *et al.* 2005; Klingbeil & Willig 2010; also see chapter 2). We used thresholds of landscape  
14 features predicting species occupancy for *Sturnira lilium* and *Myotis nigricans*. The sensitivity  
15 scenarios were more pessimistic than empirical-derived scenario for *S. lilium* and more optimistic for  
16 *M. nigricans*. We developed a second step of this comparison spatially showing that these  
17 differences were located in adjacent areas from those predicted by the scenarios. Even with these  
18 differences, we argue that scenarios of sensitivity may represent an interesting tool to foreknow  
19 impacts that species could have if they were sensitive. Predicting these impacts is important because,  
20 even knowing that a species occurs in some exposed area, sometimes it is not known if that species  
21 would persist.

22           A different approach for assessing species vulnerability to land-use changes may be verifying  
23 the exposure of species geographic range to land-use modifications instead of climate suitable areas.  
24 However, we consider that using suitable areas is a more thorough approach. Distributional areas  
25 usually have some parts with lower suitability, even if non-suitable areas have species occurrences.

1 These occurrences could be a consequence of a source-sink process, in which some occurrences in  
2 sink areas would be caused by immigration from source areas if dispersion is not limited (Pulliam  
3 2000). Bats are vagile animals (Norberg & Rayner 1987), so it would be reasonable to expect that  
4 dispersal limitations are not the major factor delimiting species distribution at a small scale such as  
5 the Cerrado biome. Considering climate suitable areas instead of geographic range may overcome  
6 the lack of information about population tendencies in different regions of distributional areas.

7 A new emergent approach integrates the impacts on species at the landscape scale with a  
8 those at a regional scale, integrating, for example, fragmentation and climate change (Faleiro *et al.*  
9 2013; Haddad *et al.* 2015; Kerr *et al.* 2007). Our approach represents a small step in this direction;  
10 our findings improve the understanding on how climate suitable areas are affected by landscape  
11 changes in Cerrado. Overall, our results showed that small suitable areas in Cerrado were  
12 determinant for predicting species vulnerability to land-use changes. However, a threatened species  
13 in Cerrado is not necessarily in also threatened in other biomes. Therefore, a wider approach  
14 considering the entire country or the continent would provide a more complete picture of bat species  
15 vulnerability. On the other hand, regional approaches are also important to focus vulnerability  
16 understanding into a regional (Ferrier *et al.* 2002) and more feasible scale for conservation  
17 management.

## 19 **Acknowledges**

20

21 We are grateful to M. Oprea and T.B. Vieira for providing occurrence data. P.M. receives a  
22 scholarship from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico). P. De  
23 Marco was funded by continuous productivity CNPq grants (305542/2010-9). P.H.C.R. receives a  
24 scholarship from PET program (Programa de Educação Tutorial) from Brazilian Educational

1 Ministry. We thank A. Andrade for helping on the evaluation of ecological niche modeling, S. Villen  
2 for comment on analysis and figures, and L.M.O. Laureto and C.E.A. Soares for the helpful  
3 comments on the text.

4

## 5 **References**

- 6 Aguiar LMS, Bernard E & Machado RB, 2014. Habitat use and movements of *Glossophaga soricina*  
7 and *Lonchophylla dekeyseri* ( Chiroptera : Phyllostomidae ) in a Neotropical savannah.  
8 *Zoologia (Curitiba, Impresso)*, 31(3):223–229.
- 9 Allouche O, Tsoar A & Kadmon R, 2006. Assessing the accuracy of species distribution models:  
10 Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43(6):1223–  
11 1232.
- 12 Bernard E, Aguiar LM & Machado RB, 2011. Discovering the Brazilian bat fauna: a task for two  
13 centuries? *Mammal Review*, 41:23–39.
- 14 Betts MG, Fahrig L, Hadley AS, *et al.*, 2014. A species-centered approach for uncovering  
15 generalities in organism responses to habitat loss and fragmentation. *Ecography*, 37(6):517–  
16 527.
- 17 Blamires D, Oliveira G De, Barreto B de S & Diniz-filho JAF, 2008. Habitat use and deconstruction  
18 of richness patterns in Cerrado birds. *Acta Oecologica*, 33:97–104.
- 19 Brown JH, 1984. On the Relationship between Abundance and Distribution of Species. *The*  
20 *American Naturalist*, 124(2):255.
- 21 Cagnolo L, Valladares G, Salvo A, Cabido M & Zak M, 2009. Habitat fragmentation and species  
22 loss across three interacting trophic levels: effects of life-history and food-web traits.  
23 *Conservation Biology*, 23(5):1167–75.
- 24 Carvalho FMV, De Marco P & Ferreira LG, 2009. The Cerrado into-pieces: Habitat fragmentation as  
25 a function of landscape use in the savannas of central Brazil. *Biological Conservation*,  
26 142(7):1392–1403.
- 27 Colwell RK, Rangel TF, Grinnell J & Elton C, 2009. Hutchinson ’ s duality : The once and future  
28 niche. 2009:1–8.
- 29 Comont RF, Roy HE, Lewis OT, *et al.*, 2012. Using biological traits to explain ladybird distribution  
30 patterns. *Journal of Biogeography*, 39(10):1772–1781.
- 31 Cuervo JJ & Møller AP, 2013. Temporal Variation in Population Size of European Bird Species:  
32 Effects of Latitude and Marginality of Distribution. *PLoS ONE*, 8(10).

- 1 Dawson TP, Jackson ST, House JJ, Prentice IC & Mace GM, 2011. Beyond predictions: biodiversity  
2 conservation in a changing climate. *Science (New York, N.Y.)*, 332(6025):53–58.
- 3 Diniz-filho JAF, Bini LM, Vieira CM, *et al.*, 2008. Spatial Patterns of Terrestrial Vertebrate Species  
4 Richness in the Brazilian Cerrado. *Zoological studies*, 47(2):146–157.
- 5 Dirzo R, Young HS, Galetti M, *et al.*, 2014. Defaunation in the Anthropocene. *Science*,  
6 345(6195):401–406.
- 7 Duchamp JE & Swihart RK, 2008. Shifts in bat community structure related to evolved traits and  
8 features of human-altered landscapes. *Landscape Ecology*, 23(7):849–860.
- 9 Elith J, Graham CH, Anderson RP, *et al.*, 2006. Novel methods improve prediction of species’  
10 distributions from occurrence data. *Ecography*, 29(2):129–151.
- 11 Elith J, Phillips SJ, Hastie T, *et al.*, 2011. A statistical explanation of MaxEnt for ecologists.  
12 *Diversity and Distributions*, 17(1):43–57.
- 13 Estrada-Villegas S, McGill BJ & Kalko EK V, 2012. Climate, habitat, and species interactions at  
14 different scales determine the structure of a Neotropical bat community. *Ecology*, 93(5):1183–  
15 93.
- 16 Faleiro F V, Machado RB & Loyola RD, 2013. Defining spatial conservation priorities in the face of  
17 land-use and climate change. *Biological Conservation*, 158:248–257.
- 18 Ferrier S, Biology S & Apr N, 2002. Mapping Spatial Pattern in Biodiversity for Regional  
19 Conservation Planning : Where to from Here? *Systematic Biology*, 51(2):331–363.
- 20 Fischer E & Grande C, Fauna de morcegos em remanescentes urbanos de Cerrado em Campo  
21 Grande , Mato Grosso do Sul Material e Métodos. 10(3).
- 22 Foley J a, Defries R, Asner GP, *et al.*, 2005. Global consequences of land use. *Science*,  
23 309(5734):570–4.
- 24 García-Morales R, Badano EI & Moreno CE, 2013. Response of Neotropical Bat Assemblages to  
25 Human Land Use. *Conservation biology : the journal of the Society for Conservation Biology*,  
26 00(0):1–11.
- 27 Gardner AL, 2007. *Mammals of South America, Volume 1: Marsupials, Xenarthrans, Shrews, and*  
28 *Bats*. New York: Chicago Press.
- 29 Gorresen PM & Willig MR, 2004. Landscape responses of bats to habitat fragmentation in Atlantic  
30 Forest of Paraguay. *Journal of mam*,
- 31 Gorresen PM, Willig MR & Strauss RE, 2005. Multivariate analysis of scale-dependent associations  
32 between bats and landscape structure. *Ecological applications*, 15(6):2126–2136.
- 33 Guisan A & Thuiller W, 2005. Predicting species distribution: offering more than simple habitat  
34 models. *Ecology Letters*, 8(9):993–1009.

- 1 Haddad NM, Brudvig LA, Clobert J, *et al.*, 2015. Habitat fragmentation and its lasting impact on  
2 Earth's ecosystems. *Science Advances*, 1(2):1–9.
- 3 Henle K, Davies KF, Kleyer M, Margules C & Settele J, 2004. Predictors of species sensitivity to  
4 fragmentation. :207–251.
- 5 Hernandez PA, Graham CH, Master LL & Albert DL, 2006. The effect of sample size and species  
6 characteristics on performance of different species distribution modeling methods. *Ecography*,  
7 29:773–785.
- 8 Hines JE, 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-  
9 PWRC.
- 10 Hutchinson GE, 1957. Concluding remarks. *Cold Spring Harbor Symp Quantitative Biol.*, 22:415–  
11 427.
- 12 Jones G, Jacobs D, Kunz T, Willig M & Racey P, 2009. Carpe noctem: the importance of bats as  
13 bioindicators. *Endangered Species Research*, 8(July):93–115.
- 14 Kadmon R, Farber O & Danin A, 2004. Effect of roadside bias on the accuracy of predictive maps  
15 produced by bioclimatic models. *Ecological Applications*, 14(2):401–413.
- 16 Kerr JT, Kharouba HM & Currie DJ, 2007. The macroecological contribution to global change  
17 solutions. *Science (New York, N.Y.)*, 316(5831):1581–4.
- 18 Klingbeil BT & Willig MR, 2010. Seasonal differences in population-, ensemble- and community-  
19 level responses of bats to landscape structure in Amazonia. *Oikos*, 119(10):1654–1664.
- 20 Klink CA & Machado RB, 2005. Conservation of the Brazilian Cerrado. *Conservation Biology*,  
21 19(3):707–713.
- 22 Liu C, White M & Newell G, 2011. Measuring and comparing the accuracy of species distribution  
23 models with presence-absence data. *Ecography*, 34(2):232–243.
- 24 López-González C, Presley SJ, Lozano A, Stevens RD & Higgins CL, 2014. Ecological  
25 biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta  
26 diversity, and environmental gradients to species richness and composition patterns. *Ecography*,  
27 37:1–12.
- 28 Mackenzie DI, Nichols JD, Royle JA, *et al.*, 2006. *Occupancy estimation and modeling: inferring*  
29 *patterns and dynamics of species occurrence*. 1<sup>o</sup> ed., Burlington.
- 30 Medellín RA, Equihua M & Amin MA, 2000. Bat Diversity and Abundance as Indicators of  
31 Disturbance in Neotropical Rainforests. 14(6):1666–1675.
- 32 Mehr M, Brandl R, Hothorn T, *et al.*, 2011. Land use is more important than climate for species  
33 richness and composition of bat assemblages on a regional scale. *Mammalian Biology -*  
34 *Zeitschrift für Säugetierkunde*, 76(4):451–460.

- 1 Meyer CFJ, Fründ J, Lizano WP & Kalko EKV, 2007. Ecological correlates of vulnerability to  
2 fragmentation in Neotropical bats. *Journal of Applied Ecology*, 45(1):381–391.
- 3 Murphy GEP & Romanuk TN, 2014. A meta-analysis of declines in local species richness from  
4 human disturbances. *Ecology and evolution*, 4(1):91–103.
- 5 Norberg UM & Rayner JM V, 1987. Ecological morphology and flight in bats (Mammalia;  
6 Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Society*,  
7 316(1179):335–427.
- 8 Oprea M, Mendes P, Vieira TB & Ditchfield AD, 2009. Do wooded streets provide connectivity for  
9 bats in an urban landscape? *Biodiversity and Conservation*, 18(9):2361–2371.
- 10 Pearce J, Pearce J, Ferrier S & Ferrier S, 2000. Evaluating the predictive performance of habitat  
11 models developed using logistic regression. *Ecological Modelling*, 133:225–245.
- 12 Peterson GD, Cumming GS & Carpenter SR, 2003. Scenario planning: A tool for conservation in an  
13 uncertain world. *Conservation Biology*, 17(2):358–366.
- 14 Phillips S, Dudík M & Schapire R, 2004. A maximum entropy approach to species distribution  
15 modeling. *Proceedings of the twenty-first ...*, :655–662.
- 16 Rangel TF & Loyola RD, 2012. Labeling Ecological Niche Models. *Natureza & Conservação*,  
17 10(2):119–126.
- 18 Rangel TFLVB, Bini LM, Diniz-Filho JAF, *et al.*, 2007. Human development and biodiversity  
19 conservation in Brazilian Cerrado. *Applied Geogrpahy*, 27:14–27.
- 20 Sano EE, Rosa R, Brito JLS & Ferreira LG, 2010. Land cover mapping of the tropical savanna  
21 region in Brazil. :113–124.
- 22 Silva D, Gonzalez V, Melo G, *et al.*, 2014. Seeking the flowers for the bees: Integrating biotic  
23 interactions into niche models to assess the distribution of the exotic bee species *Lithurgus*  
24 *huberi* in South. *Ecological ...*, 273:200–209.
- 25 Soberon J, 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology*  
26 *Letters*, 10(12):1115–1123.
- 27 Stevens RD, 2013. Gradients of Bat Diversity in Atlantic Forest of South America : Environmental  
28 Seasonality , Sampling Effort and Spatial Autocorrelation. 45(6):764–770.
- 29 Swift TL & Hannon SJ, 2010. Critical thresholds associated with habitat loss: a review of the  
30 concepts, evidence, and applications. *Biological reviews of the Cambridge Philosophical*  
31 *Society*, 85(1):35–53.
- 32 Talamoni S, Coelho D, Dias-Silva L & Amaral A, 2013. Bat assemblages in conservation areas of a  
33 metropolitan region in Southeastern Brazil. *Brazilian Journal of Biology*, 73(2):309–319.
- 34 Thomas CD, 2010. Climate, climate change and range boundaries. *Diversity and Distributions*,  
35 16(3):488–495.

- 1 Trevelin LC, Silveira M, Port-Carvalho M, Homem DH & Cruz-Neto AP, 2013. Use of space by  
2 frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil.  
3 *Forest Ecology and Management*, 291:136–143.
- 4 Turner MG, 2005. LANDSCAPE ECOLOGY : What Is the State of the Science ?
- 5 Velazco PM, Gardner AL & Patterson BD, 2010. Systematics of the *Platyrrhinus helleri* species  
6 complex (Chiroptera: Phyllostomidae), with descriptions of two new species. *Zoological*  
7 *Journal of the Linnean Society*, 159(3):785–812.
- 8 Zimbres B, Furtado MM, Jácomo AT a., *et al.*, 2012. The impact of habitat fragmentation on the  
9 ecology of xenarthrans (Mammalia) in the Brazilian Cerrado. *Landscape Ecology*, 28(2):259–  
10 269.
- 11 Zortéa M & Alho CJR, 2008. Bat diversity of a Cerrado habitat in central Brazil. *Biodiversity and*  
12 *Conservation*, 17:791–805.
- 13

## 1 Appendix 1

2 Summary of Principal Components Analysis performed to extract non-collinear axes from the 19  
3 bioclimatic variables that would be used for ecological niche modeling. Loadings of each principal  
4 component axis (PC) selected are being shown, as well as eigenvalues, proportion of explained  
5 variance and accumulated proportion of explained variance. PCs were selected until their  
6 accumulated explanation proportion reached 95%.

Bioclimatic variable	PC1	PC2	PC3	PC4	PC5	PC6
Mean Temperature of Warmest Quarter	0.189	0.318	-0.328	0.079	0.024	-0.035
Mean Temperature of Coldest Quarter	0.292	0.183	0.064	0.064	-0.104	0.054
Annual Precipitation	0.275	-0.200	-0.079	-0.209	0.138	-0.105
Precipitation of Wettest Month	0.279	-0.077	0.062	-0.309	0.244	-0.290
Precipitation of Driest Month	0.152	-0.355	-0.286	0.000	-0.106	0.355
Precipitation Seasonality (Coefficient of	-0.039	0.293	0.384	-0.386	0.119	0.097
Precipitation of Wettest Quarter	0.280	-0.086	0.059	-0.306	0.240	-0.276
Precipitation of Driest Quarter	0.162	-0.353	-0.285	-0.005	-0.079	0.319
Precipitation of Warmest Quarter	0.174	-0.185	-0.152	-0.483	-0.528	-0.203
Precipitation of Coldest Quarter	0.211	-0.204	-0.064	0.070	0.638	0.164
Annual Mean Temperature	0.269	0.256	-0.096	0.064	-0.073	0.017
Mean Diurnal Range	-0.204	0.206	-0.067	-0.495	0.087	0.481
Isothermality	0.242	-0.003	0.333	-0.054	-0.064	0.517
Temperature Seasonality	-0.245	0.033	-0.395	-0.022	0.165	-0.111
Max Temperature of Warmest Month	0.136	0.370	-0.345	-0.027	0.100	0.043
Min Temperature of Coldest Month	0.301	0.120	0.064	0.182	-0.079	-0.006
Temperature Annual Range	-0.254	0.119	-0.316	-0.230	0.161	0.037
Mean Temperature of Wettest Quarter	0.206	0.306	-0.185	-0.065	-0.195	0.043
Mean Temperature of Driest Quarter	0.269	0.178	-0.017	0.164	0.102	0.054
Principal components eigenvalue	9.853	3.860	2.272	1.055	0.753	0.472
Proportion explained by each PC (%)	51.855	20.316	11.960	5.553	3.965	2.483
Accumulated proportion explained by each PC	51.855	72.172	84.131	89.684	93.649	96.132

7

8

## 1    **CONSIDERAÇÕES FINAIS**

2  
3            Os resultados obtidos reforçam a importância da estrutura da paisagem para morcegos, não  
4 apenas da quantidade de habitat, assim como da configuração da paisagem. Isso tem uma relação  
5 direta com as mudanças no uso da terra que o planeta vem sofrendo nas últimas décadas e o impacto  
6 predito para o grupo. É importante notar que, a percepção de que esses dois componentes da  
7 estrutura da paisagem (composição da paisagem e configuração) têm efeitos diferenciados nos  
8 morcegos é um importante passo para estimular desenhos amostrais que busquem evitar a  
9 colinearidade entre ambas na amostragem. Adicionalmente, os resultados também indicam que as  
10 respostas dos morcegos à perda de habitat e fragmentação dependem da espécie em questão,  
11 evidenciando como atributos ecológicos específicos precisam ser considerados para a compreensão  
12 dos fenômenos em larga escala. Entender as causas dessas variadas respostas pode ajudar a iluminar  
13 o entendimento das consequências das mudanças no uso da terra, assim como auxiliar na criação de  
14 ferramentas de manejo que considerem essas diferenças na sensibilidade às alterações no uso da  
15 terra.

16            Nesta tese foi proposto, que os modelos de ocupação podem ser interessantes métodos para  
17 estimar limiares de sensibilidade à perda de habitat e fragmentação. Estes limiares, então, poderiam  
18 ser utilizados para prever a vulnerabilidade das espécies. A qualidade de habitat, medida na escala  
19 local, é um fator adicional importante para algumas espécies de morcegos. A inclusão da  
20 sensibilidade à qualidade de habitat para estimar a vulnerabilidade de espécies seria um importante  
21 passo para o desenvolvimento de estratégias de conservação para essas espécies. Infelizmente, a  
22 inclusão da sensibilidade à qualidade de habitat representa uma lacuna nesta tese. Contudo, o uso da  
23 sensibilidade à estrutura da paisagem já representou um grande passo nessa direção, e um maior  
24 amadurecimento dessa ideia é necessário antes da inclusão da escala local (qualidade de habitat).

1           Considerando a tendência de aumento no número de estudos que propõem separar os efeitos  
2 da perda de habitat e fragmentação, assim como estudos explorando a importância relativa da  
3 estrutura da paisagem e da qualidade do mesmo, é esperado que dentro alguns anos fosse possível  
4 avaliar através de uma meta-análise as características que predispõe espécies de morcegos a essas  
5 variáveis. Isto permitirá uma visualização de padrões gerais de resposta de morcegos a variáveis  
6 ambientais locais e da paisagem, por exemplo, a identificação de características biológicas  
7 relacionada com a sensibilidade a mudanças na estrutura da paisagem. Essa identificação  
8 proporcionará um passo a mais no entendimento da sensibilidade das espécies de morcegos. Eu  
9 espero que, em meio a tantas pesquisas científicas sobre as relações entre os morcegos e variáveis  
10 locais, da paisagem ou climáticas na região Neotropical, esse trabalho possa contribuir de alguma  
11 forma para a consolidação dos possíveis efeitos dessas variáveis na diversidade de morcegos.