

UNIVERSIDADE FEDERAL DE ALFENAS

MARIANA RANIERO

O EFEITO DA PAISAGEM NA SUBTRIBO DE ABELHAS EUGLOSSINA

(HYMENOPTERA: APIDAE)

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Dissertação apresentada para obtenção do título de Mestre no Programa de Pós-Graduação em Ecologia e Tecnologia Ambiental na Universidade Federal de Alfenas. Área de concentração: Meio Ambiente, Sociedade e Diversidade Biológica
Orientadora: Profª Drª Érica Hasui
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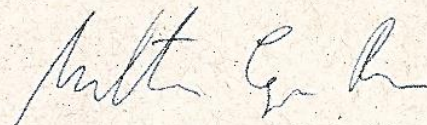
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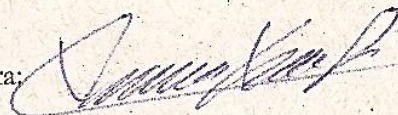
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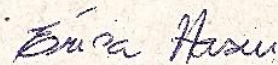
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Acaso não grita a Sabedoria? E a Inteligência não eleva a voz?
Ela se põe no cimo das colinas, nos caminhos e nas encruzilhadas.
Junto às Portas da cidade, nas vias de acesso ela brada:
“Ó homens! Clamo por vós! Grito aos filhos dos homens!
Simples, tende prudência! Tolos, tende inteligência!
Ouvi: pois tenho nobres coisas a vos dizer; dos meus lábios fluem falas de retidão.
Minha boca só proclama a verdade, o mal é abominável aos meus lábios.
Justas as palavras que eu pronuncio, sem falsidades e sem subterfúgios; são corretas a quem as
entende e exatas para quem possui o saber.
Buscai meu ensino, não a prata; e a ciência, antes que o ouro puro!”
Pois a Sabedoria é mais que pérolas e nenhuma joia lhe é comparável.
(Pr 8, 1-11)

RESUMO

O desmatamento na Mata Atlântica tem mudado a estrutura da paisagem ao longo de décadas no Brasil. Para testar a hipótese de que a estrutura da paisagem e o efeito da fragmentação pode favorecer a diversidade, nós desenvolvemos este estudo para responder a duas questões: I) Quais elementos estruturais da paisagem explicam a riqueza de abelhas Euglossina em uma paisagem altamente fragmentada? II) Qual é o limiar crítico de quantidade de habitat natural, relacionado ao polinizadores de longa distância, nesta paisagem? Apesar de nossa região estar imersa numa paisagem altamente fragmentada, características estruturais podem favorecer polinizadores de longa distância: quantidade de habitat natural e heterogeneidade em paisagens de 1000m de raio. A persistência destes polinizadores é maior em paisagens acima do limiar de 25% de habitats naturais. A quantidade de habitat e a heterogeneidade espacial melhor explicaram a diversidade e representam mecanismos de uso e forrageio dos polinizadores, como diferente recursos ao longo de diferentes habitats na paisagem. Para eles isto representa a diversa gama de recursos florais e materiais para ninhos. Para alcançar esses resultados nós usamos iscas aromáticas para amostrar abelhas Euglossina, eficientes polinizadores de longa distância, e analisamos esses dados através de modelos de regressão. Nós selecionamos o melhor modelo através do wAIC da seleção usando o Critério de Informação de Akaike (AIC), comparando modelos lineares generalizados (GLM) dos elementos estruturais da paisagem (configuração e composição) e a riqueza estimada das abelhas Euglossina.

Palavras-chave: Abelhas de orquídeas. Complexidade da paisagem. Euglossina. Grupos funcionais. Limiar crítico.

ABSTRACT

Deforestation in the Atlantic Forest has been changing the landscape structure for decades in Brazil. To test the hypothesis that landscape structure and fragmentation effects could favor diversity, we developed this study to answer two questions: I) Which structural landscape elements do best explain Euglossine richness in a highly fragmented landscape? What is the critical threshold of natural habitat amount, in respect to long-distance pollinators, in such landscape? Although our region situates in a highly fragmented landscape, structural features, such as natural habitat amount and heterogeneity, in a landscape of 1,000m radius, favored long-distance pollinators. Such pollinators have their diversity maintained in landscapes with percentage of habitat above the 25% natural habitat threshold. Habitat amount and spatial heterogeneity best explained pollinator diversity. Pollinators benefit from larger percentage of habitat and heterogeneity, given the increase in the range of floral resources available and the facility to reach them. For these pollinators, such landscapes represent a diverse range of floral and nest material. We used smell bait to sample Euglossine bees, efficient long-distance pollinators, and analyzed data by regression models. We selected the best model using wAIC from the Akaike Information Criterion, by comparing GLM of landscape structural elements (composition and configuration) and estimated richness of Euglossine bees.

Keywords: Critical threshold. Euglossine. Functional groups. Landscape complexity. Orchid bees.

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PRIMEIRA PARTE

1 INTRODUÇÃO

Apresentação da proposta do projeto de pesquisa desenvolvido ao longo do curso de pós graduação de Ecologia e Tecnologia Ambiental. Com base na literatura, apresentamos o problema, as diversas relações entre as mudanças antrópicas e a diversidade remanescente, em áreas que sofrem altos níveis de degradação, como o caso do município de Alfenas, o qual a pesquisa foi realizada. O estudo com foco na ecologia de paisagem relacionada a abelhas silvestres, teve o apoio de ferramentas tecnológicas para análise do ambiente biótico e abiótico.

1.1 DESENVOLVIMENTO

1.1.1 Mata Atlântica e Fragmentação

O desmatamento florestal, gerado pelo desenvolvimento humano e sistemas agropecuários causa grandes alterações nas paisagens naturais (TILMAN et al., 2001; ALTIERI, 2009; MICHALSKI et al., 2008). No Brasil, a Mata Atlântica é um bioma amplamente afetado por esses processos. Desde o início do sistema colonial este bioma foi explorado e sofreu grandes surtos de devastação devido aos ciclos de uso do solo e da urbanização em toda sua extensão devido a facilidades de sua posição geográfica (RODRIGUES et al., 2009). Atualmente menos de 16% de sua área original ainda é remanescente, grande parte com fragmentos florestais menores que 100ha (RIBEIRO et al., 2009). Por possuir grande número de espécies endêmicas e sofrer grandes perdas ao longo do tempo, é classificado como um 'hottest hotspot', situado entre os oito mais importantes hotspots no mundo (MYERS et al., 2000).

Esse desmatamento faz com que o bioma sofra o processo antrópico de fragmentação de habitat. Tal processo ocorre com a retirada de habitat natural e a conversão desta área em uso antrópico. A matriz antrópica, ambiente natural convertido em pastagens, plantações e áreas urbanas, geralmente é denominada como a área que se encontra em maior quantidade, ou simplesmente o habitat adjacente ou circundante ao natural. Essa matriz além de ser constituída através da retirada de habitat natural, também causa ruptura dos remanescentes florestais, e assim gera o e isolamento dos habitats anteriormente contínuos (BASCOMPTE; SOLÉ, 1996; FAHRIG, 2003; BOSCOLO; METZGER, 2011). Desta maneira a

fragmentação altera a quantidade e também o movimento das espécies (FAHRIG, 2001; TSCHARNTKE et al., 2005; HADLEY; BETTS, 2012). Esse novo ambiente, geralmente composto por plantações exóticas ou pastagens, ainda pode refletir no habitat remanescente gerando diversos efeitos de borda (MESQUITA et al., 1999; POULIN; VILLARD 2011).

A borda florestal, ambiente que foi bruscamente alterado, se encontra em contato tanto com a matriz quanto com ao habitat original, geralmente em estado climático. Desta forma compõe-se de alta heterogeneidade de habitat e espécies. Por apresentar grande contato com a área alterada, pode sofrer perturbações, além de favorecer a chegada e estabelecimento de espécies exóticas (HARPER et al., 2005; EWERS; DIDHAM 2006). Dessa forma a fragmentação de habitat altera a composição e a configuração da paisagem original alterando assim a biodiversidade e os processos ecológicos envolvidos (FAHRIG, 2003; FISCHER; LINDENMAYER, 2007; FAHRIG et al., 2011).

De acordo com estudos a perda de habitat é o fenômeno que mais causa efeito negativo na biodiversidade e desestruturação dos processos ecológicos, diminuindo a riqueza de espécies, alterando taxas de crescimento e reprodução além da diversidade genética (FAHRIG, 2003). Porém, a fragmentação em si, em termos de configuração da paisagem, é capaz de gerar efeitos positivos. Se mantida a quantidade de habitat, a subdivisão das áreas naturais pode favorecer a taxa de imigração, a capacidade competitiva; gerar diferentes habitats, favorecendo espécies dependentes de diversos tipos de ambiente, além de gerar efeitos de borda, os quais também são conhecidos por efeitos positivos, como aumento da diversidade de espécies, e ambientes heterogêneos (FAHRIG, 2003). Assim a fragmentação de habitat é várias vezes definida como um fenômeno negativo devido aos efeitos que a perda de habitat, e não a fragmentação por si só, gera na biodiversidade. É importante avaliar esses aspectos da paisagem fragmentada de forma a verificar qual a causa real de perdas e ganhos no ecossistema, para assim podermos agir da melhor maneira.

1.1.2 Paisagem e Heterogeneidade

De acordo com isso se torna indispensável considerar essas mudanças a nível de paisagem, já que a fragmentação é um processo que ocorre a este nível (FAHRIG, 2003). A paisagem fragmentada apresenta componentes de composição, como os diversos tipos de habitats, sejam naturais, monoculturas, pastagens, ou mesmo áreas urbanas. Apresenta também componentes de configuração, que evidenciam o arranjo e a complexidade estrutural ou física da paisagem. Estudos de paisagem geralmente conseguem entender de forma mais

ampla como essas mudanças atingem os organismos e processos ecológicos. Além disso também consideram a matriz como habitat adjacente ao original e passível de uso e movimentação pelas espécies (METZGER, 2008; TSCHARNTKE et al. 2008; BANKS-LEITE et al., 2011). A fragmentação pode causar diferentes aspectos estruturais em cada paisagem, como arranjo desordenado ou simples, e diversos habitats naturais e antrópicos compondo um mosaico heterogêneo. Neste contexto, a ecologia de paisagens procuram entender como essa heterogeneidade em áreas já fragmentadas, é percebida pelos organismos (METZGER, 2001; TSCHARNTKE et al. 2005; BIANCHI; BOOIJ; TSCHARNTKE, 2006; FAHRIG et al. 2011).

A visão heterogênea da paisagem, diferente da visão binária habitat-matriz, considera os diversos ambientes criados na paisagem fragmentada como habitats que podem fornecer recursos suplementares ou complementares ao habitat natural (FAHRIG, 2003; HOLZSCHUH *et al.*, 2010; HADLEY; BETTS, 2012). Tanto a heterogeneidade de habitats quanto a complexidade deste, como arranjo e permeabilidade, são percebidos de maneira diferente pelas espécies (METZGER, 2001; CONCEPCION et al., 2008; BOSCOLO; METZGER, 2009; WINQVIST; AHNSTRÖM; BENGTSSON, 2012). As espécies reagem de acordo com sua capacidade de movimentação e percepção do tipo de habitat, constituindo assim a heterogeneidade funcional da paisagem (WITH; CRIST, 1995; EWERS; DIDHAM, 2006; FISCHER; LINDENMAYER, 2007). Se as espécies são capazes de perceber os diferentes habitats e os utilizar como fonte heterogênea de recursos para diversas atividades, este ambiente é funcionalmente heterogêneo. Através da caracterização da paisagem de acordo com essa visão de heterogeneidade funcional, é possível adquirir respostas mais precisas da biodiversidade do que considerando apenas a heterogeneidade estrutural da paisagem (FAHRIG et al., 2011). Isso se deve a características de locomoção e comportamento das espécies, bem como as necessidade para sua sobrevivência, como recursos alimentares, locais para nidificação e reprodução.

De acordo com isso, se insere a hipótese de uma heterogeneidade intermediária, na qual tanto a heterogeneidade de habitats, quanto a heterogeneidade configuracional da paisagem favoreçam mais a biodiversidade num nível intermediário (FAHRIG et al., 2011). Uma situação abaixo ou acima do nível intermediário de heterogeneidade, pode gerar perda de biodiversidade, já que ou haveria pouca diversificação de habitat, ou uma altíssima heterogeneidade poderia resultar na diminuição de área de cada tipo de habitat. Estas e outras características das espécies devem ser consideradas quando se quer entender sua resposta frente a fragmentação nas paisagens. Tomando como base a escala que melhor represente

suas necessidades e características, podemos melhor descrever a resposta da biodiversidade ou de processos ecológicos na paisagem fragmentada.

1.1.3 Limiar crítico de fragmentação

Um mecanismo que vem sendo utilizado é a definição de um limiar crítico de habitat natural (FAHRIG, 2002; HUGGETT, 2005; KEITT, 2009; SWIFT; HANNON, 2010; KATO; AHERN, 2011). Esse valor é observado através de uma relação não-linear entre a perda de habitat na paisagem e a resposta biológica, a qual apresenta um momento de queda acentuada. O limiar crítico é determinado pela proporção de habitat natural observada antes deste ponto de queda, que representa a proporção de habitat na paisagem que ainda mantém a persistência da diversidade (LANDE, 1987; revisado por DYKSTRA, 2004 e SWIFT; HANNON, 2010). A princípio, a não linearidade desta relação foi baseada na teoria de percolação, na qual a queda da resposta biológica se deve puramente à perda de habitat. Esta, atinge uma situação em que as manchas diminuem de tamanho, mas ainda compartilham de bordas verticais e horizontais (“four neighbour rule”). O limiar crítico ocorre com uma proporção de habitat em torno de 60% na paisagem (GARDNER; O’NEILL 1991; BASTA; PICCIARELLI; DIPARTHENTO, 1994; BASCOMPTE; SOLÉ, 1996). Com a persistência da perda de habitat o processo de fragmentação se torna acentuado, atingindo uma situação de limiar crítico quando o arranjo da paisagem se torna um aspecto determinante para biodiversidade, em torno de 10 a 30% de habitat natural (ANDRÉN, 1994; METZGER; DECÁMPS, 1997). Nestas paisagens altamente fragmentadas o limiar reflete o isolamento entre os habitats naturais e assim, o efeito no fluxo e uso pelos organismos (GIBBS, 1998; WITH; KING, 1999; MARTENSEN et al., 2012). Se o processo de fragmentação persistir, efeitos da perda de habitat e da conectividade na paisagem dependerão ainda do tipo de habitat adjacente e de características de dispersão e comportamento das espécies, podendo leva-las à extinção ou auxiliar sua sobrevivência ao longo do desmatamento (LANDE 1987; OVASKAINEN et al., 2002).

Ao longo do processo de fragmentação a perda de habitat gera perda da biodiversidade, como visto anteriormente. A biodiversidade sofrerá ainda mais quando a estrutura e a configuração da paisagem heterogênea gerar efeitos negativos na capacidade de dispersão de uso do habitat modificado e de dependência do habitat natural, o que geralmente ocorre em altos níveis de fragmentação (FAHRIG, 2003; DRINNAN, 2005; ROMPRÉ et al., 2010). A definição desse valor crítico permite que entendamos como o processo de fragmentação

afeta a biodiversidade e os grupos funcionais, bem como a função que estes exercem. De acordo com a literatura recente, esse limiar crítico tem se apresentado em vários grupos, sendo grande parte descrita entre 10 e 30% (revisado por ANDRÉN, 1994 e SWIFT; HANNON, 2010). Entretanto, há uma grande variação de acordo com o grupo utilizado, as características das espécies, tanto físicas quanto comportamentais, requerem diferentes exigências quanto ao ambiente, e isso pode provocar essa divergência. Enquanto certas espécies têm grandes habilidades como dispersoras e são capazes de encontrar recursos além de seu habitat usual, outras podem ter a dispersão restrita devido ao comportamento territorial, por exemplo, e serem incapazes de resistir ao efeito da fragmentação (HOMAN et al., 2004; GIBBS, 1998). Além disso, elementos da paisagem como a conectividade, tamanho e forma e complexidade podem alterar o valor deste limiar, já que podem amenizar a perda do habitat natural (KEITT, 2009; HADLEY E BETTS, 2012).

Assim, não podemos estabelecer um limiar comum, ou único, já que este valor depende tanto de características das paisagens, escalas adotadas, bem como os organismos e suas necessidades e habilidades em questão (KEITT, 2009; SWIFT; HANNON, 2010; MARTENSEN, et al., 2012). Porém, a determinação destes limiares seria de grande contribuição à conservação e mesmo à restauração de ecossistemas se realizadas em grupos funcionais, os quais são imprescindíveis na geração de serviços ecossistêmicos, como animais nectarívoros, frugívoros (dispersores), polinizadores, sendo, portanto, tanto ecologicamente quanto economicamente relevantes (HUGGET, 2005; BROSI; ARMSWORTH; DAILY, 2008). Pesquisas ainda demonstram que o conhecimento e a determinação deste limiar necessita de mais atenção, atentando para o fato de que grupos funcionais podem ser fortes determinantes de mudanças no funcionamento do ecossistema, e pouco ainda se sabe sobre essa abordagem funcional (TILMAN et al., 1997; HOMAN et al. 2004; CARRIÉ; GEORGE; WÄCKERS, 2012; HADLEY; BETTS, 2012; VIANA, et al., 2012). Tais grupos são compostos por organismos que participam de processos ecológicos e desempenham assim, funções ambientais. Tais processos ocorrem geralmente através de relações entre várias espécies, gerando serviços ecossistêmicos, e com isso, benefícios e produtos à sociedade humana (RICKETTS, 2004; ZHANG et al., 2007; LAUTENBACH et al., 2011). Uma importante função ecossistêmica é a polinização, através da qual ocorre o processo de reprodução das plantas. Nesta relação geralmente mutualística, enquanto os polinizadores são beneficiados ao consumir e utilizar recursos florais, as plantas são beneficiadas com o transporte do pólen e conseqüente reprodução. Além disso, a ocorrência deste processo pode gerar diversos serviços ecossistêmicos, como o fornecimento de frutos e madeira, o controle

da qualidade da água, e ainda de suporte dos solos (MILLENNIUM ECOSYSTEM ASSESSMENT, 2005). Apesar de sua importância, o conhecimento de como esses grupos são afetados pelo processo de perda de habitat e fragmentação ainda é escasso (HADLEY; BETTS, 2012; VIANA et al. 2012).

1.1.4 Polinização e Abelhas Euglossina

Dentro deste contexto o estudo presente foi desenvolvido para descrever a resposta de polinizadores frente ao processo de fragmentação, utilizando essa hipótese de limiar crítico e a relação com aspectos da paisagem fragmentada. A polinização vem sofrendo grandes perdas com o avanço agrícola e a fragmentação (ROUBIK, 2000; CRANMER; MCCOLLIN; OLLERTON, 2012). Alterações na paisagem podem afetar a polinização de diversas formas, como diminuindo locais para nidificação ou plantas hospedeiras para larvas, no caso dos polinizadores serem insetos; ou a retirada de recursos florais, a qual interfere de várias maneiras no desenvolvimento do organismo; além do uso de fertilizantes e inseticidas em áreas convertidas, cujo efeito atinge diretamente a abundância de abelhas polinizadoras e a heterogeneidade de áreas e de plantas usadas na busca de recursos florais (BATÁRY et al., 2011; KOVÁCS-HOSTYÁNSZKI et al., 2011). De acordo com revisões recentes pouco se sabe como a estrutura da paisagem afeta os polinizadores, e qual a proporção de habitat representa um possível limiar crítico para estes organismos (HADLEY; BETTS, 2012; VIANA et al., 2012). Apesar disso é possível que haja concílio entre a conversão da terra para uso agrícola, ou pecuário, e a manutenção de habitats necessários para sobrevivência de agentes polinizadores. Estudos demonstram que muitos cultivos são beneficiados com a proximidade de áreas de florestas nativas (RICKETTS et al., 2008; TAKI et al., 2010; WATSON; WOLF; ASCHER, 2011). Assim como a diversidade de polinizadores pode ser também beneficiada pela presença de sistemas agrícolas, já que estes fornecem uma maior gama de diferentes tipos de habitats, que propiciam diferentes recursos alimentares e variados locais para forrageio e nidificação ao longo das diferentes estações do ano (ROMEY, et al., 2007; WINFREE; GRISWOLD; KREMEN, 2007).

As abelhas são conhecidas por serem os mais importantes organismos polinizadores (AIZEN; FEINSINGER, 2003; KLEIN et al. 2007). Apesar disso estão sofrendo grandes declínios, assim como a polinização, com o avanço agrícola e urbano (ROUBIK, 2000; CRANMER; MCCOLLIN; OLLERTON, 2012). A polinização por abelhas é um serviço que pode ser beneficiado, ou menos agredido, se manejado em agroecossistemas ou

agrossistemas que ainda possuem habitats naturais (WATSON; WOLF; ASCHER, 2011; WINFREE; BARTOMEUS; CARIVEAU, 2011). Muitos cultivos são beneficiados com a proximidade de áreas de florestas nativas, já que 35% das plantas cultiváveis agrícolas são dependentes de polinizadores nativos (KLEIN et al., 2007; RICKETTS et al., 2008; TAKI et al., 2010; WATSON; WOLF; ASCHER, 2011). Por outro lado, a diversidade de polinizadores pode ser também beneficiada pela presença de sistemas agrícolas, já que estes geram paisagens mais heterogêneas, quando não dominados por monoculturas, propiciando diferentes recursos alimentares e variados locais para forrageio e nidificação ao longo das diferentes estações do ano (ROMEY, et al., 2007; WINFREE; GRISWOLD; KREMEN, 2007; FAHRIG, et al., 2011). Com o aumento da atividade das abelhas nas paisagens alteradas pelo homem é provável que estas mesmas paisagens sejam beneficiadas pelo serviço gerado por tais polinizadoras (RICKETTS, 2004; KLEIN, 2009). É possível estabelecer modelos de manejo a fim de garantir a persistência e sobrevivência de abelhas em paisagens agrícolas, garantindo assim o serviço ecológico (BROSI; ARMSWORTH; DAILY, 2008). Para isso, é importante que todo o contexto da paisagem seja estruturado de forma a satisfazer também as necessidades essenciais dos grupos que promovem esse serviço, como as abelhas (KEITT, 2009). Assim, é preciso avaliar a paisagem de acordo com mecanismos que assegurem a persistência dos polinizadores e assim da polinização (GROFFMAN et al., 2006; HADLEY; BETTS, 2012; VIANA et al., 2012).

Polinizadores como as abelhas da subtribo Euglossina (Hymenoptera: Apidae) são consideradas importantes organismos prestadores deste serviço. Através da síntese de substâncias aromáticas, como óleos e resinas, produzidos por plantas polinizadas por estas abelhas, seu estudo foi facilitado e aspectos da biologia e comportamental destes organismos foram melhor compreendidos (POWELL; POWELL 1987; REBÊLO; GARÓFALO 1991; TONHASCA; BLACKMER; ALBUQUERQUE, 2002). De acordo com pesquisas, machos destas abelhas utilizam estas substâncias na produção de feromônios para atração de fêmeas, na construção de ninhos construídos no solo, em troncos e folhas secas, entre outras atividades ainda não descritas. Possuem ciclo de vida composto por fase larval e adulta, e assim dependem de diferentes habitats para completa-lo. São capazes de voar longas distâncias em busca de diversos recursos, utilizando variados ambientes para sobreviver, podendo atravessar áreas abertas e presentes até mesmo em ambientes antrópicos (CANE, 2001; SOFIA; SUZUKI 2004; BROSI, 2009). Desta maneira demonstram serem sensíveis ao processo de fragmentação já que utilizam grande variedade de recursos na paisagem heterogênea (BEZERRA; MARTINS, 2001; BROSI; DAILY; EHRLICH, 2007;

NEMÉSIO; SILVEIRA, 2007; RAMALHO; GAGLIANONE; OLIVEIRA, 2009). Dos cinco gêneros que compõem essa subtribo, *Aglae*, *Exaerete*, *Eufriesea*, *Eulaema* e *Englossa*, os quatro últimos são encontrados em ambientes de Mata Atlântica. Dentre estes, diversas espécies apresentam dependência de ambientes preservados, porém outras mostram suportar mudanças antrópicas (DRESSLER, 1982; TYLIANAKIS; KLEIN; TSCHARNTKE, 2005; CANE et al., 2006; BROSI et al., 2008). Assim é possível considerar o grupo como organismos funcionais que possuem necessidade e recursos similares, podendo assim descrever melhor a resposta da biodiversidade e do funcionamento ecológico em questão (TILMAN, 1997).

1.2 OBJETIVOS

Dentro deste contexto o nosso estudo foi baseado na seguinte hipótese: os diferentes aspectos da paisagem fragmentada podem favorecer polinizadores como abelhas Euglossina. Assim, tivemos como objetivos responder às perguntas: I) quais elementos da paisagem favorecem a diversidade de abelhas Euglossina em áreas altamente fragmentadas? II) qual o limiar crítico de quantidade de habitat natural na paisagem relativo às abelhas Euglossina nestas áreas? De acordo com a literatura, analisando a capacidade de movimentação e as necessidades das abelhas, é possível esperar que elementos como a quantidade de habitat natural e os diversos tipos de habitats antrópicos, bem como habitats heterogêneos e transitórios sejam importantes elementos para estas abelhas. Para testar esta hipótese e responder às nossas perguntas, nós analisamos 14 paisagens agrícolas, ao redor de Alfenas-MG, município imerso numa região de Mata Atlântica altamente fragmentada. Através de substâncias aromáticas as abelhas foram amostradas e analisadas através de sua riqueza estimada ao longo de um gradiente de habitat natural, dentre as paisagens. Utilizando regressões lineares e não-lineares foi possível detectar quais elementos explicam melhor a resposta das abelhas, e qual o limiar crítico desses organismos, sendo assim possível testar nossa hipótese principal.

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SEGUNDA PARTE

2 ARTIGO

Artigo desenvolvido como produto do curso de pós-graduação em Ecologia e Tecnologia Ambiental.

2.1 HABITAT AMOUNT AND SPATIAL HETEROGENEITY FAVOR LONG DISTANCE POLLINATORS IN A HIGHLY FRAGMENTED LANDSCAPE

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Artigo redigido sob as normas da revista científica *Biodiversity and Conservation*.

Introduction

Human development has been altering entire natural landscapes, deforesting and changing land use composition. The Atlantic Forest, after centuries of degradation since colonial times, has less than 16% of the original area remaining (Ribeiro et al. 2009). After vast habitat loss, fragmentation processes generate disconnection and increased isolation among areas through the creation of an anthropic matrix, directly affecting biodiversity and ecological process (Fahrig 2003; Altieri 2009).

Through the use of Metapopulation and Island Biogeography Theory in continent studies, we could understand how forest surrounding habitats, known as ‘matrix’, may be important to forest diversity (Fahrig 2001). Instead of such binary view of habitat, the landscape heterogeneity concept includes the distinct ways that different animal groups behave and use the entire landscape, be it natural or anthropogenic (Fahrig et al. 2011). Even with land use changes and the fragmentation process, some organisms are able to persist in agricultural areas since they can use different matrix types and/or secondary habitats as complementary sources to nest and feed (Fahrig 2003; Keitt 2009; Mandelik et al. 2012). Therefore, fragmentation effect per se, besides habitat loss, could favor diversity by provisioning diverse suitable habitats and well arranged in space, regarding the species needs. Matrix quality, according to the functional view of species, also contributes to species use range. Accordingly, studies may focus on the home range or the dispersion capability of focal organisms to choose the landscape scale that is coherent with its needs and reflects their specific response (With and Crist 1995; Fahrig 2001; Dryska 2004; Hadley and Betts 2012).

A better understanding of landscape use can be achieved by replacing the binary view of the landscape with a functional one. Such functional approach incorporates the way animals perceive landscape structural, such as composition and configuration features (Swift and Hannon 2010; Viana et al. 2012). A diverse range of habitats and arrangement among them could provide different resources for organisms. The matrix quality could promote a permeability between patches and favor the functional connectivity in landscape, allowing a flow of organisms and the proper species usage of it (Fahrig 2001; Prevedello and Vieira 2010, review). Fahrig and colleagues (2011) showed that a heterogeneous landscape promotes increase in diversity, regarding matrix type and configuration. Configuration elements, such as connectivity and complexity of landscape, could improve species movement; therefore resulting in the possibility of species survival in changed landscapes (Ricketts 2004; Drinnan 2005; Lindenmayer and Cunningham 2005; Holzschuh et al. 2010).

To understand biological responses to landscape changes, fragmentation hypotheses are proposed, which describe the relationship between biodiversity and the decrease of the natural habitat amount. Such hypotheses predict this relationship to be non-linear, and the existence of a critical threshold of habitat amount. Below the threshold, diversity drops abruptly and other structural factors influence diversity besides habitat loss (Andr n 1994; Metzger and Dec mps 1997; Rompr  et al. 2010). The critical threshold indicates how much natural habitat in landscape is sufficient for diversity persistence; below this value, a minimal decrease of natural habitat causes very abrupt changes in ecological stability, increasing extinction trends (Dykstra 2004; Hadley and Betts 2012). We identify the nonlinearity in the biological response to the amount of natural habitat in landscapes by observing a breakpoint in regression models (Metzger and Dec mps 1997; Murandin 2001; Martensen et al. 2012). Studies have shown the threshold value is not universal, ranging between 20 and 30%; varying at different spatial scales and groups (revised by Swift and Hannon 2010; Pardini et al. 2010; Martensen et al. 2012). However, threshold analyses were carried out with a binary approach. Therefore, there is room for improvement via the incorporation of a functional approach.

Since landscape structural changes could affect species differently, better than describe a threshold to diversity, is to regard functional groups and providers of services. Such organisms strongly affected by these changes, promote a cascade effect in ecological functioning if threatened (MEA 2005; Groffman et al. 2006; Klein et al. 2007; Holzschuh et al. 2010; Viana et al. 2012). Pollination is an important function in the ecological processes, which promotes both native and cultivated plant reproduction. In addition, pollination can increase the resiliency and ability of ecological recovery (Lindenmayer et al. 2008; Bennet et al. 2009). However, agricultural development and constant landscape changes convert large natural areas into simple monocultures,

with widespread use of chemical compounds and farm machinery, which results in decline in pollinator diversity in these areas (Fahrig et al. 2011; Cranmer et al. 2012; Mandelik et al. 2012). Bees such as Euglossine sub tribe, known as orchid bees, are able to fly long-distance foraging and pollinating in agricultural areas. They are efficient pollinators of a range of plant families, ecologically and economically important, present in crop, open, and small habitats (Janzen 1971; Roubik and Hanson 2004; Wikelsike et al. 2010; Brosi et al. 2008a; Aguiar and Gaglianone 2012). Establishing how these pollinators respond to landscape structures will help us better understand how they recognize features and use the different habitats in agricultural landscapes (Nemesio 2010). Identifying elements that favor pollinator diversity, and describing a critical threshold of habitat amount in landscape, provides tools to manage land conversion. This is important for supporting pollinator needs, which in turn offers several benefits to human welfare (MEA 2005; Winfree et al. 2011).

In this context, our hypothesis is that a heterogeneous landscape structure could favor Euglossine pollinators. We considered heterogeneous habitats and arrangements on the landscape scale that they are able to percept. Since bees are able to fly to different habitats, we expect that heterogeneous habitats provide a diverse range of resources available to them, increasing diversity and possibility of survival in highly fragmented landscapes (Brosi 2008b; Fahrig 2011). Accordingly, our study aims to address two questions: I) Which landscape structure aspects favor Euglossine bees in a highly fragmented landscape? II) What is the critical threshold of natural habitat amount, related to Euglossine bees, in such landscape? Our study addressed these questions and confirmed the hypothesis. The natural habitat amount and the spatial heterogeneity best explained richness of Euglossine pollinators. If well managed, landscape could enhance diversity and functionality, and promote sustainable exploitation, above the 25% natural habitat threshold found for these pollinators.

Material and methods

Study site

We carried out this study in 14 agricultural landscapes following a gradient of natural habitat amount (Figure 1), surrounding the city of Alfenas, south of Minas Gerais State, Brazil. The region belongs to a highly degraded, semi-deciduous, seasonal forest, with less than 4% original ground cover (Fundação SOS Mata Atlântica and INPE, 2011). The selection of sampled landscapes followed a land cover map generated from digital image processing from the Sino-Brazilian satellite CBERS-2B, from 2009 and with resolution of 20m. We used the criteria: i) similarity of degradation, by observing spectral attributes such color and texture; ii)

minimum distance of four kilometers between areas, to ensure sample independence, and; iii) a gradient of natural habitat amount from 8 to 62%, throughout the selected landscapes, in a 1,000m radius.

To test whether and how landscape structure affects Euglossine diversity, we related landscape composition and configuration measures to estimate species richness. Over the natural habitat amount gradient throughout the 14 landscapes, we sampled the central forest fragment to obtain and analyze these variables as follows:

Bee sampling

The sample occurred bimonthly during the wet season (from December/2012 to March/2013), when Euglossine species present higher activity. We sampled five hours a day and five landscapes per day, completing each sample cycle in three days. Therewith, we minimized abiotic differences among areas, and avoided cloudy and rainy days in our sampling (Abrahamczyk et al. 2011).

To capture bees, six attractive substances (benzyl acetate, eucalyptol, eugenol, methyl cinamate, methyl salicylate and vanillin) used commonly in Euglossine studies were placed in smell baits in each central fragment forest (Dodson et al. 1969; Aguiar and Gaglianone 2008). We placed the six traps in the forest interior, 100m from the edge, 1.5m from the ground, spaced 10m from each other (according to Sofia and Suzuki 2004).

We released species of easy identification and known by collectors (*Enfriesea violaceae* Blanchard and *Eulaema nigrita* Lepeletier) to minimize adverse effects on them. We collected the other species for identification at the Zoology Department of Federal University of Paraná - (UFPR), the entomological collection where the specimens remain.

Landscape analyzes

We delimited a radius of 1000m around the central point of each forest fragment sampled (Wikelski et al. 2010; Watson et al. 2011). We carried out the landscape classification by manual supervised vectorization, presenting the landscape composition by land use classes, which we validated by Google Earth satellite images (dated 2009) and in the field (Figure 2).

To landscape analyzes, we used the software ArcGis (Version 10.0, ESRI). We used three main landscape parameters related to Euglossine richness (McGarigal and Marks 1995). Group 1: landscape complexity and structure, we mainly adopted Area Weighted Mean Patch Fractal Dimension (awmpfd) metric, calculated to

avoid patch area effect regarding only its complexity; group 2: landscape connectivity and fragmentation degree and; group 3: landscape composition and its quality in landscape (Table 1).

Such quality index is determined through a value between 0.0 and 1.0. Values near 1.0 are for habitats more suitable to Euglossine bees, which could provide more resources needed for their survival (Table 2). We determined these values through the Expert Knowledge approach, defining a mean value among those obtained (EK, McBride and Burgman 2012). The four researchers who collaborated in this study are specialists in taxonomy and ecology of Euglossine bee groups. They were asked to analyze the different habitats as a Euglossine organism, and settle it in accord to the bees' use.

By using ArcGis extensions, V-LATE and Patch Analyst 5.0, we calculated these and other landscape metrics (Newton 2007). We tested the correlations among metrics (Table 3) to avoid redundancy in results, using values ≥ 0.70 to consider a correlation, and only used the non-related ones (Table 4).

Data Analyzes

We used the Bootstrapping estimator to estimate Euglossine richness data (Tonhasca et al. 2002; Ramírez et al. 2010). This richness estimator considers patterns with a few dominant and many rare species, the same pattern found here in the Euglossine community (Magurran 2004).

In order to identify the landscape variables that best explain the Euglossine richness, we used generalized linear models and Akaike Information Criterion and its derived parameters by using the R package 'bbmle' (Burnham and Anderson 2002; Bolker 2008). The AICc parameter provides a correction to small samples ($n < 70$) and number of parameters used in each model. The derived $\Delta AICc$ parameter is the difference of each model to the most plausible one; hence, the best model should have a value of zero. We considered models equally plausible if their values had $\Delta AICc < 2$ of difference. The parameter $wAICc$ is the 'weight' of the model and represent its relative likelihood from the others, from 0 to 1. Finally, the $wAICacc$ is the sum of the likelihood of the best models, representing the total likelihood of these models to explain the biological response.

To find the critical threshold of habitat amount in euglossines, we related these data with the landscape natural cover gradient and constructed nonlinear regression models to find the most appropriate to explain such relationship (Table 5). To identify the critical point by break lines at the asymptotic curve of the relationship, we used the R package 'segmented', and a resampling of 1000 times.

Results

After 3,600 field hours, our sample comprised 1,479 specimens of 10 species within four genera: *Eufriesea* (Cockerell 1908), *Euglossa* (Latreille 1802), *Eulaema* (Lepeletier 1841) and *Excaerete* (Hoffmannsegg 1817). The genus of Euglossine sub tribe which we expected to found in the Atlantic Forest Domain (Nemesio 2009). The data showed *Euglossa* (60% of species) as the richest genre, and *Eulaema* (70% of specimens) and *Eufriesea* (26%) as the most abundant, an expected pattern as well (Table 6).

To relate and obtain the best explanation for the Euglossine response, we mainly tested richness. Sampling showed a dominance in abundance for two main species (*Eulaema nigrita* and *Eufriesea violacea*). Community richness, estimated by bootstrapping, showed a satisfactory asymptotic curve, representing a reasonable sample effort of diversity (Figure 3).

Habitat amount proportion in landscape was the model that best explained Euglossine richness, followed by its effect and spatial heterogeneity (awmpfd measure, Sh2) added to the model. The best models comprised more than 70% of wAICacc, 50% with respect to natural habitat effect alone and 21% of natural habitat and heterogeneity effects combined, demonstrating its consistency from other models and the null one (Table 7). Such variables represent the best explanation of Euglossine richness variation in agricultural landscapes (Figure 4). This means that a higher habitat amount proportion showing higher spatial heterogeneity leads to higher Euglossine richness, showing the better landscape structure to bees (Figure 5). We had hypothesized that connectivity measures would compound a consistent model to explain bee richness. However, one of the connectivity measures (Prx1) showed high correlation with habitat amount (Prx1), since it is related to the area of each neighbor fragment. Thus, it had to be excluded from the analyses. The other measure (Prx2) did not show any considerable weight in the models. In addition, the quality index of matrix habitats also showed no consistency among models.

Results to determine a critical threshold of habitat amount showed the nonlinear model 'Power' with the best fitness and significant patterns ($R = 0.69$; $p < 0.01$), best even than the GLM ($R = 0.13$; $p < 0.01$). Therewith, we estimated the value of the critical threshold of natural habitat amount with the resultant equation of this model by the 'segmented' package. Through this we determined the mean value of the critical threshold as 24.3% (min = 23.6; max = 24.5) of habitat amount (Figure 6).

Discussion

Euglossine pollinators respond positively to some aspects of landscape structure in a highly fragmented region. Habitat amount, mainly, followed by spatial heterogeneity of landscape, best explained bee richness, despite the fragmentation process. The gradient of habitat amount in landscapes presents a nonlinear relationship with richness, and generates a critical threshold of around 25%. The value represents when fragmentation process is effect of structural features, besides natural habitat decrease, and become effect of spatial heterogeneity as well.

Natural habitat, as already known, is the main element affecting landscape biodiversity, being important to several groups. Many studies have demonstrated the strong relationship between natural habitat amount in landscape, on several spatial scales, and diversity of several groups (Andr n 1994; Fahrig 2001; Swift and Hannon 2010; Hadley and Betts 2012). Such element in the landscape represent the primary habitat and the sites where organisms could find a wide range of resources. These places offer safe locations to nest and forage, and disturbance do not occur frequently and abruptly as in anthropic habitats. In addition to habitat loss, studies have shown structural changes in landscapes as effects of fragmentation (Metzger and Dec mps 1997; With and King 1999; Fahrig 2003). The region studied here, present quite advanced stages of such processes, where diversity remains dependent on habitat amount, but also on the arrangement of landscape elements. We could observed this through the response of bees to spatial heterogeneity here, reported also in other research (Steffan-Dewenter et al. 2002; Holzschuh et al. 2010).

Here we show the spatial heterogeneity as an element that eases habitat amount effects on pollinators. In addition to natural habitat amount, landscape heterogeneity, in terms of complexity, showed to be as quite strong and complement the explanation of biological response. Spatial heterogeneity of landscapes represents how habitat types arranges to each other, taking their contact zones as parameter. Therefore, this parameter shows interlacement among habitats of every type: ecotones and edge areas, corridors, small patches and matrix habitats; which could offer complementary sites and increase richness (Ries and Sisk 2004). Features regarding heterogeneity that pollinators use functionally (Brosi 2009; Abrahamczyk et al. 2011; Aguiar and Gaglianone 2012). These heterogenic environments offer different resources, as materials and cavities for nesting, floral sources from diverse succession stage and phenology seasonality (Gathmann et al. 1994; Roubik and Hanson 2004; Holzschuh 2010). Such features of agricultural landscapes improve the quality and possibility for organisms to exploit other habitats, since their primary one is almost depleted (Fahrig 2003; Fahrig 2011; Hadley and Betts 2012).

Accordingly, studies have shown the existence of a critical threshold of natural habitat in landscapes (Martensen et al., 2012). This threshold indicates how much habitat is sufficient to maintain the persistence of diversity on landscape level (Huggett 2005). This approach indicates the effect of habitat loss in biological response until a certain level, after this, effect of landscape structure also plays a role (Andr n 1994; Keitt 2009). Our results showed a critical threshold around 25% of natural habitat amount in landscape. Such set value is in the defined range of diverse group responses, regarding biodiversity and ecological processes (revised by Swift and Hannon 2010; Hadley and Betts 2012). Tschardt et al. (2011) describe a threshold of 20% for pollination and biological control, in addition to biodiversity. Some studies reveal the existence of more than a unique threshold (Morandin and Winston 2006; Pardini et al. 2010; Tschardt et al. 2011; Martensen et al. 2012). Depending on the degree of fragmentation of the region, abrupt changes could occur. Low fragmented areas (around 60% of natural habitats) could promote the percolation threshold due to the physical separation of natural habitats (Gardner and O'Neill 1991). Medium fragmented areas (around 30% of natural habitats), could promote the connectivity threshold, besides the habitat loss, due to the functional separation of habitats, preventing species movement (Metzger and Decamps 1997). Highly fragmented areas (<10% natural habitat) could ultimately promote, an extinction threshold due to abrupt changes in features in respect the needs of species until a scale in which they perceive such changes (Keitt et al. 2001; Swift and Hannon 2010). Our studied landscapes, the sample points, located in a highly fragmented region with less than 10% of habitat remaining, showed to be able to support Euglossine pollinators and maintain its richness. Diversity was maintained at a finer-grained level, at landscapes (1000m radii) showing at least 25% of habitat. Studies with Euglossine, or similar guild has not defined a threshold of habitat amount in degraded areas, but still confirm the positive response of bees to this parameter and landscape structure (Brosi et al. 2008b, Brosi 2009; Keitt et al. 2009; Viana et al. 2012). The use of the scale that reflects the species-specific response, regarding the movement capacity of focal organisms, is important as well. Different results might be due to this, while considering just local or too broad scale could not explain well the relationship to changes in landscape (Steffan-Dewenter et al. 2002; Hadley and Betts 2012). Besides habitat amount effect, spatial heterogeneity showed to be a landscape structure that positively affects the pollinators' response in a fragmented area.

According to other studies, Euglossine bees are able to fly long distances to find resources, and are efficient pollinators, by supporting reproduction of native and cultivated plants. These solitary bees take advantage of their high dispersion ability, and fly to different habitats including open and crop areas, searching for floral sources and materials for nest construction (Dressler 1968; Janzen 1971; Wikelski et al. 2010). The

four genera found in our sample use several types of materials disposed in such sites: sand, fallen tree logs, leaves, resin, pollen, nectar, several kinds of resources present in several kinds of habitats in landscape (Cameron 2004). Studies demonstrate that heterogenic habitats as well intermediate ones could increase bee richness and their use of it, but still depend on the original (Sofia and Suzuki 2004; Nemesio and Silveira, 2007; Ramalho et al. 2009). The habitat heterogeneity generates a wider range of microhabitats and niches, supported by different abiotic aspects that produce richer assemblages (MacArthur and MacArthur 1961; Parris 2004; Nemesio and Silveira 2006). This knowledge corroborate our findings, illustrating the dependence of these pollinators in natural habitats, but also the use of intermediate areas, which allows them to search for new resources and keep close to primary habitats, thus enhancing richness.

Euglossine pollinators are able to persist in highly fragmented landscapes, as seen here; moreover, they are able to exploit altered and anthropic habitats. Our deforestation situation represents the real situation of degraded areas, which suffer from intense agricultural development and dramatic landscape changes. Therefore, a better understanding of relationships of biological responses to habitat loss and landscape changes in less fragmented areas is important too, since it could show the threshold below which significant losses could occur, thus helping to prevent them to reach such a degraded situation as ours. We showed that it is still possible to maintain diversity, and that well managed landscape structure and anthropic matrices could enhance the use by species (Hadley and Betts 2012). Pollinator richness decays with decreases along the natural habitat amount gradient. Until the threshold value, biological responses relate to habitat loss. Below this value, a decrease of spatial heterogeneity explains the decline in pollinator richness, since bees are not capable of efficiently using highly fragmented landscapes. If a landscape has a low amount of habitat but shows a heterogeneous structure, then diversity tolerates fragmentation and persists in altered landscapes.

Based on our results, it is possible to define managements to attend a wide range of pollinator diversity. Bees are the most important group for such a functional service (Winfree 2010). Studies reveal that wild bees could enhance the production of crop areas when near natural habitats (Ricketts 2004). The maintenance of these functional organisms could improve the range of this service in cultivated plants as well as native ones. This service brings benefits such as reproduction of plants, increasing production and maintaining the forests and its ability to recover, as well as soil and water regulation and indirect goods it yields (MEA 2005; Kremen et al 2007). Paying attention to habitat requirements of this important group, we would be able to explore landscapes, while still allowing the persistence of environmental processes.

Future studies are needed to understand how landscape structure, habitat loss and spatial heterogeneity in landscapes, affect long-distance pollinators in regions with low and medium fragmentation (e.g. Pardini et al. 2010; Martensen et al. 2012). The response in such environments could provide information on a range of diversity greater than our study, and explain how and why pollinators decline. By studying these responses, we could understand which processes and landscape structures play a role in pollinator diversity before they become concerned; therefore, avoiding such situations and predicting threats, saving a wide range of species that could be already lost here. We would use this information to provide guidelines for sustainable exploitation; thus, promoting human welfare and biodiversity conservation, in the present and future.

In conclusion, our study shows that besides habitat amount, spatial heterogeneity is an important feature of landscape that favors long-distance pollinators. The critical threshold presented in our highly fragmented area showed that bees could persist despite changes in landscape, and satisfy different needs through the heterogeneity of landscape including the natural habitat.

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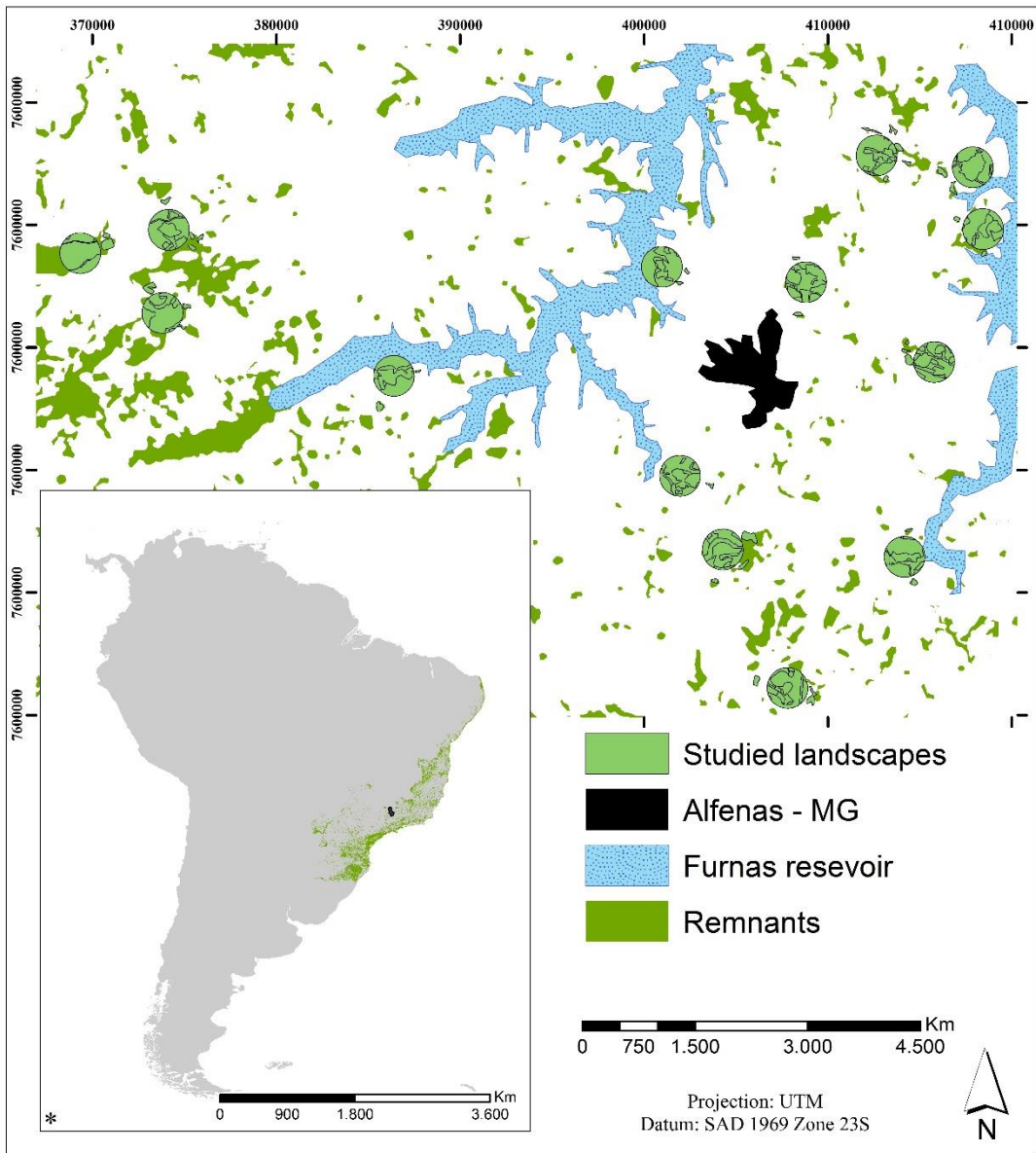
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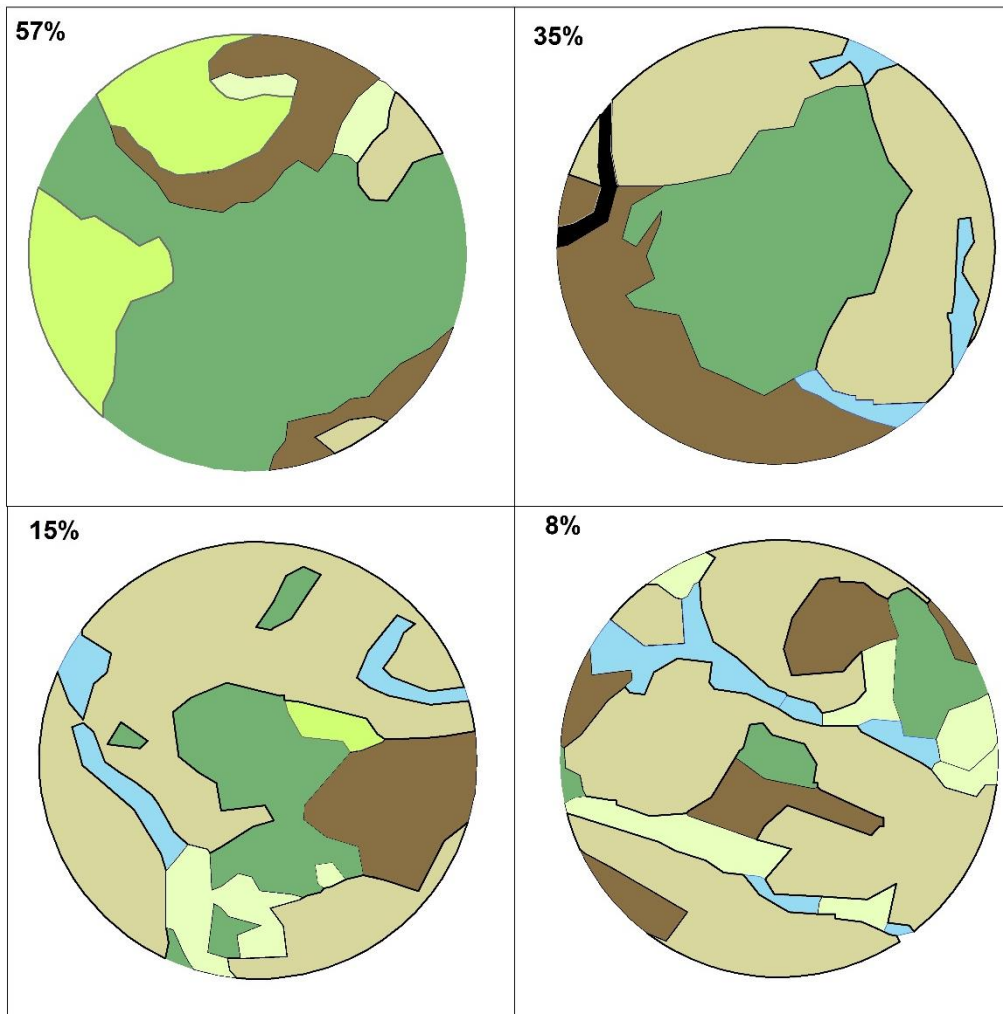
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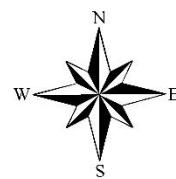
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- Water
- Coffee
- Sugar cane
- Forest undergrowth
- Natural cover
- Pasture
- Road



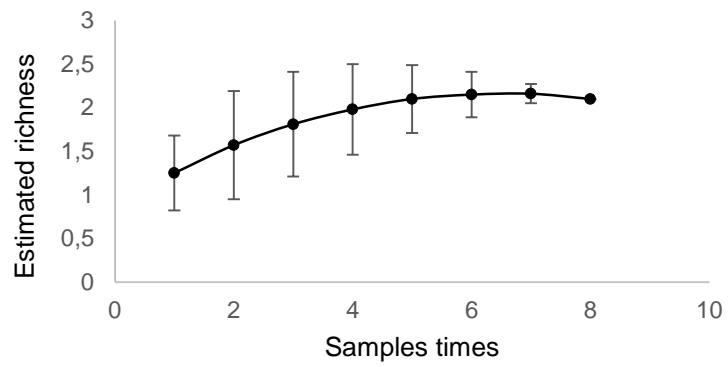


Fig. 3 Collector effort represented by the distribution of Bootstrapping estimated curve throughout samples. It is possible to observe an asymptotic relationship, representing a reasonable effort.

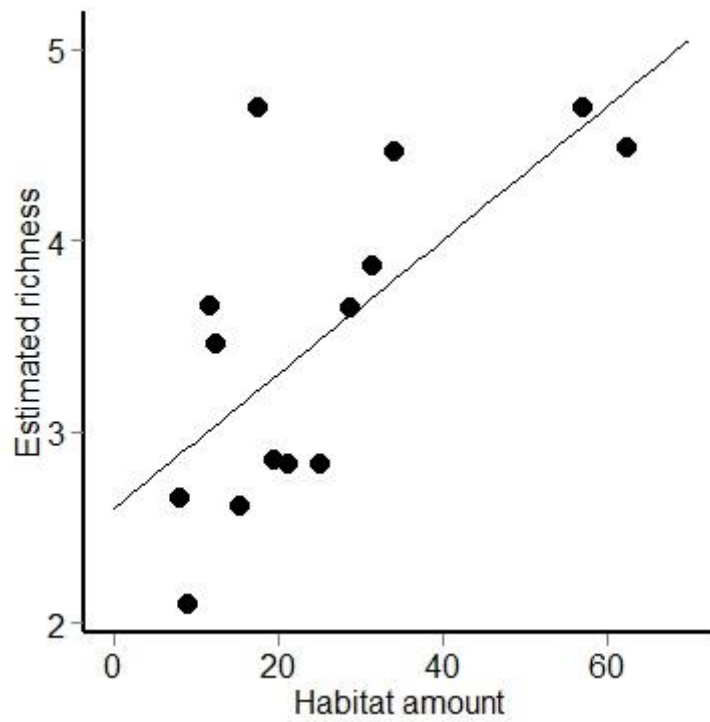


Fig 4 Relationship between habitat amount (%) and the bootstrapping estimated richness. We could see a positive increase of Euglossine bee diversity to habitat amount.

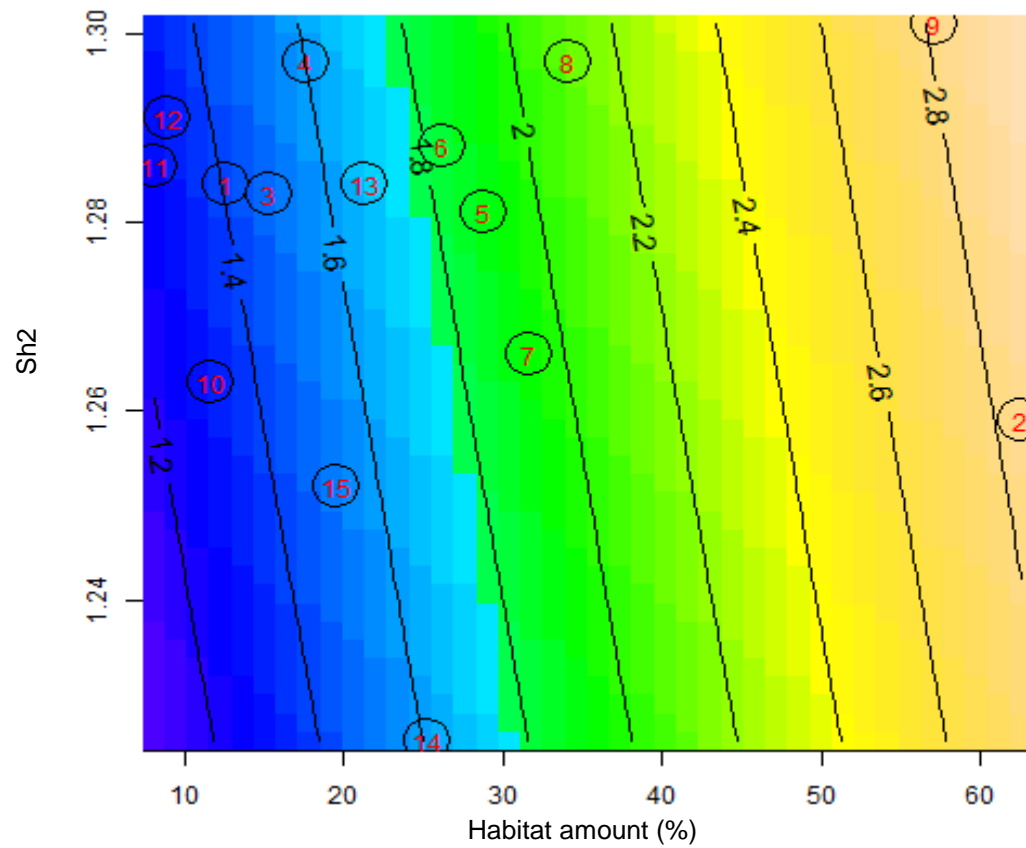


Fig 5 Effects of both habitat amount (C1) and the complexity landscape parameter (Sh2) on estimated richness of Euglossine bees (circles). . A higher habitat proportion supports a higher richness, which become even higher, after making the landscape structure more complex.

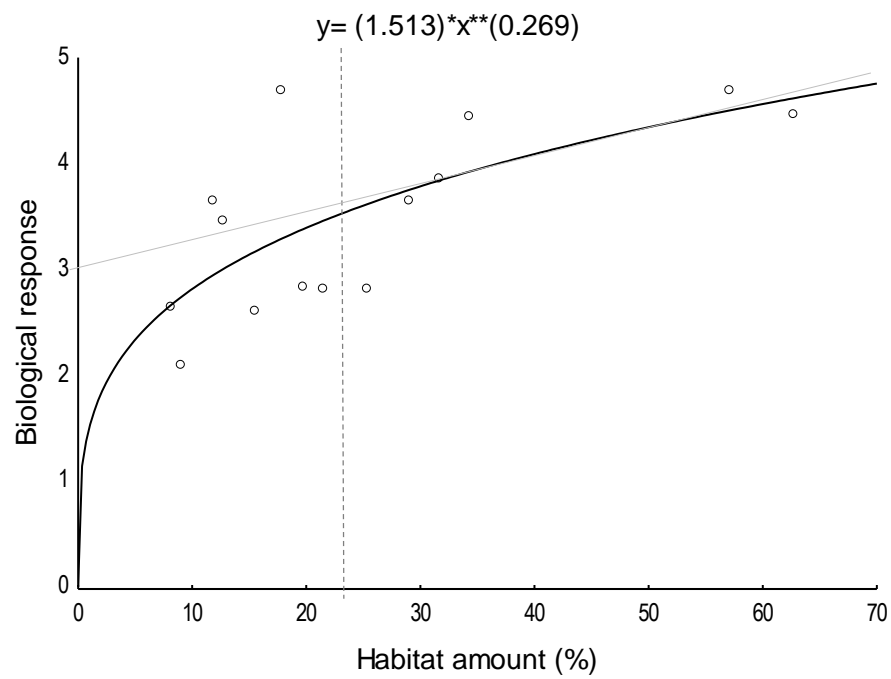


Fig. 6 Nonlinear regression Model, 'Power', presenting the relationship between biological response, euglossine richness, and habitat amount gradient on landscape. It is possible to note a threshold around 24% of habitat amount, below it the richness tends to decay abruptly. Critical threshold represents the diversity decay over habitat loss effect. In this study, we observed spatial heterogeneity besides natural cover as a landscape structure to support diversity despite perturbation, decreasing threshold value.

Table 1 Three measures groups used to construct and select the model which best explain Euglossine estimated richness. We determined three features: group 1: landscape complexity and structure; group 2: landscape connectivity and fragmentation degree and; group 3: landscape composition and its quality on region; group 4: no effects. Groups have the respective prefixes: Sh, Prx, C and Null.

G	Model	Variable	Numeric meaning	Ecological meaning	Reference
1	Sh1	Shape habitat amount	Area weighted mean patch fractal dimension (awmpfd) is a shape measure that do not considers patch area; values around 1 determine simple perimeters and around 2 complex ones. It regards only natural cover on landscape.	Edge effect	Brosi et al. (2008) Brosi (2009)
	Sh2	Shape landscape	Awmpfd measure; it regards spatial heterogeneity of entire landscape.	Heterogeneity and complexity of the landscape, complementary and transitional habitats.	
2	Prx1	Connectivity	Proximity index regarding distance and area of the nearest neighbors on landscapes.	Landscape connectivity and fragmentation.	Brosi (2009)
	Prx2	Connectivity	Nearest Neighbor distances mean on landscape (m).	Mean landscape connectivity	
3	C1	Habitat amount	Natural cover proportion on landscape (%).	Primary habitat amount.	Brosi et al (2008) Brosi et al (2009)
	C2	Matrix a, b, c	a) Sugar cane plantation proportion on landscape (%); b) Coffee plantation proportion on landscape (%); c) Pasture proportion on landscape (%).	Proportion of original habitat and surrounding habitats where bees could take floral source and nest material, but the use of conventional manage allow agricultural compounds on landscapes.	Nemesio and Silveira (2006) Ricketts et al (2004)
	C3	Landscape quality index	Quality index based on EK; it regards mean quality of all classes on each landscape.	Quality and landscape use by Euglossine bees	
	C4	Matrix quality index	Quality index based on EK; it regards mean quality of all matrix classes on each landscape.	Quality and matrix permeability	
4	Null model	Constant	Constant parameter and β_0 .	Absence of effects	

Table 2 Expert knowledge approach. The value given by experts to the different habitat types express their opinion on the value of these types for the bees (for foraging, movement or nesting). Values can range from 0 (completely inhospitable) to 1 (the best possible habitat, such as a mature forest).

Problem definition	Expert knowledge (EK)			
	W1	W2	W3	W4
Habitat types				
Water: wet areas, rivers, lakes and deepest swamps.	0.0	0.2	0.1	0.0
Road: paved highway.	0.0	0.6	0.1	0.0
Exposed soil: areas without vegetation	0.0	0.1	0.2	0.0
Sugar cane: plantation areas where the cut uses fire, machines, besides the agricultural compounds use.	0.3	0.5	0.3	0.2
Silviculture: eucalyptus areas may suffer cut or not.	0.3	0.4	0.7	0.3
Pasture: cattle areas and grasslands.	0.3	0.6	0.4	0.1
Coffee: plantation areas of conventional managed coffee.	0.5	0.4	0.6	0.2
Initial Succession stage: abounded areas with herbs and shrubs predominant vegetation.	0.7	0.8	0.5	0.4
Forest: original areas	1.0	1.0	1.0	1.0

Land use classes defined by landscape composition. Feature classified by the EK, which attributed a value weight (W) to each class type of landscapes. Three expert guesses (W1, W2, W3) used here represented the quality of landscape. We used it to calculate the entire landscape quality and matrix quality (without consider forest areas), through a mean value of the quality index generated by EK. To reach a unique value for landscapes we multiplied each value of W for its respective class area and divided by the entire landscape area.

Table 3 Correlation test of landscape measures. Observing correlation values, we excluded variable up 0.7, which indicates a relation of 70% between correlated ones, in bold, to avoid redundancy in results. Those correlated that did not have a logical explanation to produce redundant results we analyzed separately. We used R Version 2.15.3 software for such analysis.

Variable	C1	C1C2a	C1C2b	C1C2c	C2a	C2b	C2c	Sh1	Sh2	Prx1	Prx2	C3	C4
C1	1.00												
C1C2a	0.73	1.00											
C1C2b	0.46	0.13	1.00										
C1C2c	0.19	-0.32	-0.23	1.00									
C2a	0.27	0.86	-0.16	-0.59	1.00								
C2b	-0.28	-0.42	0.72	-0.40	-0.38	1.00							
C2c	-0.49	-0.76	-0.51	0.76	-0.71	-0.17	1.00						
Sh1	-0.58	-0.25	-0.53	-0.15	0.09	-0.13	0.25	1.00					
Sh2	-0.04	-0.29	0.08	0.14	-0.38	0.11	0.14	-0.31	1.00				
Prx1	0.88	0.62	0.50	0.08	0.21	-0.15	-0.51	-0.41	0.06	1.00			
Prx2	-0.33	-0.41	0.22	-0.05	-0.32	0.49	0.17	0.11	-0.42	-0.48	1.00		
C3	-0.30	-0.42	0.24	-0.20	-0.37	0.50	0.02	0.04	-0.08	-0.25	0.62	1.00	
C4	0.45	0.35	0.14	-0.05	0.15	-0.20	-0.34	-0.11	0.03	0.66	-0.29	0.02	1.00

C1 = Habitat amount (%); C1C2a = Natural cover + sugar cane proportion (%); C1C2b = Natural cover + coffee proportion (%); C1C2c = Natural cover + pasture proportion (%); C2a = Sugar cane plantations (%); C2b = coffee farms (%); C2c = pasture areas (%); Sh1 = awmpfd measure of natural cover on landscape ($1 \leq \text{awmpfd} \leq 2$); Sh2 = awmpfd measure of entire landscape (spatial heterogeneity); Prx1 = mean proximity index of landscape; Prx2 = mean nearest neighbor distance (m); C3 = quality index of landscape classes; C4 = quality index of matrices on landscape.

Table 4 Bootstrapping richness estimator of Euglossine bees (ascending order), and landscape variables of 14 landscapes studied. Selected measures of the three groups, g1: Sh1 and Sh2; g2: Prx; g3: C1C2b, C1C2c, C1, C4.

Lat.-S (m)	Long-W (m)	Land	Boots	Sh1	Sh2	Prx2	C1C2b	C1C2c	C1	C4
396847.66	7635804.63	12	2.10	1.25	1.29	255.47	13.32	64.44	9.02	0.3178
368290.84	7636589.13	3	2.61	1.27	1.28	196.95	62.56	64.92	15.37	0.2838
408810.01	7621732.89	11	2.65	1.26	1.29	157.33	15.37	85.13	8.11	0.3261
397786.20	7625600.06	13	2.83	1.23	1.28	180.24	29.57	80.08	21.41	0.2713
383700.08	7630586.34	14	2.83	1.29	1.23	414.82	28.89	44.69	25.29	0.2812
381036.69	7628203.35	15	2.85	1.31	1.25	139.86	34.59	53.51	19.59	0.288
399887.50	7621906.22	1	3.46	1.28	1.28	247.03	63.56	45.06	12.60	0.3356
412091.33	7640839.75	5	3.65	1.29	1.28	240.41	55.60	75.75	28.89	0.4115
372498.22	7633498.98	10	3.66	1.26	1.26	477.11	71.40	66.13	11.72	0.2954
412713.70	7637938.19	7	3.87	1.27	1.27	158.48	80.58	31.20	31.62	0.2868
410197.96	7631290.36	8	4.46	1.22	1.30	275.76	22.07	72.79	34.15	0.1752
402972.40	7615327.18	2	4.48	1.20	1.26	149.76	61.22	27.91	62.56	0.4098
372752.26	7637756.64	4	4.69	1.28	1.30	172.28	25.92	27.42	17.66	0.2863
404006.25	7635247.68	9	4.69	1.23	1.30	131.52	26.53	79.55	57.09	0.4196

Lands = number of each studied landscape; Boots. = the bootstrapping estimator value; Sh1 = awmpfd measure of natural cover on landscape ($1 \leq \text{awmpfd} \leq 2$); Sh2 = awmpfd measure of entire landscape; Prx2= mean nearest neighbor distance in landscape (m); C2a = sugar cane plantation proportion in landscape (%); C2b = coffee farms (%); C2c = pasture areas (%); C1 = natural cover (%); C4= quality index of matrices in landscape.

Table 5 Nonlinear Regression Models used to define the critical threshold of natural cover to Euglossine bee community.

Models	Equations	References
Cumulative Weibull	$y= a(1-\exp(-bx^c))$	Weibull (1951); Flather (1996)
Exponential	$y= a+b \log(x)$	Gleason (1925); Fisher et al. (1943)
Piece-Wise	$y= a+b*x+c*(x-Breakpnt)*(x>Breakpnt)$	Lomolino e Weiser (2001)
Power	$y= ax^b$	Arrhenius (1921); Preston (1962)
Rational Function	$y= (a+bx)/(1+cx)$	Ratkowsky (1983)

Table 6 Species sampled in the 14 landscapes. We could observe two dominant species among them. *Ef. violacea* and *El. nigrita*. Despite this, we set a richness estimator that presented the euglossine distribution pattern. The bootstrapping estimator take into account the divergence in data presenting few species with many individuals, and many species with few individuals.

Species	Abundance
<i>Euglossa amazonica</i> Dressler, 1982	1
<i>Euglossa truncata</i> Rebêlo and Moure, 1996	1
<i>Euglossa townsendi</i> Cockerell, 1904	2
<i>Eulaema pseudocingulata</i> Oliveira, 2006	2
<i>Euglossa cordata</i> (Linnaeus, 1758)	3
<i>Exaerete smaragdina</i> (Perty, 1833)	9
<i>Euglossa annectans</i> Dressler, 1982	16
<i>Euglossa fimbriata</i> Rebêlo and Moure, 1996	18
<i>Efriesea violacea</i> (Blanchard, 1840)	388
<i>Eulaema nigrita</i> Lepeletier, 1841	1039
Total specimens	1479
Total species	10

Table 7 Generalized linear models selected by AIC. Habitat amount (C1), followed by habitat amount plus awmpfd measure (Sh2) were the models that best explained Euglossine richness. The combined weight of the amount of habitat reaches 71%.

Models	ΔAIC	wAICc	wAICacc
C1	0.0	0.50	0.71
C1_Sh2	1.8	0.21	
Null	5.3	0.03	

Akaike Information Criterion (AIC) provided the best model. We refined its results for small sample correction and the calculus of the derived parameters Δ AICc and wAICc. These represent the dimension between each model and the best one; and the weight of the model, or the probability of it being the best one, respectively. The wAICacc presents the accumulated value of the best models, calculated by the sum of wAICc of the best models.