UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE CIÊNCIAS BIOLÓGICAS

DEPARTAMENTO DE ZOOLOGIA

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

BRUNO KAROL CORDEIRO FILGUEIRAS

RESPOSTA DOS BESOUROS ESCARABEÍNEOS (SCARABAEIDAE) E BORBOLETAS FRUGÍVORAS (NYMPHALIDAE) À MODIFICAÇÃO DE HABITAT NA FLORESTA ATLÂNTICA NORDESTINA

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de doutor em Biologia Animall.

Orientadora: Prof.ªDr.ª Luciana Iannuzzi

Co-orientadora: Prof.ªDr.ª Inara Roberta Leal

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Aprovada em ____ /___/ ________.

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Dedico:

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ñAquele que sabe que possui o
suficiente é ricoò.
(Tao Te Ching)

RESUMO

Com a expansão de paisagens modificadas pelo homem nos ecossistemas tropicais, o uso de indicadores ambientais torna-se importante para verificar como a biodiversidade está respondendo as diferentes condições de habitat. Na presente tese, verificou-se a resposta dos besouros escarabeíneos e das borboletas frugívoras à modificação de habitat em uma paisagem modificada pelo homem da Floresta Atlântica. Para isso, subdividiram-se os seguintes tópicos: (1) persistência de besouros escarabeíneos em paisagens modificadas pelo homem: combinando espécies indicadoras com o uso antropogênico da terra e efeitos relacionados à fragmentação; (2) *turnover* spacial das assembléias de besouros escarabeíneos neotropicais em habitats de borda: implicações para conservação em paisagens modificadas pelo homem e (3) o valor de habitats dominados por borda na persistência de borboletas frugívoras em uma paisagem modificada pelo homem na Floresta Atlântica. Foi selecionada para o estudo uma paisagem hiper-fragmentada (Paisagem Serra Grande), localizada na Floresta Atlântica do Nordeste brasileiro. Verificou-se que (1) a distinção taxonômica entre os habitats é associada com a presença de espécies indicadoras, com algumas espécies beneficiando-se ou sendo dependentes de habitats alterados, como os afetados por borda e as matrizes não florestais; (2) o *turnover* espacial dos besouros escarabeíneos é influenciado pelos efeitos relacionados à fragmentação (efeito da área, borda e isolamento), aumentando em locais alterados (habitats afetados por borda e matrizes não florestais) o que corrobora a hipótese de diferenciação desses besouros em paisagens antropizadas; e (3) fragmentos florestais pequenos, dominados por borda, isolados e com alta proporção de árvores pioneiras afetam a persistência de borboletas frugívoras favorecendo espécies de borda adptadas a elevada intensidade luminosa em paisagens fragmentadas. Tal composição ecológica demonstrada nesse estudo sugere que embora as florestas primárias e suas áreas interiores sejam insubistituíveis para a biodiversidade, os habitats afetados por borda retêm espécies de besouros escarabeíneos e borboletas frugívoras. Esses resultados adicionam novas perspectivas sobre a manutenção da biodiversidade em paisagens tropicais severamente degradadas e podem ser utilizados em futuros planos de conservação da biodiversidade na Floresta Atlântica.

Palavras-Chave: Floresta Atlântica. Fragmentação. Indicadores Ecológicos. Mudança de Habitat. Nymphalidae. Scarabaeinae.

ABSTRACT

With the expansion and consolidation of human-modified landscapes, identifying and making use of ecological indicators becomes an essential task to verify the biodiversity response to different habitat condition. Here, I analyze the response of dung beetles and frui-feeding butterflies to habitat change in a human-modified Atlantic Forest landscape. For this, I analyze the following aspects: (1) dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land use and fragmentation-related effects; (2) spatial turnover of Neotropical forest dung beetle assemblages in edge-dominated habitats: conservation implications for human-modified landscapes, and (3) the value of edge-dominated habitats for fruit-feeding butterfly persistence in a human-modified Atlantic Forest landscape. I found that (1) cross-habitat taxonomic distinctness is associated with the presence of indicator species, some species benefit or are dependent of open habitats created by human-disturbances, such as forest edges and matrices; (2) there is a strong influence of fragmentation-related effects on dung beetle beta diversity with the spatial turnover increase in altered habitats (edge-affected and matrix habitats), which in turn corroborate the hypothesis of dung beetle differentiation in altered landscapes, and (3) small and isolated remnants (edge-dominated habitats) with high proportion of pioneer trees are important habitats for fruit-feeding butterfly persistence favouring edge species more tolerant to sunlight in fragmented landscapes. Such ecological composition suggests that although forest interior represents an irreplaceable habitat for biodiversity, edge-affected habitats are able to retain species of dung beetles and fruit-feeding butterflies. These findings add further approachs to the maintenance of biodiversity in severely deforested tropical landscapes and have ecological implications for biodiversity conservation planning in Atlantic Forest.

Key-words: Atlantic Forest. Ecological Indicators. Fragmentation. Habitat change. Nymphalidae. Scarabaeinae. Species persistence.

SUMÁRIO

1. INTRODUÇÃO GERAL

O declínio de grandes áreas florestais intactas, principalmente nos ecossistemas tropicais, tem levado os ecólogos a depositarem suas esperanças no manejo de paisagens modificadas pelo homem para conservar a biodiversidade (MELO et al., 2013; WRIGHT e MULLER-LANDAU, 2006). A falta de grandes áreas intactas torna a concepção de mega-reservas utópica nos trópicos, onde paisagens antropizadas com práticas agrícolas sustentáveis coexistindo com florestas naturais têm emergido como foco para a conservação de espécies (TILMAN et al., 2011). Entre as forças motrizes formadoras de paisagens modificadas que ameaçam a conservação das espécies tropicais, destaca-se a fragmentação de habitat (LAURANCE e BIERREGARD, 1997; TURNER, 1996). A fragmentação de habitat envolve três processos distintos, porém inter-relacionados. Primeiro, a quantidade de habitat original na paisagem é reduzida. Segundo, fragmentos de variados tamanhos e com diferentes graus de isolamento são formados (FAHRIG, 2003; LAURANCE, 2008). Terceiro, a interação entre a floresta e a matriz não florestada resulta no efeito de borda (BIERREGAARD et al. 1992; FAHRIG, 2003; MURCIA, 1995). Em geral, paisagens fragmentadas não sustentam a mesma diversidade de espécies encontradas no habitat original (LOVEJOY et al., 1986; TABARELLI et al., 1999). As perturbações antrópicas que são impostas aos sistemas naturais levam à desestruturação do conjunto das condições ideais para muitos organismos (BROWN, 1991).

Um modo de detectar e monitorar os padrões de mudança na biota é utilizar espécies, ou grupo de espécies, que funcionam como bioindicadoras de degradação ambiental. Vários grupos de insetos, como libélulas, borboletas, abelhas, formigas e besouros têm sido utilizados como bioindicadores (AGOSTI et al., 2000; FREITAS et al., 2006; HALFFTER et al., 1992; LUKE et al., 2014; UEHARA-PRADO et al., 2009). Os besouros escarabeíneos e as borboletas frugívoras, por responderem à conversão de florestas intactas em paisagens antropizadas (BARLOW et al., 2010; BARNES et al., 2014; HALFFTER et al., 1992; KLEIN, 1989; NYAFWONO et al., 2014; RIBEIRO et al., 2012) e por apresentarem padronização de amostragem e taxonomia relativamente bem resolvida, são considerados excelentes indicadores ambientais nos trópicos (FREITAS et al., 2006; HALFFTER e FAVILLA, 1993).

Os besouros escarabeíneos são componentes conspícuos de muitos ecossistemas terrestres, sendo abundantes e diversos nos trópicos (HANSKI e CAMBEFOT, 1991). Depois de localizar uma fonte de recurso, geralmente fezes ou carcaça, a maior parte dos besouros escarabeíneos remove rapidamente o recurso, enterrando-o sob a superfície do solo para a alimentação dos adultos, oviposição e posterior alimentação das larvas (HALFFTER e EDMONDS, 1982). Esse comportamento tem importantes consequências ecológicas como aeração e fertilização do solo (HALFFTER e MATTHEWS, 1966), ciclagem de nutrientes (NEALIS, 1977) e dispersão secundária de sementes defecadas por vertebrados frugívoros (ANDRESEN, 2001). Fatores como o tipo de solo (JANZEN, 1983; NEALIS, 1977), variáveis microclimáticas (OSBERG et al., 1994), abundância de fontes de alimento (ESTRADA et al., 1999; ESCOBAR, 2000) e cobertura vegetacional (DAVIS, 1994; ESCOBAR, 1997, 2000; FILGUEIRAS et al., 2011; HALFFTER e ARELLANO, 2002; HILL, 1996), influenciam as comunidades desses besouros. Nos trópicos, os besouros escarabeíneos são estenotípicos em relação à vegetação, já que associada com a cobertura vegetal está uma assembléia de fatores que promove oscilações na umidade e temperatura, incluindo a temperatura da superfície do solo, e direção de insolação (HALFFTER, 1991). Além disso, mudanças na cobertura vegetacional podem alterar populações de vertebrados e, assim influenciar as comunidades de besouros escarabeíneos (CULOT et al., 2013; DOUBE, 1983; HOWDEN e NEALIS, 1975; NEALIS, 1977; NICHOLS et al., 2009;).

A influência da modificação de habitat sobre as borboletas frugívoras tem sido documentada na literatura com diferentes respostas. De acordo com a Teoria de Biogeografia de Ilhas (TBI), BENEDICK et al., (2006) encontraram em Borneo que a riqueza e a diversidade de borboletas frugívoras são positivamente influenciadas pelo tamanho das áreas florestais e negativamente relacionadas com o isolamento das áreas presentes. A influência da área dos fragmentos sobre a riqueza de espécies também foi identificada em outras áreas da Indonésia, enquanto o isolamento entre as áreas florestais não teve efeito significativo sobre as borboletas (VEDDELER et al., 2005). Por outro lado, SHAHABUDDIN e TERBORGH (1999) encontraram na Venezuela que a distância de isolamento tem um papel decisivo na diversidade de borboletas frugívoras, enquanto a área dos fragmentos não teve efeito sobre a mesma. Ao comparar duas paisagens, uma contínua e outra adjacente fragmentada na Floresta Atlântica do Sudeste brasileiro, UEHARA-PRADO et al. (2007) viram que essas paisagens são similares em termos de riqueza de espécies, mas apresentam composição de espécies diferentes. Além dessas diferentes respostas em relação à perda e fragmentação de habitat, alguns estudos apontam que florestas secundárias podem apresentar maior (BOBO et al., 2006; RAMOS et al., 2000) ou menor (VEDDELER et al., 2005) diversidade e riqueza de borboletas frugívoras do que florestas primárias. Contudo, segundo BARLOW et al. (2007), essas diferentes respostas devem-se principalmente à falta de replicação sazonal e ao tamanho amostral empregado nesses estudos.

Essas incertezas quanto à resposta da biodiversidade às mudanças de habitat têm desafiado os ecólogos a planejarem e executarem estratégias de conservação nas paisagens modificadas pelo homem. Além da restrição dos estudos a poucas espécies, em geral, apenas um grupo taxonômico, e erros de amostragem e no levantamento de dados, outros fatores contribuem para tais incertezas. O fato da mudança de habitat afetar cada grupo taxonômico de maneira peculiar, com cada táxon apresentando respostas comportamentais, reprodutivas e ecológicas distintas pode mascarar determinada resposta (GARDNER et al., 2009). O contexto paisagem é outro fator determinante nessas incertezas. A escala espacial e a falta de dependência de padrões que ocorrem muitas vezes sinergicamente dificultam o entendimento das respostas da biodiversidade às alterações ambientais (GARDNER et al., 2009). Adicionalmente, para o conhecimento real de como a modificação de habitat altera a composição das espécies florestais, faz-se necessária uma comparação das áreas alteradas com a floresta intacta (primária), o que pode remeter ao erro da extrapolação, uma vez que em determinadas áreas com ausência de florestas conservadas, faz-se impossível tal comparação. Nesse caso, apenas florestas secundárias com diferentes estados de conservação podem vir a ser comparadas, o que pode gerar inferências errôneas, pois florestas primárias e secundárias são obviamente áreas florestais distintas com, portanto, padrões e processos agindo de maneira diferente sobre elas.

Nesse contexto, há uma grande discussão sobre a importância dos remanescentes florestais secundários e florestas primárias na persistência de espécies tropicais. Estudos de habitats dominados por borda, como os pequenos fragmentos florestais remanescentes nos trópicos, fornecem respostas divergentes sobre a persistência de espécies florestais (MELO et al., 2013). Mais de 80% dos remanescentes florestais situados na Floresta Atlântica são menores que 50 ha e aproximadamente metade da floresta existente está a menos de 100 m de uma área antropizada (RIBEIRO et al., 2009). Sendo assim, conhecer como as espécies de besouros escarabeíneos e borboletas frugívoras respondem a diferentes estados ambientais, ressaltando as respostas desses grupos em habitats afetados por borda, pode fornecer subsídios para ações contundentes de conservação para essas espécies e garantir suas funções ecológicas nas paisagens modificadas pelo homem da Floresta Atlântica. Estudos que elucidem como a biodiversidade está respondendo a mudança de habitat podem estabelecer diretrizes para conservação das espécies florestais presentes na Floresta Atlântica.

2. OBJETIVOS

O objetivo geral da presente tese é compreender como os besouros escarabeíneos e as borboletas frugívoras respondem a modificação de habitat em uma paisagem modificada pelo homem na Floresta Atlântica. Com a expansão das atividades humanas sobre os ambientes florestais, tendo como força motriz a fragmentação e a perda de habitat, há um incremento de habitats afetados por borda. Assim, deseja-se verificar o papel desses habitats na retenção da biodiversidade. Partindo dessa premissa, espera-se que os habitats afetados por borda apresentem uma menor diversidade de espécies assim como uma simplificação na composição dessas, levando à homogeneização das assembléias desses grupos analizados. Nesse contexto de múltiplas respostas dos besouros escarabeíneos e borboletas frugívoras com relação às estruturas e modificações de habitat, o presente estudo apresenta-se dividido em três capítulos com seus respectivos objetivos: no primeiro, ñPersistência de besouros escarabeíneos em paisagens modificadas pelo homem: combinando espécies indicadoras com o uso antropogênico da terra e efeitos relacionados à fragmentaçãoò, foram mensuradas as respostas de besouros escarabeíneos à modificação de habitat (ou seja, uso da terra e efeitos relacionados à fragmentação de habitat), analisando-se a existência ou não de espécies indicadoras das alterações ambientais em habitats dominados por borda. Espera-se que haja distinção na riqueza de espécies, abundância e biomassa entre os habitats, cada qual com espécies indicadoras. Adicionalmente, espera-se que distâncias mais afastadas das áreas abertas (matrizes de não habitat) retenham mais espécies de besouros escarabeíneos do que distâncias mais próximas. No segundo, ñ*Turnover* espacial das assembléias de besouros escarabeíneos neotropicais em habitats dominados por borda: implicações para conservação em paisagens modificadas pelo homemò, foi investigado como os habitats dominados por borda influenciam o *turnover e* o padrão de aninhamento espacial dos besouros escarabeíneos, avaliando-se se os efeitos relacionados a fragmentação tendem a homogenizar ou diferenciar as assembléias desses besouros. Espera-se que, ou os habitats afetados por borda apresentem baixo *turnover* contribuindo para a homogeneização das assembléias de besouros escarabeíneos, ou que os mesmos incrementem o *turnover* contribuindo para a diferenciação dos mesmos. No terceiro e último, ñO valor dos habitats dominados por borda para a persistência de borboletas frugívoras em uma paisagem modificada pelo homem da Floresta Atlânticaò, verifica-se se há um efeito cascata da fragmentação de habitat, testando se as mudanças nas assembléias de árvores nos habitats dominados por borda são refletidas pelas comunidades de borboletas frugívoras. Espera-se que a convergência existente em termos de assembléias de árvores entre as bordas e os pequenos fragmentos florestais também ocorra para as borboletas frugívoras. Dessa forma, habitats com alta proporção de árvores pioneiras e simplificação da estratificação vertical estariam afetando a riqueza, a abundância e a composição de espécies de borboletas frugívoras nesses habitats afetados por borda.

3. REVISÃO BIBLIOGRÁFICA

3.1. FRAGMENTAÇAO DE HABITAT E PAISAGENS MODIFICADAS PELO HOMEM

A fragmentação de uma paisagem pode ocorrer naturalmente ou ter origem em atividades antrópicas (LAURANCE, 2008; OLIFIERS e CERQUEIRA, 2006), sendo essas as principais ameaças atuais à biodiversidade global (LAURANCE e BIERREGAARD, 1997). A fragmentação reduz a diversidade de espécies de muitos taxa (EWERS e DIDHAM, 2006; KLEIN, 1989; LAURANCE et al., 2002; LOVEJOY et al., 1986; MARSH e PEARMAN, 1997; STOUFFER e BIERREGAARD, 2005) e altera processos ecológicos como a herbivoria (WIRTH et al., 2008), a polinização (GHAZOUL, 2005; KWAK et al., 1998) e a dispersão de sementes (ANDRESEN, 2003; GHAZOUL, 2005).

O processo de fragmentação de habitats leva a mudanças significativas na configuração da paisagem (AWADE e METZGER, 2008). O efeito mais imediato do processo de fragmentação é a subdivisão do habitat original. Subsequentemente pode ocorrer uma diminuição adicional do tamanho dos habitats e o aumento do isolamento entre os habitats remanescentes. Com a progressiva fragmentação da paisagem, um grande número de fragmentos de variados tamanhos e formas são criados (FAHRIG, 2003).

Como resultado da supressão vegetal e subdivisão da floresta continua (fragmentação), manchas de habitat em regeneração ou florestas secundárias são características de paisagens modificadas pelo homem representando em termos globais 50% dos remanescentes florestais (WRIGHT, 2010). Alguns estudos identificaram porções significativas da biota original nesses habitats (SODHI et al., 2010), enquanto outros argumentam que essa áreas retêm assembléias empobrecidas da biota local (GIBSON et al., 2011). Devido às diferentes respostas da biota as paisagens antrópicas, MELO et al., (2013) descreveram modelos conceituais retratando as possíveis trajetórias das paisagens tropicais que podem favorecer ou não a persistência de espécies florestais. Inicialmente com o desmatamento as *paisagens naturais* passam a ser utilizadas pelo homem, sendo chamadas de *paisagens de conservação*, as quais ainda retêm setores de crescimento tardio da floresta e baixa proporção de áreas afetadas por borda, bem como há manejo do solo e o desmatamento foi interrompido. Com a futura fragmentação e perda de habitat essas paisagens movem-se para o conceito de *paisagens funcionais*, onde há setores florestais com idade intermediária -florestas secundárias (apresentando elevada proporção de cobertura vegetacional), e proteção dessas áreas. Essas paisagens são consideradas *amigas da biodiversidade*, uma vez que espécies florestais persistem assim como os serviços ecológicos. Todavia, essas *paisagens funcionais* podem tomar rumos diferentes. Primeiro, caso o abandono da terra ocorra concomitante com a proteção das áreas florestais, grandes blocos de floresta em regeneração podem retornar a ser *paisagens de conservação*. No sentido oposto, com o aumento do uso da terra e mais perda de habitat, tende a se formar *paisagens degradadas*, formadas por pequenos fragmentos florestais com elevada proporção de habitats afetados por borda e baixa conectividade entre os mesmos, levando a uma baixa diversidade e colapso nos serviços ecossistêmicos (MELO et al., 2013). Essas diferentes formas de paisagens torna importante compreender a resposta de espécies à modificação de habitat visando um plano de conservação e manejo para essas áreas.

3.2. EFEITO DE BORDA E MATRIZ CIRCUNDANTE

Uma consequência inevitável da fragmentação é o drástico aumento de habitats de borda. A variabilidade nos efeitos da fragmentação deve-se, principalmente, ao efeito de borda (FAHRIG, 2003). Na medida em que os fragmentos se tornam menores e com forma mais irregular, eles passam a ser crescentemente dominados por habitats de borda (SAUNDERS et al., 1991). A transição entre o fragmento florestal e o ecossistema adjacente é muito abrupta, criando uma borda que expõe a floresta às condições encontradas na matriz (YOUNG e MITCHEL, 1994). Como as paisagens são tidas como fragmentos de habitat e não-habitat (METZGER, 1999), os efeitos de borda vêm sendo conceituados como alterações nas condições ecológicas resultantes da interação entre habitat e não-habitat. Esse efeito refere-se a mudanças bióticas e abióticas resultantes das disparidades abióticas relacionadas ao ecótono que se forma entre o fragmento e seu entorno (LOVEJOY et al., 1986; MURCIA, 1995). O efeito de borda pode ser compreendido por meio de dois componentes: magnitude e extensão. O primeiro remete à diferença entre os valores máximos e mínimos de uma dada característica ecológica os quais são mensurados em zonas de transição, enquanto o segundo refere-se à distância na qual as mudanças nas características mensuradas são detectadas (EWERS e DIDHAM, 2006). Dessa forma, para inferir plausivamente o efeito de borda, torna-se imprescindível mensurar ambos os lados da área transicional (EWERS e DIDHAM, 2006).

Com a formação de bordas, tem-se um aumento da incidência de luz, temperatura e diminuição na umidade relativa (MURCIA, 1995; TABARELLI et al., 2008; TURNER, 1996). Essas condições, por sua vez, levam à mortalidade de árvores tolerantes à sombra e ao aumento no recrutamento de espécies pioneiras (LAURENCE et al. 1998). Além disso, o aumento da relação perímetro/superfície causado pelo processo da fragmentação florestal incrementa a penetração de espécies exóticas encontradas nos habitats periféricos, podendo representar uma ameaça às espécies locais (TURNER, 1996).

Assim como os efeitos da formação de borda, a matriz circundante também exerce influência sobre a dinâmica do fragmento (GASCON et al., 1999). Essa influência inclui a interação da paisagem num nível mais amplo de configuração do habitat (FAHRIG e MERRIAM, 1994). A persistência de determinadas espécies em áreas fragmentadas pode estar relacionada com a capacidade de dispersão através da matriz (LAURANCE e BIERREGAARD, 1997). A natureza da matriz pode modificar a probabilidade de ocorrência de dispersão entre os fragmentos e entre esses e outras fontes colonizadoras (FAHRIG e MERRIAM, 1994). A vegetação que circunda o fragmento, favorecendo essa conectividade, é de extrema importância para a sobrevivência de uma metapopulação em habitats fragmentados (METZGER e DECAMPS, 1997). Assim, fatores como a natureza do entorno e as alterações abióticas da paisagem decorrentes do processo de fragmentação influenciam e determinam a composição de espécies em paisagens fragmentadas (FAHRIG e MERRIAM, 1994).

Como a perda e a fragmentação de habitat alteram drasticamente a diversidade biológica (EWERS e DIDHAM, 2006; FAHRIG, 2003; LAURANCE, 2001), entender como esses processos afetam a biota das florestas tropicais é de fundamental importância para a permanência dessas florestas (LAURANCE e BIERREGAARD, 1997; TABARELLI et al., 1999). Por outro lado, o efeito de borda é camuflado em vários estudos pelo efeito da perda de área (FLETCHER et al., 2007). Com base na resposta de aves de sub-bosque, BANKS-LEITE et al., (2010) viram que comparando-se fragmentos florestais na Floresta Atlântica e uma floresta primária na Amazônia a resposta das aves ao efeito de borda foi semelhante. Todavia, fixando-se o efeito de borda, a área dos fragmentos deixou de ser uma variável importante (BANKS-LEITE et al., 2010). Isso demonstra a necessidade de entender a dinâmica biológica em domínios extremamente alterados, onde há predomínio de habitats afetados por borda nos segmentos florestais, como a Floresta Atlântica, onde a maior parte dos fragmentos é menor que 50 ha e estão próximos a áres abertas (RIBEIRO et al. 2009).

3.3. FLORESTA ATLÂNTICA ï CENTRO DE ENDEMISMO PERNAMBUCO

No vasto conjunto do território intertropical e subtropical brasileiro destaca-se o contínuo norte-sul das Florestas Atlânticas, na categoria de segundo grande complexo de florestas tropicais biodiversas brasileiras, que outrora estendia-se ao longo da costa brasileira, penetrando até o leste do Paraguai e nordeste da Argentina em sua porção sul (ABôSÁBER, 2005; GALINDO-LEAL e CÂMARA, 2003). Estimativas referem-se a 1,36 milhões de km² de floresta distribuídos ao longo de 28 graus de latitude (CONSERVATION INTERNATIONAL et al., 2000). A Floresta Atlântica é uma das 35 prioridades para a conservação da diversidade biológica mundial, sendo um ñhotspotò da biodiversidade (TABARELLI et al., 2005) que, segundo MYERS et al. (2000), denotam regiões que possuem uma alta diversidade e grande taxa de endemismo de espécies, associados a uma alta incidência de perda de habitats.

Embora tenha sido em grande parte destruída, pois já perdeu 87% de sua área (RIBEIRO et al., 2009), a Floresta Atlântica ainda abriga 8.567 espécies endêmicas entre 21.361 espécies de plantas vasculares, anfíbios, répteis, aves e mamíferos (MYERS et al., 2000). Parte desse endemismo está restrita a um bloco de florestas úmidas e semidecíduas no extremo norte da costa Atlântica brasileira ï o Centro de Endemismo Pernambuco (sensu PRANCE, 1982) ou Floresta Atlântica nordestina (sensu SILVA e TABARELLI, 2000).

O Centro de Endemismo Pernambuco (CEP), localizado entre os paralelos 5°00ô e 10°30ô sul e meridianos 34°50ô e 37°12ô oeste, corresponde ao segmento sob o Domínio da Floresta Atlântica que se inicia ao norte do Rio Grande do Norte e se estende ao longo da costa brasileira até o sul do estado de Alagoas às margens do Rio São Francisco (SILVA e CASTELETI, 2003). Biogeograficamente, esta região é também importante para a compreensão da evolução das biotas Amazônica e Atlântica, pois foi através do CEP que as trocas bióticas entre as duas grandes regiões de florestas sul-americanas ocorreram durante o Cenozóico (Prance, 1982). No CEP, podem ser observados cinco tipos de vegetação: floresta ombrófila aberta, floresta ombrófila densa, áreas de tensão ecológica, floresta estacional semidecidual e formações pioneiras, fisionomias que cobriam originalmente uma área equivalente a 56.400 km² (COIMBRA-FILHO e CÂMARA, 1996). Comparado com outros setores da Floresta Atlântica, o CEP é o mais desmatado, o mais desconhecido e o menos protegido (COIMBRA-FILHO e CÂMARA, 1996; SILVA e TABARELLI 2001). De acordo com RANTA et al., (1998), grande parte do que restou desta floresta (entre 2-7%) é composta por arquipélagos de fragmentos florestais; a maioria deles menores que 10 ha e totalmente circundados por cana-de-açúcar. De acordo com Silva e Tabarelli (2000), aproximadamente 49% da flora de plantas lenhosas desta floresta pode se extinguir no nível regional, consequência da interrupção do processo de dispersão de seus diásporos. Tal interrupção está associada ao desaparecimento de vertebrados frugívoros, consequência direta da fragmentação, da perda de hábitat e da caça (SILVA e TABARELLI, 2000).

Mesmo com essa constante degradação, o CEP comporta 1.213 espécies vegetais entre árvores e arbustos, ou seja, 6% de todas as espécies de vegetais superiores encontradas na Floresta Atlântica brasileira (TABARELLI e SANTOS, 2005). Apesar da sua diversidade, o CEP é o setor da Floresta Atlântica com menor número de unidades de conservação (MACHADO et al., 1998, UCHÔA NETO, 2002). Além de serem poucas e pequenas, as unidades de conservação do CEP não estão devidamente implantadas (UCHÔA NETO, 2002). Para se evitar mais desmatamentos e perda massiva de espécies na Floresta Atlântica, o desafio consiste na integração dos diversos instrumentos regulatórios, políticas públicas e novas oportunidades e mecanismos de incentivo para a proteção e restauração florestal, em uma única e abrangente estratégia para o estabelecimento de redes de paisagens sustentáveis ao longo da região (TABARELLI et al., 2005). Além da criação de unidades de conservação, a implementação de corredores de biodiversidade pode facilitar a viabilização dessa rede de paisagens sustentáveis (SANTOS et al., 2008). A conectividade de fragmentos em uma paisagem fragmentada através da implementação de corredores de fauna e flora pode favorecer a diversidade biológica local reduzindo a taxa de extinção de espécies (SOULÉ e TERBORGH, 1999). Os corredores conectam populações de fragmentos separados, permitindo o aumento da população viável e o aumento do fluxo gênico (FONSECA et al., 2004). SOULÉ e TERBORGH (1999) defendem não só fragmentos conectados, mas também paisagens conectadas dentro de diferentes regiões. Essa conectividade de paisagens pode ser um processo chave para a manutenção de populações em paisagens fragmentadas (FAHRIG, 2003; EWERS e DIDHAM, 2006).

3.4. INDICADORES AMBIENTAIS

Devido à escassez de tempo, dinheiro e disponibilidade de taxonomistas para levantamentos completos de todos os grupos de organismos, vários tipos de inventários rápidos têm sido desenvolvidos e implementados. Uma abordagem utilizada para maximizar e qualificar inventários é enfocar os levantamentos em certos grupos taxonômicos, referidos como indicadores biológicos ou bioindicadores. Na sua revisão sobre o assunto, MCGEOCH (1998) define indicador biológico como uma espécie, ou grupo de espécies, que apresenta alguma das seguintes características: (1) indica o estado biótico ou abiótico de um ambiente (indicador ambiental); (2) representa o impacto da mudança ambiental em um habitat, comunidade ou ecossistema (indicador ecológico); (3) indica a diversidade de um subconjunto taxonômico, ou de toda a diversidade, dentro de uma área (indicador de biodiversidade).

O desenvolvimento da bioindicação inicialmente se deu em ambientes aquáticos e a sua aplicação a ecossistemas terrestres ganhou força apenas a partir da década de 80 (MCGEOCH, 1998). Desde então, diversos critérios foram propostos para a escolha de indicadores biológicos adequados aos sistemas terrestres (BROWN, 1991; 1997; DALE e BEYELER, 2001). Alguns desses critérios são:

1 ï Taxonomia relativamente bem resolvida ï grupos com problemas taxonômicos fornecem informação de baixa qualidade, devido à dificuldade ou impossibilidade de definição dos limites entre as espécies;

2 ï Conhecimento a respeito da história natural, genética, química e outros aspectos da biologia ï ajudam a definir as preferências e associações de habitat e recursos das espécies;

3 ï Diversidade conveniente ï um número de espécies muito alto pode inviabilizar o processo de triagem e análise, e um número muito baixo (por exemplo, menos de cinco) pode comprometer a qualidade dos dados e dificultar as previsões;

4 ï Ciclo de vida curto ï em teoria, quanto menor o tempo de geração, mais rapidamente os efeitos da alteração ambiental são percebidos;

5 ï Diversidade ecológica ï um grupo que tenha espécies com diferentes associações ecológicas fornece informações sobre diferentes compartimentos do habitat;

6 ï Fidelidade de habitat ï espécies com pouca fidelidade de habitat não fornecem informação específica;

7 ï Associação estreita a recursos ou outras espécies ï não é essencial, mas espécies estreitamente relacionadas a outras são mais informativas (representam outro grupo taxonômico ou recurso);

8 ï ñSedentarismoò relativo ï num extremo, espécies migratórias ou muito dispersivas podem estar presentes em um ambiente sem relação nenhuma com as condições ambientais do mesmo;

9 ï Facilidade na amostragem, triagem e identificação;

10 ï Pouco uso humano ï grupos cujas espécies tem valor econômico alto (por exemplo caçadas para consumo e/ou ornamentação) podem desaparecer do sistema independente do seu estado de conservação.

De acordo com esses critérios, vários grupos tidos como ñcarismáticosò, como primatas e aves, por exemplo, são indicadores pouco confiáveis, geralmente pouco diversos em comparação com muitos grupos de invertebrados e sujeitos a influências adicionais externas à qualidade do sistema, isto é, a ausência de certas espécies sensíveis à alteração ambiental pode estar mais relacionada à eliminação por caça do que à falta de condições mínimas para a manutenção de populações viáveis das mesmas, e devem ser utilizados com extremo cuidado, em situações particulares (BROWN, 1997).

Em países de clima temperado, diversos invertebrados, particularmente insetos, vêm sendo usados com sucesso em estudos de bioindicação em ambientes terrestres. Nos trópicos, onde a diversidade desses grupos é muito alta e a taxonomia da maioria deles incipiente, o desenvolvimento da bioindicação ainda é embrionário para muitos grupos. Dentre alguns taxa que têm sido usados com sucesso podem ser destacados muitos insetos, entre eles libélulas, borboletas, formigas, abelhas e algumas famílias de besouros (BROWN, 1991; BROWN e FREITAS, 2000a, b, 2003; FREITAS et al., 2003, 2006). No Brasil, apesar de alguns trabalhos iniciais já terem identificado formigas, borboletas e besouros como indicadores ambientais e de diversidade (BROWN, 1991; BROWN e FREITAS, 2000a, b, 2003, 2006; IANNUZZI et al., 2003; LEAL, 2003), essa abordagem ainda não tem sido aplicada nos planos de conservação. Por exemplo, a identificação de áreas prioritárias da Floresta Atlântica nordestina foi feita quase que exclusivamente com dados de vertebrados (CONSERVAÇÃO INTERNACIONAL DO BRASIL et al., 2000).

Com o aumento de paisagens modificadas pelo homem em detrimento dos habitats antes naturais, determinados grupos de organismos permanecem nas paisagens alteradas (resilientes) aumentando suas populações e tornando-se dominantes (vencedores), enquanto as espécies nativas não toleram os distúrbios provocados pelo homem (perdedores) (TABARELLI et al., 2012). Grandes mamíferos (BENCHIMOL e PERES, 2013), árvores tolerantes à sombra (TABARELLI et al., 2012) e besouros escarabeíneos especializados (NICHOLS et al., 2009) são exemplos de grupos considerados perdedores. Enquanto besouros escarabeíneos pouco especializados (NICHOLS et al., 2009), árvores pioneiras (TABARELLI et al., 2012) e espécies arbóreas exóticas em geral (SOHDI et al., 2008) são considerados vencedores. Sendo assim, compreender como grupos ecologicamente importantes de insetos ï no caso borboletas frugívoras e besouros escarabeíneos ï que respondem ao processo de perda, fragmentação e mudança de habitat (NICHOLS et al., 2007; UEHARA-PRADO et al., 2007) e cujas respostas podem ser usadas para indicar áreas relevantes para a conservação da biota da Floresta Atlântica nordestina, torna-se útil para futuros diagnósticos e monitoramentos ambientais nessas áreas.

3.6. BESOUROS ESCARABEÍNEOS: COLEOPTERA (SCARABAEIDAE: SCARABAEINAE) COMO INDICADORES AMBIENTAIS

Os coleópteros pertencentes à subfamília Scarabaeinae são vulgarmente chamados de ñrola-bostaò e são considerados cosmopolitas, sendo em geral encontrados em locais com precipitação e temperatura mínima anual de 250 mm e 15ºC, respectivamente (HALFFTER e MATTHEWS, 1966). Os besouros escarabeíneos realizam funções ecológicas importantes para o meio em que vivem (NICHOLS et al., 2008). A ciclagem eficiente e rápida de nutrientes com o processamento da matéria orgânica com sua disponibilização para o meio (BORNEMISSA e WILLIAMS, 1970; HALFFTER e MATTHEWS, 1966; NEALIS, 1977); a dispersão secundária de sementes de muitas espécies de árvores nas florestas neotropicais, sendo importantes no processo natural de regeneração da floresta (ESTRADA e COATES-ESTRADA, 1991) e no controle de possíveis vetores de parasitos e enfermidades (CAMBEFORT e HANSKI, 1991; ESTRADA e COATES-ESTRADA, 1991).

A oferta de alimento, bem como as características ecológicas do ambiente (tipo de bioma, composição de solo, insolação) determina a distribuição dos besouros escarabeíneos (CAMBEFORT e HANSKI, 1991; SPECTOR, 2006). Em relação ao hábito alimentar, pode-se dividir as espécies dessa subfamília nas seguintes dietas: (a) saprófagas, que se alimentam de frutos, matéria vegetal e fungos em decomposição; (b) necrófagas, que se utilizam de carcaças de animais frescas ou em decomposição; (c) coprófagas, que se alimentam de fezes; (d) generalistas, que usam combinações alimentares, podendo ser: copro-necrófagas, copro-saprófagas, copro-necro-saprófagas, (HALFFTER e MATTHEWS, 1966; HALFFTER et al., 1992). Entretanto, grupos primitivos desses besouros não possuíam tanta variedade em relação a seus hábitos alimentares. Esses grupos utilizavam raízes vivas, vegetais mortos e fungos em decomposição como recursos alimentar. Desse último grupo de saprófagos é que derivam os Scarabaeidae coprófagos: Aphodinae, Geotrupinae e Scarabaeinae. Os besouros escarabeíneos saprófagos e necrófagos atuais derivam de uma linhagem ancestral de coprófagos (HALFFTER e MATTHEWS, 1966). A presença de excrementos em abundância, resultado do aparecimento dos grandes vertebrados terrestres no Mesozóico, forneceu subsídios para a coprofagia. O excremento estava ao alcance dos besouros, sendo troficamente aceitável devido a sua similaridade com a matéria vegetal em decomposição, porém, estava exposto às intempéries ambientais. Dessa forma, para resolver esse problema, o excremento poderia ser comido *in situ* pela larva, ou os besouros poderiam também transportar esse recurso enterrando-o no solo ou conduzindo-o até uma sombra para que não viesse a ressecar (HALFFTER e MATTHEWS, 1966).

A maioria das espécies de besouros escarabeíneos (tanto no estágio larval como no adulto) utiliza excrementos, principalmente de grandes mamíferos, como recurso alimentar. Esses excrementos contêm resíduos que não foram digeridos, produtos de secreção e excreção, bactérias, leveduras, entre outros. Dentre os excrementos, as fezes humanas e as de bovídeos são as mais utilizadas pelos escarabeíneos na sua alimentação. Nas grandes savanas africanas, por exemplo, devido ao grande número de mamíferos herbívoros, a abundância de besouros coprófagos é expressiva (HALFFTER e MATTHEWS, 1966). Nesses locais, onde há elevado número de grandes mamíferos, podem ocorrer espécies de escarabeíneos tidas como estenofágicas, ou seja, que são atraídas somente por fezes de uma espécie de mamífero em particular (HALFFTER e MATTHEWS, 1966). Nas florestas tropicais, a falta de uma fauna numerosa de mamíferos herbívoros fez com que os besouros sofressem uma evolução paralela, tendo como resultado dessa pressão seletiva novas especializações tróficas, como é o caso da saprofagia secundária e da necrofagia (HALFFTER e MATTHEWS, 1966).

A alimentação e a reprodução, uma vez que os Scarabaeinae utilizam o recurso que se alimentam também para nidificar, estão relacionadas com o transporte de uma parte do recurso alimentar para um local distante da fonte original, o que evita a pressão de competição com outros grupos de detritívoros, como dípteros e mamíferos (CAMBEFORT e HANSKI, 1991), além de proteger a comida contra condições adversas do meio, como excessivo calor e seca (SCHEFFLER, 2002). Dessa forma, desenvolveram-se estratégias de alocação de recurso relacionadas a características morfológicas, comportamentais e necessidades ecológicas próprias.

Os Scarabaeinae são divididos de acordo com a forma de alocação de recurso em três grupos: os roladores (telecoprídeos), os escavadores (paracoprídeos) e os residentes (endocoprídeos). As espécies roladoras apresentam tíbias posteriores com um formato curvo e alongado, o que facilita a rolagem do recurso, podendo esse ser deslocado do local de origem de 5 a 18 metros (HANSKI e CAMBEFORT, 1991). Os escavadores apresentam tíbias anteriores bem desenvolvidas, o que facilita a escavação, sendo o túnel construído antes do alimento ser levado para baixo (HALFFTER e MATTHEWS, 1966). As espécies escavadoras da América do Sul pertencem às tribos Dichotomiini, Phanaeini e Onthophagini (HANSKI e CAMBEFORT, 1991). Os residentes, por sua vez, permanecem na localização do recurso, não o relocando dentro do habitat, tendo um desenvolvimento exagerado das pernas médias. É representativa dessa guilda na América do Sul a tribo Euristernini (HANSKI e CAMBEFORT, 1991).

Fatores referentes ao ambiente, como a cobertura vegetacional, também estão relacionados com a distribuição de Scarabaeinae. Nos trópicos, os escarabeíneos são estenotípicos em relação à vegetação, já que, associada com a cobertura vegetacional, está um conjunto de fatores que promove oscilações na umidade e temperatura, incluindo a temperatura da superfície do solo, e direção de insolação (HALFFTER, 1991). Dessa forma, há espécies exclusivas de ambientes abertos e espécies que nunca se afastam de coberturas vegetais (HOWDEN e NEALIS, 1975; NEALIS, 1977). Além dessas especificidades de ambiente e condições físicas do meio, o fato de responderem à destruição, fragmentação e isolamento de florestas tropicais (HALFFTER et al., 1992; KLEIN, 1989; FILGUEIRAS et al., 2011), processos que representam uma barreira para o movimento e dispersão de espécies (KLEIN, 1989), os besouros escarabeíneos são considerados bons indicadores ambientais nos trópicos.

Na maioria dos estudos relacionando a fragmentação de habitat e paisagens modificadas pelo homem aos besouros escarabeíneos, a riqueza e a abundância desses besouros variaram drasticamente em fragmentos pequenos, isolados bem como em áreas alteradas (e.g. pastagens, plantações), embora, nesse caso, a resposta dos besouros dependa da natureza da matriz (BARNES et al., 2014; FILGUEIRAS et al., 2011; KLEIN, 1989). Estudos diretos sobre a resposta dos besouros escarabeíneos ao efeito de borda são escassos. SPECTOR e AYZAMA (2003) realizaram um estudo na Bolívia verificando a resposta desses besouros a um ecótone, os quais detectaram um declínio na abundância e riqueza de besouros escarabeíneos da floresta para a savana. Na Floresta Atlântica Argentina, PEYRAS et al. (2013), compararam como diferentes tipos de ecótones floresta-plantações em gradientes de distâncias afetam os besouros escarabeíneos, encontrando que a resposta depende do grau de especialização das espécies e da dissimilaridade dos habitats.

Por outro lado, estudos sobre como os besouros escarabeíneos respondem a diferentes habitats antropizados são intensificadamente contemplados. Plantações de eucalipto (GARDNER et al., 2008; GRIES et al., 2011), pastos (LOPES et al., 2011; LOUZADA e CARVALHO E SILVA, 2009), e agroflorestas (NEITA e ESCOBAR, 2012) são exemplos de áreas antropizadas exploradas por besouros escarabeíneos florestais. Todavia, não se conhece como uma matriz de cana-de-açúcar adjacente a áreas florestais pode influenciar esses besouros. Em estudo realizado em Uganda, NYEKO (2009) encontrou comunidades de besouros escarabeíneos similares entre fragmentos florestais imersos em matrizes de cana-de-açúcar, sugerindo uma possível permeabilidade dessas plantações para as espécies florestais.

Em revisão liderada por NICHOLS et al. (2007), os autores realizaram meta-análise e afirmaram que áreas florestais modificadas podem reter diversidade de besouros escarabeíneos similar a florestas intactas. Contudo, estudos realizados na Amazônia apontam as florestas primárias como áreas de elevada diversidade de besouros escarabeíneos em comparação com áreas de crescimento secundário ou paisagens modificadas, como pastagens e plantações (GARDNER et al., 2008). Na Floresta Atlântica presente em Alagoas, FILGUEIRAS et al., (2011) demonstraram que fragmentos pequenos e isolados com elevada proporção de árvores pioneiras e baixa riqueza de árvores, apresentam assembléias de besouros escarabeíneos drasticamente empobrecidas. Em outro setor da Floresta Atlântica situada no Sul da Bahia, AUDINO et al., (2014) viram que áreas em recuperação e pastagens não apresentam diversidade de besouros escarabeíneos similares a floresta intacta. Diferentes contextos biogeográficos, problemas com amostragem e a qualidade da paisagem são os fatores que podem ajudar a explicar as diferentes respostas dos besouros escarabeíneos às mudanças de habitat (GARDNER et al., 2008).

3.7. BORBOLETAS FRUGÍVORAS (NYMPHALIDAE) COMO INDICADORES AMBIENTAIS

Em torno de 90% das espécies de borboletas são encontradas nos trópicos (BONEBRAKE et al., 2010). Na Região Neotropical as borboletas somam quase 8.000 espécies (LAMAS, 2004), ocorrendo cerca de 3.280 no Brasil e 2.200 espécies na Floresta Atlântica (BROWN e FREITAS, 1999). As borboletas divididem-se em duas superfamílias, sendo representadas por seis famílias, Hesperioidea (Hesperiidae) e Papilionoidea

(Papilionidae, Pieridae, Nymphalidae, Lycaenidae e Riodinidae). As famílias Hesperiidae, Nymphalidae e Riodinidae são as três famílias mais representativas no Brasil, seguidas por Lycaenidae, Pieridae e Papilionidae (BROWN e FREITAS, 1999).

A fase adulta possui hábito alimentar diferente do seu estágio juvenil. Enquanto as lagartas são fitófagas, alimentando-se de material vegetal, sendo assim comumente encontradas em suas plantas hospedeiras, os adultos alimentam-se sugando líquidos. As borboletas podem ser separadas em duas guildas, quando considerado o modo de alimentação dos adultos (DEVRIES, 1987): (1) as nectarívoras, que se alimentam de néctar durante a sua vida adulta, compreendendo as espécies das famílias Papilionidae, Pieridae, Lycaenidae, Riodinidae e Hesperiidae e alguns grupos de Nymphalidae; (2) as frugívoras, que incluem as espécies que se alimentam de frutas fermentadas, pertencentes a quatro subfamílias de Nymphalidae: Biblidinae, Charaxinae, Satyrinae e pela tripo Coeini de Nymphalinae (WAHLBERG et al., 2009). Borboletas frugívoras também podem se alimentar de fezes de vertebrados e seiva secretada por algumas espécies de plantas e carniça (DEVRIES, 1987).

A amostragem de borboletas frugívoras apresenta algumas vantagens práticas, que facilitam o estudo de suas populações. Elas são facilmente capturadas em armadilhas contendo isca de fruta fermentada, de modo que a amostragem pode ser simultânea e o esforço pode ser padronizado em diferentes áreas e meses do ano (DEVRIES, 1987). Os indivíduos podem ser marcados e soltos depois de identificados, com um mínimo de manuseio, permitindo que um estudo não destrutivo seja efetuado com confiança. Ademais, a atração da borboleta pela isca, um recurso alimentar, reduz a possibilidade de capturas ao acaso, presentes em outros métodos (FREITAS et al. 2003, UEHARA-PRADO et al., 2007).

Do mesmo modo, por apresentarem uma amostragem prática e responderem a perturbações ambientais, as borboletas frugívoras são consideradas bioindicadoras (BROWN, 1997; DE VRIES, 1987; UEHARA-PRADO et al., 2009). Essa guilda de borboletas tem sido amplamente utilizada em estudos que avaliam a distribuição de espécies e indivíduos em paisagens com diferentes graus de perturbação, principalmente em ambientes florestais na América do Sul (BROWN 1991, 1997; BROWN e FREITAS, 2000; UEHARA-PRADO et al. 2009). Alguns estudos prévios tem elucidado alterações significativas na composição das comunidades de borboletas frugívoras depois do distúrbio (BONEBRAKE et al., 2010; NYAFWONO et al., 2014; UEHARA-PRADO et al., 2007). Contudo, não há consenso na resposta das borboletas aos ambientes modificados pelo homem. Estudos apontam um decaimento na abundância, riqueza de espécies e diversidade de borboletas (AKITE, 2008), enquanto outros têm reportado um padrão oposto (BOBO et al. 2006; HORNER-DEVINE et al. 2003). Essa variação nos resultados pode ser atribuída a diferenças metodológicas (BARLOW et al., 2007), contrastes nas escalas espaciais e diferenças regionais entre os locais amostrados (HAMER e HILL, 2000) e o tipo de distúrbio (AKITE, 2008). As diferentes respostas das borboletas frugívoras aos ambientes modificados faz com que novos estudos em paisagens antrópicas sejam necessários para tornar claro qual o real papel desempenhado por essas paisagens na retenção da diversidade de borboletas frugívoras, em particular compreender se e como os habitats afetados por borda afetam as memas.

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CAPÍTULO 1

Dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land use and fragmentation-related effects

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Dung beetle persistence in human-modified landscapes: Combining indicator species with anthropogenic land use and fragmentation-related effects

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Abstract

Identifying and making use of ecological indicators becomes an essential task in the conservation of tropical systems, mainly in fragmented landscapes where land use intensification and habitat loss are confounding factors in the detection of speciesô responses to human-caused disturbance. We aimed to analyze the importance of anthropogenic land use and fragmentation-related effects on dung beetle (Coleoptera: Scarabaeinae) persistence according to the interior-exterior non-linear gradient (forest + matrix) in a fragmented Atlantic Forest landscape used to sugar cane production and cattle ranching/farming. We offer scores for a comprehensive set of community-level attributes, from beetle abundance to taxonomic and ecological composition (i.e. species body size), including a list of indicator species of different forest habitats and adjacent matrix. Dung beetles were surveyed by traps across forest interiors (i.e. core forest areas) and edges of a primary forest, small fragments, sugar cane fields and pastures in a total of 60 sites. Indicator analyses were conducted across the landscape, using two well-established methods (IndVal and SIMPER). Our results suggest that (1) cross-habitat taxonomic distinctness is associated with the presence of indicator species, (2) some species benefit or are dependent of open habitats created by human-disturbances, such as forest edges (e.g. *Canthon nigripennis*) and matrices (e.g. *Canthon* aff. *piluliformis*, *Dichotomius nisus* and *Trichilum externepunctatum*) (3) although landscape habitats exhibit reduced beta diversity, dung beetle assemblages are spatially organized in response to the presence of both forest habitats and matrix and fragment area, (4) forest interior supports beetle assemblages biased toward large-bodied species, (5) accordingly forest interior, forest edges and matrix support taxonomically distinct assemblages, both contributing to the bulk of species richness at landscape level, (6) the response of dung beetles to the interior-exterior non-linear gradient (i.e. forest edge + matrix) reveals a similar pattern regardless of the nature of the matrix, and (7) there is no within-habitat variation in beetle abundance and species richness associated with distance from forest edge. Given that there is a high number of forest-dependent or forest-interior specialist species (e.g. *Aphengium* aff. *sordidum*, *Ateuchus* aff. *alipioi*, *Dichotomius mormon*, *Ontherus* aff. *erosus* and *Onthophagus* aff. *clypeatus*) dung beetle persistence in human-modified landscape is highly dependent on the presence of core areas, although edge-affected and matrix habitats may be complementary. This information is essential to permit a better prospect for dung beetle persistence in human-modified landscapes as they continue to move towards edge-dominated landscapes with intensively managed matrices.

Keywords: agricultural frontiers, ecological indicators, forest-dependent species, matrix, Scarabaeinae.

1. Introduction

A myriad of human-associated processes, such as agriculture, forestry and urbanization, has imposed increasing rates of habitat loss and fragmentation on tropical forests, which has threatened native biodiversity across the tropics (Tabarelli et al., 2010). In fact, such an expansion of human-modified landscapes (HMLs) and the consequent reduction of old-growth forests poses a challenge to conservation practitioners devoted to guaranteeing biodiversity persistence (Melo et al., 2013). Understanding the relationship between HML and species persistence is a major issue of interest in applied ecology because of its direct relationship with biodiversity conservation (De Angelo et al., 2013).

Studies in HMLs on biodiversity persistence based on data of focal species groups do not exhibit a consistent pattern of response. Generally, forest biodiversity declines along a coarse gradient from old-growth forest patches through agroforestry, plantations, secondary forest stands and small forest remnants or edge-affected habitats (Harvey et al., 2006; Nyafwono et al., 2014). However, other studies support the notion that for certain taxonomic groups small forest patches, secondary forest stands and even some crops are able to retain an important fraction of the original biodiversity (Thornton et al., 2011; Melo et al., 2013).

Tropical biodiversity has been roughly assigned into two mutually excluding groups: forest-dependent species as those with persistence depending on the presence of old-growth forest stands (Melo et al., 2013), and disturbance-adapted species as those able to persist or even proliferate in HMLs dominated by edge-affected habitats (Tabarelli et al., 2010). Particularly in the case of animals, discrepant abilities to persist in HML are related to (1) dispersal ability, particularly the ability to cross non-forested habitats (Schtickzelle and Baguette, 2003), (2) capacity of species to move in the matrix (Uezu et al., 2008), (3) use of edge-affected habitats (Banks-Leite et al., 2010), and (4) lack of collection or hunting by human-populations (Benchimol and Peres, 2013).

Dung beetles (Coleoptera: Scarabaeinae) are well-represented insects in tropical regions and have been used in biodiversity monitoring studies (Nichols et al., 2007, 2013; Audino et al., 2014; Campos and Hernández, 2015). These beetles are very sensitive to habitat alterations and have distinct organization patterns when studied in tropical forest fragments (Klein, 1989; Filgueiras et al., 2011) or in areas that have deteriorated due to human activities (Gardner et al., 2008; Barlow et al., 2010a; Korasaki et al., 2013). Such characteristics make dung beetles indicators of natural or anthropogenic environmental disturbances in tropical forests (Halffter and Favilla, 1993). However, dung beetle persistence in such altered landscapes remains controversial (Nichols et al., 2007; Gardner et al., 2008); it is particularly unclear how much, and for how long, tropical dung beetles can persist in HMLs under current land uses, mainly in fragmented landscapes where anthropogenic land use and fragmentation-related effects are confounding factors in the detection of speciesô responses to human-caused disturbance. In this way, dung beetle responses across edge gradients effectively integrate many facets of habitat degradation, providing a generalized indication of the role played by HMLs on species persistence (Barnes et al., 2014).

In the Brazilian Atlantic Forest, more than 80% of the fragments are <50 ha, almost half the remaining forest is <100 m from its edge (Ribeiro et al., 2009). This is one of the most diverse ecosystems in the world, presenting high rates of endemism but also experiencing huge habitat loss (Tabarelli et al., 2010). Seventy percent of the Brazilian population lives in the Brazilian Atlantic Forest region where there are unprecedented levels of habitat loss and other human disturbances going back to the 16th century (Silva and Casteleti, 2003). Approximately 88% of the natural vegetation in this ecosystem/biome/region has been modified or replaced by anthropogenic environments (Ribeiro et al., 2009). The historical and current land-use trajectory of Brazilian Atlantic Forest offers an excellent opportunity to examine the role played by HMLs in terms of forest species persistence (Melo et al., 2013).

Here, we discuss the uncovered patterns of dung beetle assemblage organization in core areas and edges of a large tract of primary forest, small fragments, sugar-cane fields, and cattle pastures in a human-modified Atlantic Forest landscape of northeastern Brazil. We aimed to analyze the importance of anthropogenic land use and fragmentation-related effects on dung beetle persistence according to the interior-exterior non-linear gradient (forest + matrix). This issue was addressed by a set of predictions: 1) habitats largely differ in terms of species richness and taxonomic and ecological composition, with each habitat supporting exclusive and indicator species; 2) edge-affected habitats (i.e. edges of primary forest and small fragments) are able to retain less species of dung beetles than core primary forest patches independently of fragment characteristics (i.e. fragment area, isolation, soil type and vegetation type) and matrix type; and 3) although both factors (i.e., land use and habitat fragmentation) negatively affect dung beetle persistence, land use exerts a stronger effect with matrix habitats harbor a set of species consisting of anthropogenic-specialists.

2. Materials and methods

2.1. Study sites

The Serra Grande landscape is located within the Pernambuco Centre of Endemism (Fig. 1), the most threatened bioregion of the Brazilian Atlantic Forest (Silva and Casteleti, 2003). Annual precipitation is 2000 mm with a dry season (<60 mm/month) occurring from November to January (Santos et al., 2008) and with the wettest period between April and August (Pimentel and Tabarelli, 2004). This hyper-fragmented landscape (667 km^2) contains approximately 9000 ha of forest (9.2% forest cover) distributed in a total of 109 forest remnants, ranging from 1.67 to 3500 ha, which are almost all completely surrounded by sugar-cane fields (Santos et al., 2008). The presence of Coimbra forest (3500 ha), the largest remnant of Atlantic Forest in northeast Brazil, makes Serra Grande landscape an excellent scenario for understanding the long-term effects of habitat fragmentation on plant (Santos et al., 2008) and animal (Filgueiras et al., 2011; Leal et al., 2012) communities. We are aware, however, that Coimbra forest does not fully represent a ócontinuous forestö, limiting our study design. But it is the single, unreplicated tract of primary forest has several large-seeded tree species and medium-sized frugivorous vertebrates at the landscape and regional scales (Pimentel and Tabarelli, 2004). In addition Coimbra forest is surrounded by different types of matrix besides the predominant sugar cane fields, such as pastures and plantations maintained for subsistence by local human communities.

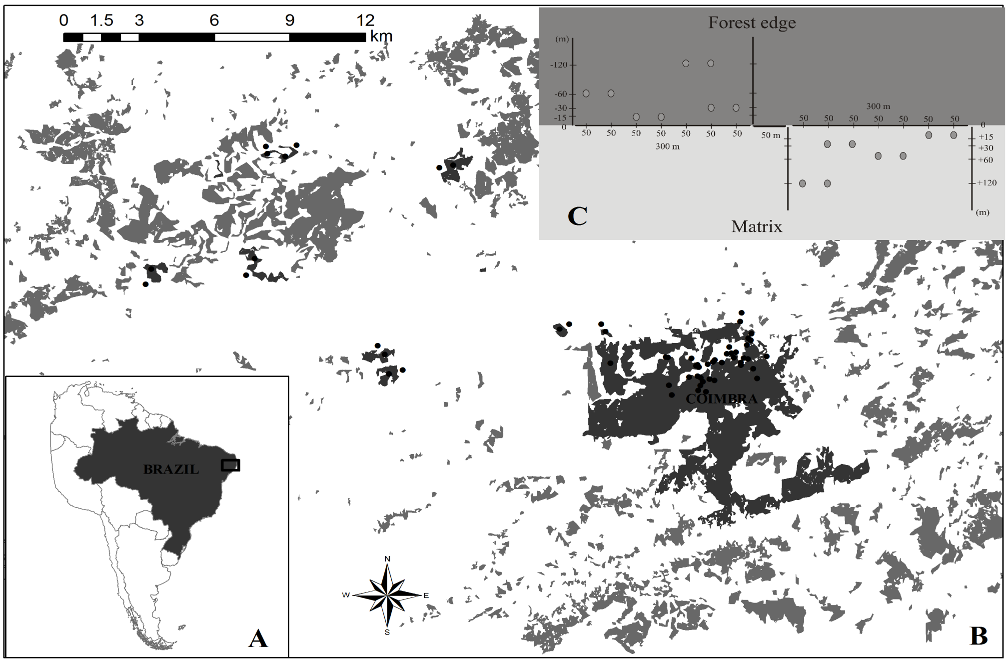
2.2. Habitats and dung beetle surveys

Beetles were surveyed using equal sampling effort across six habitats arranged in two spatially independent setups: (A) 10 sampling units in the Coimbra forest interior (control), 10 in Coimbra forest edges, 10 in the sugar-cane plantation and 10 in pastures surrounding Coimbra forest. Forest interior referred to forest stands > 200 m from the nearest edge (Santos et al., 2008). (B) 10 units in the edges of 10 small forest fragments (range in size = 8.25-91 ha), and 10 in the surrounding sugar-cane matrix (Fig. 1). We therefore sampled a total of 60 sites. Sampling units across surrounding matrix and small forest fragments were randomly selected considering fragments with little (< 1ha) or no forest interior habitat.

Dung beetle surveys were carried out between October 2011 and February 2012. To avoid the effects of seasonality on dung beetle communities, trapping was carried out under generally similar climatic conditions, avoiding rainy days (Estrada et al., 1999), and was conducted once at each site. In the interior of Coimbra forest, sampling units were located randomly with a minimum distance of 300 m. Each sampling unit consisted of four pairs of pitfall traps, each pair 50 m apart and set along a linear transect. This spatial independence was confirmed by a Mantel test - no significant correlation was observed ($R = 0.17$, $p = 0.11$) between the spatial arrangement of sampling units and patterns of species similarity (Bray-

Curtis index). In forest edges, trap-pairs were set at 120, 60, 30 and 15 m from forest edge towards forest interior, while in matrix habitats (pasture and sugar cane) they were set 15, 30, 60 and 120 m from forest edge toward the matrix (see Fig.1). The total sampling effort consisted of 480 traps. To avoid a lack of independence (Larsen and Forsyth, 2005), the trap-pairs were separated at least 50 m apart and arranged according to a non-linear interior-exterior gradient (i.e. sampling points were staggered laterally- parallel to the forest edge) (see Fig.1).

Figure 1. Map of the Usina Serra Grande landscape of northeastern Brazil (A) showing the 60 sampling sites in Atlantic Forest (B). Schematic figure showing an example of the sampling design used to assess dung beetle communities in interior-exterior non-linear gradient in forest edges and matrix habitats. Pitfall traps (dark shaded circles) (C). The forest fragments sampled are represented by black circles. Light-shaded areas represent remaining Atlantic Forest remnants that were not sampled. Blank spaces represent uniform matrix of sugar-cane monoculture and pastures.



Traps consisted of plastic containers (15 cm in diameter by 13 cm in height) with a bait-holding recipient (3 cm in diameter by 4.8 cm in height) containing ~30 g of human feces. Forty-eight hours after installing the traps, the dung beetles were collected and taken to the Serra Grande study base, where the insects were sorted. The dung beetles were then taken to the Insect Taxonomy and Ecology Laboratory at the Universidade Federal de Pernambuco for storage. After drying, beetles were weighed (scales accurate to 0.0001g). A sample of between 1 and 10 individuals was used to obtain body mass estimates. The biomass of each species in each habitat was estimate by multiplying the mean body mass by species total abundance. Dung beetles were identified to species level at the Universidade Federal de Pernambuco and Universidade Federal de Mato Grosso, Brazil. Voucher specimens were deposited at both institutions.

2.3. Patch and landscape metrics

We estimated the amount of forest cover retained in the surrounding landscape as a measure of patch isolation (Gorresen and Willig, 2004). It was defined as the percentage of forest within 1-km of the fragment perimeter. The area of fragments and the amount of forest cover retained in the surrounding landscape were quantified using two GIS packages (ArcView 3.2 and Erdas Imagine 8.4) on the basis of: (1) three Landsat and Spot images (years 1989, 1998, 2003) and (2) a set of 160 aerial photos (1:8000) taken from helicopter overflights commissioned in April 2003 (provided by Conservação Internacional do Brasil) (Appendix A).

We computed a core area metric to make sure that small forest fragments used in this study were edge-dominated habitats (Appendix A). We defined this as the total remaining core area per class after the application of a buffer (MacGarigal et al., 2001). Soil type was based on the Brazilian soil classification system (IBGE 1985) and involved two soil classes:

yellow-red latosols (L) and yellow-red podzols (P). With respect to vegetation type, the Serra Grande landscape included two physiognomic subtypes: evergreen (E) and semi-deciduous forests (S) (Veloso et al., 1991) (Appendix A).

2.4. Data analysis

We assessed the completeness of each habitat by calculating the number of observed species as a percentage of the total richness, which was estimated based on the average of three abundance-based nonparametric estimators, Bootstrap, Chao 1 and Jack 1 (Colwell 2013). We compared patterns of richness between forest habitats and matrix after standardizing for differences in abundance with individual-based rarefaction analysis (Gotelli and Colwell, 2001). The completeness and rarefaction analysis were calculated in EstimateS v. 9.1 (Colwell, 2013). An analysis of indicator species (*sensu* Dufrêne and Legendre, 1997) was also performed to determine the fidelity and specificity of the dung beetles to three groups of habitats: forest interiors (Group 1), forest edges (i.e. edges of Coimbra forest and of small fragments) (Group 2) and matrix habitats (i.e. sugar-cane plantations and pastures) (Group 3). We used SIMPER (Primer v.6, Clarke and Gorley, 2001) to determine the contribution that individual species made toward distinguishing differences in quantitative community structure among these habitats.

To analyze dung beetle communities in different forest edges (edges of Coimbra forest and of small forest fragments) with the same type of matrix (sugar-cane plantation), we first used Generalized Linear Models (GLM) with poisson error in order to test whether forest species, in terms of total observed species richness, total estimated richness and number of individuals are influenced by different types of vegetation (i.e. evergreen or semi-deciduous forest), soil (i.e. latosols or podzols), fragment area (transformed log10) and isolation (forest cover within 1 km around fragments). The performance of GLM was assessed using Akaikeôs Information Criterion (AIC). We used three measures associated with the AIC to determine the optimal model given the data: the φAIC ranks alternative models according to their AIC values; the AIC for each model (rescaled based on the best model) and w_iAICc - chance for the model to be selected, which varies from 0 to 1 (Burnham and Anderson, 1998). Models were run using the ć*glmer*ô function in the đ*m4*ô package in the R environment (R Core Team 2014). Second, to analyze the species composition between forest edges and matrix habitats, non-metric multidimensional scaling (NMDS - Clarke and Gorley, 2001) was performed using a Bray-Curtis similarity matrix with 1000 random restarts. We used analysis of similarities (ANOSIM - Clarke and Gorley, 2001) to test for significant differences in dung beetle communities in the landscape. These analyses (i.e. NMDS and ANOSIM - Clarke and Gorley, 2001) were also used to evaluate dung beetle communities in different forest environments (forest edges and interiors) with distinct types of matrix (pastures and sugar-cane plantation) as compared to Coimbra forest. Ordinations were performed based on both abundance and biomass. Data were transformed (square root) (*sensu* Clarke and Gorley, 2001) in order to avoid any bias resulting from highly abundant species. ANOSIM and NMDS were performed using Primer v.6 (Clarke and Gorley, 2001).

Finally, we analyzed dung beetle diversity comparing the sampling designs by the additive partitioning of total diversity expressed by species richness. This consists of partitioning the total species diversity (***ɔ***) into additive components representing within-community diversity (***Ŭ***) and between-community diversity (***ɓ***) (see Veech et al., 2002). Additive diversity partitioning is flexible in that ɔ diversity can be partitioned on the basis of any categorical factor (e.g. habitat, host or resource use); therefore, it can potentially be used to analyze any postulated determinant of species diversity (Veech et al., 2002).

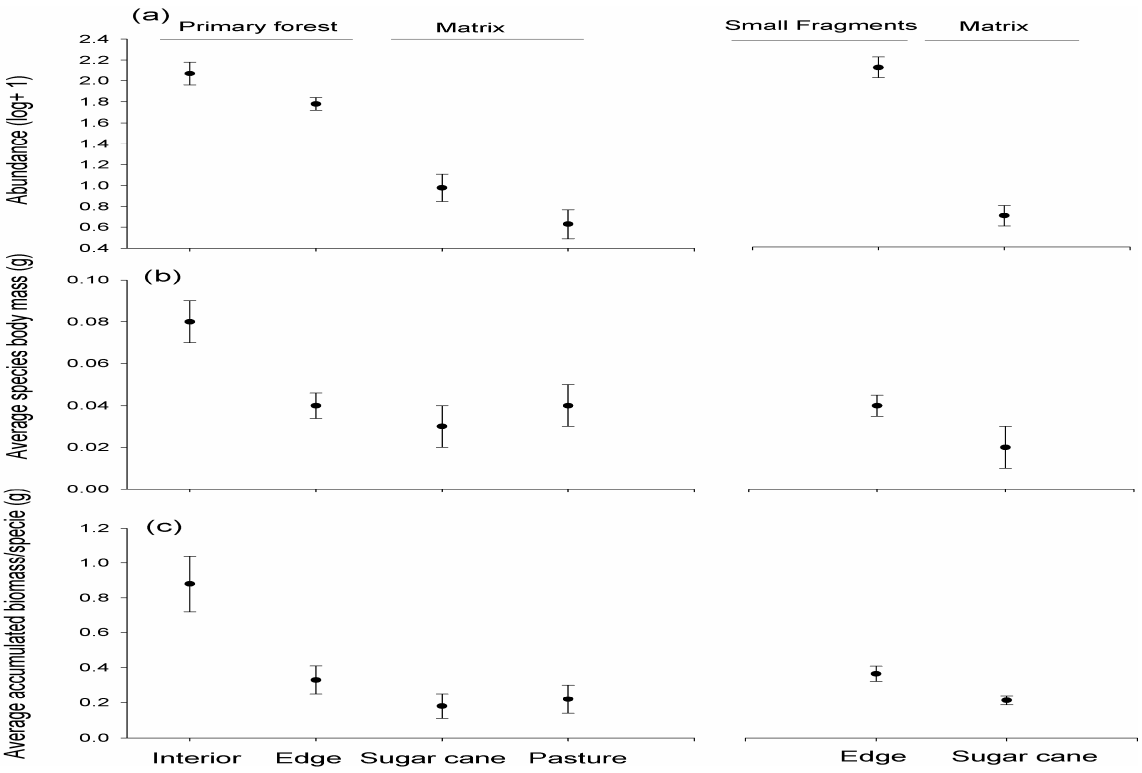
3. Results

3.1. Abundance, species richness, biomass and body mass

A total of 4218 individuals from 45 dung beetle species were recorded in the Serra Grande landscape as follow: 1570 individuals from 20 species in Coimbra forest interior (control habitat), 675 individuals from 20 species in Coimbra forest edges, 119 individuals from 12 species in sugar-cane plantation and 54 individuals from 11 species in the pasture surrounding the Coimbra forest. In addition, we recorded 1764 individuals from 20 species in the edges of small forest fragments and 36 individuals from 11 species in sugar-cane plantations adjacent to fragments (Appendix B).

Habitats largely differed in terms of assemblage structure as follows. First, forest interior supported many more large-bodied species resulting in a significant difference in terms of average species body mass and average biomass accumulated per species (Fig. 2).

Figure 2. Abundance (Mean ± SE) (a), average species body mass (± SE) (b) and average accumulated biomass per species (± SE) (c) for dung beetles collected in Serra Grande landscape, northeast Brazil. FI (forest interior of Coimbra forest), FE (forest edge of Coimbra forest), SF (forest edge of small fragments), SCSF (sugar-cane around fragments), SCC (sugar-cane around Coimbra forest), PC (pastures around Coimbra forest).



Additionally, forest interior supported more species-rich assemblages than forest edge and landscape matrices (Table 1). We refer to a Ó50%-reduction in species richness from interior (mean ± SE: 9.2 ± 0.69 species/sampling unit) to sugar cane or pasture (mean ± SE: 2.5 ± 0.65 species). Please note that although beetles were as abundant in the edges of small fragments as in forest interior, species richness was much lower in fragments (mean ± SE: 4.7 ± 0.55 species). Higher species richness in forest interiors (i.e. the observed number of species) was also confirmed by estimates of species richness, such as species numbers based on rarefaction procedures (see Table 1). Thus it is not surprisingly that forest interior exhibited the highest scores of species completeness (mean ± SE: 20.3 ± 1.61 species) and coverage (> 87.3%) as compared to other habitats (Table 1). However, pastures and sugar cane plantations no differed in terms of abundance, species richness and sample completeness (see Table 1).

Table 1. Mean value and standard error (SE) for species richness, abundance and sample completeness for dung beetles collected in Serra Grande landscape, northeast Brazil.

Habitats	Abundance (Mean ± SE)	Richness (Mean ± SE)	Rarefaction À(Mean ± SE)	Estimators ÿ (Mean ± SE)	Coverage(%)§ (Mean ± SE)	Completeness¶ (Mean ± SE)
Coimbra forest interior	156.8 (40.7)	9.2 (0.69)	6.18 (0.33)	10.57 (0.83)	87.3 (2.71)	20.3 (1.61)
Coimbra forest edges	67.7 (9.59)	7.1 (0.75)	5.41 (0.29)	9.35 (1.61)	81.5 (4.31)	15.2 (1.5)
Coimbra sugar-cane matrix	11.9 (2.79)	3.7 (0.7)	2.6 (0.33)	5.37 (1.11)	67.5 (9.63)	6.5 (1.59)
Coimbra pasture matrix	5.4 (1.43)	2.5 (0.65)	1.85 (0.53)	3.39 (1.0)	43.4 (12.14)	5.4 (1.44)

Edges of small fragments	176.3 (48.8)	4.7 (0.55)	3.38 (0.3)	5.93 (0.82)	81.2 (4.48)	9.27 (1.25)
Fragment sugar-cane matrix	3.5 (1.1)	1.7 (0.42)	0.93 (0.31)	2.19 (0.75)	32.7 (11.1)	3.5 (0.9)

ÀAdjusted species richness from individual-based rarefaction.

ÿEstimated species richness based on the average of three abundance-based richness estimators, Bootstrap, Chao 1 and Jack 1 (see Colwell 2013).

§Number of species observed as a percentage of the total estimated richness.

¶Number of species observed as a percentage of the landscape total.

*P<0.01, **P < 0.0001.

3.2. Assemblage response, additive partitioning and indicator analyses

Both observed and estimated total species richness in forest edges of small fragments correlated positively with fragment area (Table 2), although forest cover and soil type played a minor role.

Table 2. Results of the Generalized Linear Models for the effects of fragment area ($\log_{10}$-transformed) (AREA), forest cover (FC) retained in the surrounding landscape (buffer of 1000 m), soil type (ST) and vegetation type (VT) on total observed richness, total estimated richness and abundance of dung beetles in habitat edges (edges of Coimbra forest and small forest fragments) sampled in Serra Grande landscape, northeast Brazil. Models are ranked from best to worst according to model φAICc. We also show the number of predictor variables (K), Akaike weights (**ɤ** *i*) and cumulative Akaike weights (c**ɤ** *i)*.

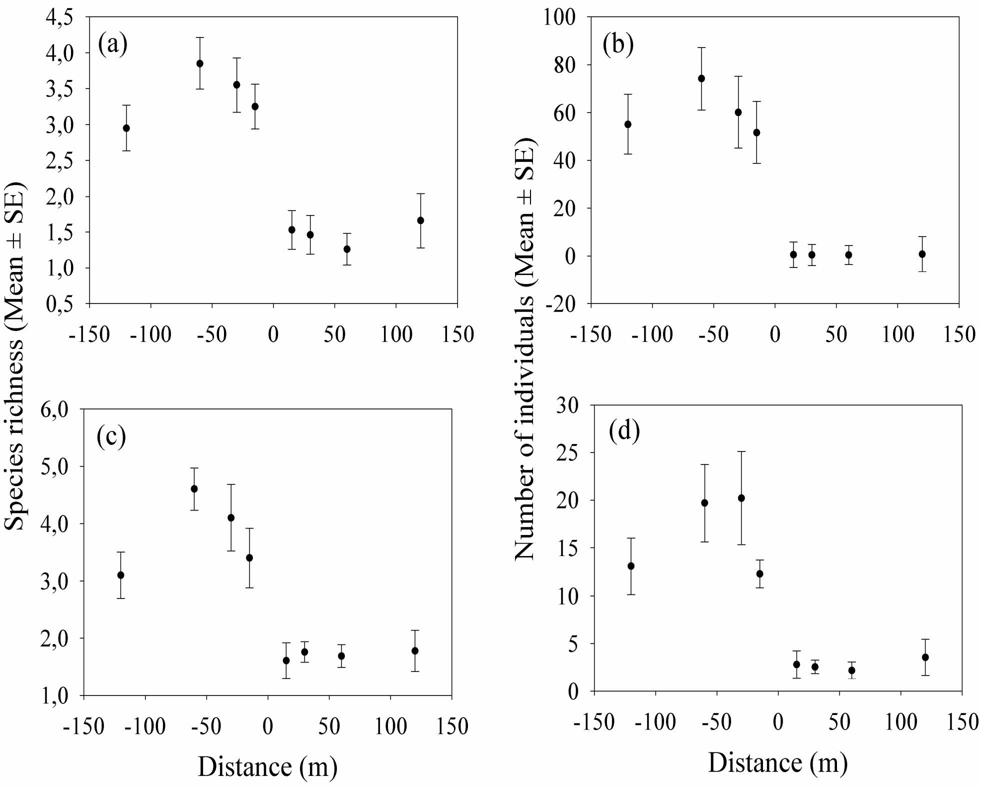
Response variables	Models	AICc	φAICc	K	**ɤ** i	*c***ɤ** *i*
Total observed richness	AREA	89.71	0	2	0.4	0.4
	AREA + FC	91.2	1.49	3	0.19	0.59
	AREA + ST	91.7	1.99	3	0.15	0.74

	AREA + VT	92.03	2.32	3	0.13	0.87
	AREA + FC + ST	93.96	4.25	4	0.05	0.91
	AREA + FC + VT	94.27	4.56	4	0.04	0.95
Total estimated richnessÀ	AREA + VT	99.62	0	4	0.31	0.31
	AREA	99.74	0.13	3	0.29	0.59
	AREA + ST	101.06	1.44	4	0.15	0.74
	AREA + FC	102.06	2.44	4	0.09	0.83
	AREA + VT + ST	102.54	2.92	5	0.07	0.91
	AREA + FC + VT	103.12	3.5	5	0.05	0.96
Abundance	AREA + FC + VT + ST	1281	0	5	1	1
	AREA + VT + ST	1300	18.68	4	0	1
	AREA + FC + VT	1352	70.63	4	0	1
	AREA + VT	1382	100.41	3	0	1
	FC + VT	1520	238.49	3	0	1
	FC + VT + ST	1522	240.97	2	0	1

À Estimated species richness based on the average of three abundance-based richness estimators, Bootstrap, Chao 1 and Jack 1 (Colwell 2013).

Overall, all habitats exhibited reduced beta diversity (from 4% to 14%) with little contribution to gamma diversity at habitat level as follow: (a) 10% in forest edges of small fragments and 14% in the adjacent sugar cane plantation, (b) 4%, 4% and 12% of total gamma diversity for forest interior, edge and matrix (sugar cane and pasture) surrounding Coimbra forest respectively. The response of dung beetles to the interior-exterior non-linear gradient (i.e. forest edge + matrix) revealed a similar pattern regardless of the nature of the matrix, i.e. there was no within-habitat variation in beetle abundance and species richness associated with distance from forest edge (Fig. 3).

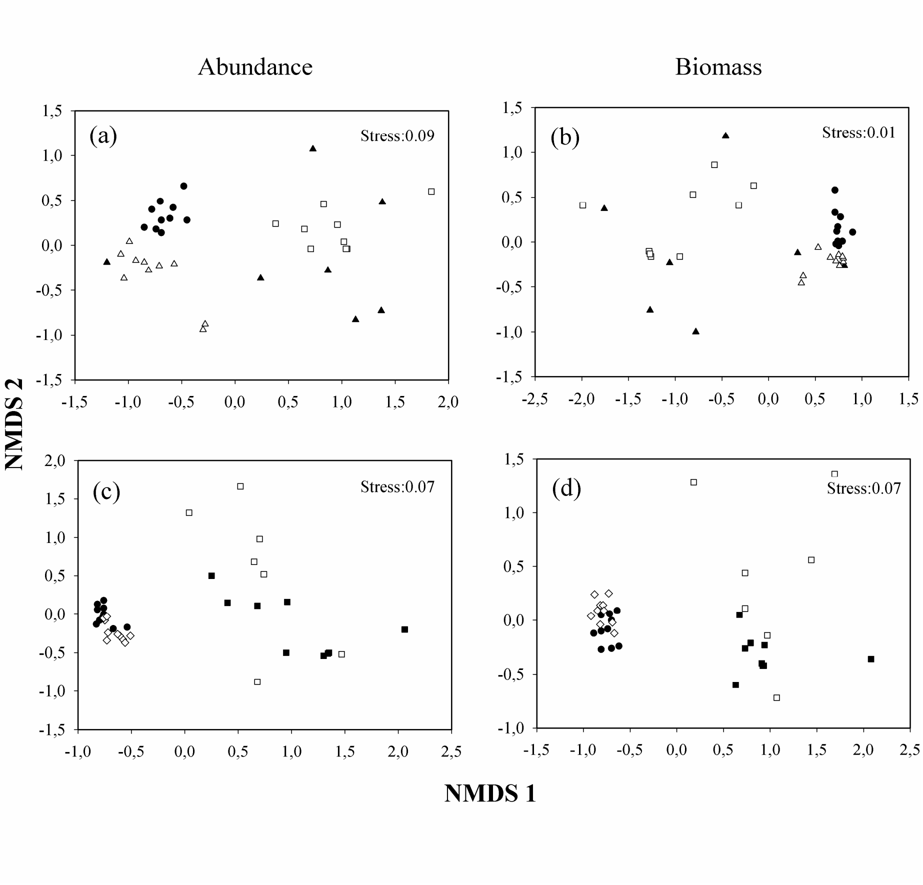
Figure 3. Patterns of dung beetle response to the interior-exterior non-linear gradient in Serra Grande landscape, northeast Brazil: (a) and (b) edges of small fragments vs. sugar-cane plantation; (c) and (d) edges of Coimbra forest vs. pastures and sugar-cane plantation. Negative values represent forest edges and positive values matrix habitats.



NMDS ordination of sampling units based on similarity of species abundance and biomass resulted in consistent and segregated groups as follow: (a) one formed by forest edges of Coimbra forest and small fragments and another formed by sugar cane units (Fig. 4a and Fig. 4b), and (b) one group formed by forest edges and forest interior and another group formed by matrix units (Fig. 4c and Fig. 4d). This clear segregation, particularly in terms of forest vs. matrix were supported by ANOSIM tests, which detected a strong effect of habitat type ($R = 0.56$-0.68, $p < 0.01$).

Figure 4. NMDS based on dung beetle community structure across forest and matrix habitats: (a) and (b) forest edges (open triangles) and sugar-cane plantation (dark shaded triangles) of small forest fragments, forest edge (dark shaded circles) and sugar-cane plantation (open squares) of Coimbra forest; (c) and (d) forest edges (dark shaded circles),

interior forest areas (open diamonds), pastures (dark shaded squares) and sugar-cane plantations (open squares) of Coimbra forest.



Accordingly, the average dissimilarity (SIMPER analysis) for differentiation between habitats varied from 54.51% to 94.7% as in the case of forest interior and pastures (Table 3). This differentiation was more pronounced when we compared forest and matrix habitats (Table 3) and was due to a small number of species such as *Dichotomius* aff. *sericeus*, *Canthon* sp.2 and *Canthon* aff. *piluliformis*.

Table 3. Pairwise dissimilarities among habitats of Serra Grande landscape, northeast Brazil. FI = Forest Interiors (Coimbra forest); FE = Forest Edges (including edges of Coimbra forest and small forest fragments); M = Matrix Habitats of Coimbra forest and small forest fragments (including sugar-cane plantations and pastures). We present species that make a >

5% contribution only. Average dissimilarity (Av. diss) with standard deviation (SD) and contributions (Cum %) for all species is explained between habitats.

Comparison	Av. diss (overall)	Species	Average abundance		Av. diss	Av. diss SD	Contrib (%)	Cum. (%)
FI vs. FE	54.51	*Dichotomius* aff. *sericeus*	29.23	42.2	8.84	1.24	16.22	16.22
		Ontherus aff. *erosus*	17.35	6.65	6.64	1.81	12.17	28.39
		Onthophagus aff. *clypeatus*	10.92	2.32	4.99	1.28	9.15	37.54
		Eurysternus hirtellus	3.15	11.28	4.94	1.32	9.05	46.6
		Canthidium sp. 1	11.85	9.03	4.9	1.47	8.98	55.58
FI vs. M	94.7	*Dichotomius* aff. *sericeus*	29.23	6.57	14.37	2.37	15.17	15.17
		Canthon aff. *piluliformis*	0	26.62	13.31	0.93	14.06	29.23
		Canthon sp. 2	0	20.29	10.14	1.17	10.71	39.94
		Ontherus aff. *erosus*	17.35	0	8.67	3.17	9.16	49.1
		Trichilum externepunctatum	0	12.12	6.06	0.85	6.4	55.5
		Canthidium sp. 1	11.85	2.89	6.01	1.76	6.35	61.85
		Onthophagus aff. *clypeatus*	10.92	0	5.46	1.36	5.77	67.61
		Deltochilum irroratum	0	9.94	4.97	0.46	5.25	72.86
FE vs. M	93.7	*Dichotomius* aff. *sericeus*	42.2	6.57	20.32	2.14	21.68	21.68
		Canthon aff. *piluliformis*	0	26.62	13.31	0.93	14.21	35.89
		Canthon sp. 2	0	20.29	10.14	1.18	10.83	46.71
		Eurysternus hirtellus	11.28	3.54	6.49	1.11	6.92	53.64
		Trichilum externepunctatum	0	12.12	6.06	0.85	6.47	60.11
		Deltochilum irroratum	0.51	9.94	5.07	0.47	5.42	65.52
		Canthidium sp. 1	9.03	2.89	4.98	1	5.31	70.83

Finally, indicator species accounted for 36% of all species recorded in the Serra Grande landscape according to the following categories: forest interior indicators (seven species, 15%), forest edge-indicators (one species, 3%), and matrix indicators (five species, 11%, see Table 4). Moreover, the majority of species recorded in forest habitats (such as the large-bodied *Deltochilum calcaratum*, and *Dichotomius mormon*) were not recorded across matrix habitats, while *Canthon* aff. *piluliformis*, *Canthon* sp. 2, *Dichotomius nisus* and *Trichilum externepunctatum* were unique to these environments.

Table 4. Analysis of indicator species (*sensu* Dufrêne and Legendre, 1997) of dung beetles (> 10 individuals) characteristic of forest interiors (Group 1), forest edges (edges of Coimbra forest and small forest fragments) (Group 2) and those characteristic of matrix habitats (Group 3) in Serra Grande landscape, northeast Brazil.

Species	Indicator value	Groups	*P*
Aphengium aff. *sordidum*	77	1	0.001
Ateuchus aff. *alipioi*	91	1	0.001
Ateuchus sp. 1	60	1	0.007
Canthon nigripennis	45	2	0.025
Canthon aff. *piluliformis*	80	3	0.002
Canthon sp. 2	82	3	0.001
Coprophanaeus dardanus	76	1	0.001
Deltochilum irroratum	52	3	0.025
Dichotomius nisus	58	3	0.003
Dichotomius aff. *sericeus*	92	1 and 2	0.001
Dichotomius mormon	81	1	0.001
Eurysternus hirtellus	84	1 and 2	0.001
Ontherus aff. *erosus*	92	1	0.001
Onthophagus aff. *clypeatus*	93	1	0.001
Sylvicanthon aff. *machadoi*	52	1 and 2	0.032
Trichilum externepunctatum	68	3	0.003

4. Discussion

4.1. Dung beetles as ecological indicators

Our results suggest that (1) cross-habitat taxonomic distinctness is associated with the presence of indicator species, (2) some species benefit or are dependent of open habitats created by human-disturbances, such as forest edges and matrices, (3) although landscape habitats exhibit reduced beta diversity, dung beetle assemblages are spatially organized in response to the presence of both forest habitats and matrix and fragment area, (4) forest habitats represent the most species-rich habitat in HMLs of Atlantic Forest, while pastures and sugar cane fields represent the most impoverished, (5) forest interior supports beetle assemblages biased toward large-bodied species, (6) accordingly forest interior, forest edges and matrix support taxonomically distinct assemblages, both contributing to the bulk of species richness at landscape level, (7) the response of dung beetles to the interior-exterior non-linear gradient (i.e. forest edge + matrix) reveals a similar pattern regardless of the nature of the matrix, and (8) there is no within-habitat variation in beetle abundance and species richness associated with distance from forest edge.

These statements are in accordance with the notion that dung beetle assemblages are sensitive to habitat loss (Klein, 1989) and the creation of forest edges, due to the fact that a considerable number of species are forest-dependent or forest-interior specialist species (Filgueiras et al., 2011). Many others are able to eventually exploit forest edges and the surrounding matrix for additional resources (Prevedello et al., 2012), while others are matrix or even edge-specialists (Peyras et al., 2013). Such ecological composition suggests that HMLs are able to retain a significant proportion of dung beetle fauna, although forest interior represents an irreplaceable habitat (Gardner et al., 2008) as shown by the indicator species analysis.

In fact, the conversion of natural landscapes into HMLs results in some key-processes: habitat loss and fragmentation, creation of forest edges, proliferation of small forest fragments and the establishment of open-habitats. Both forest edges and small fragments (edge-affected habitats) have been frequently described as being more desiccated and wind-disturbed as having higher light levels, and as supporting impoverished and small-statured tree assemblages dominated by pioneer plants (Santos et al., 2008). Edge-effects and reduced patch area have been frequently referenced in the literature as habitats that are unsuitable for a myriad of animals (Laurance et al., 2001), including large-bodied mammals and associated coprophagous-specialist beetles (Estrada et al., 1999). Coimbra forest still retains a full complement of large and medium-bodied mammals (from to agoutis to peccaries) while small fragments in the Serra Grande landscape could be designated empty forests (Fernandes, 2003; Pimentel and Tabarelli, 2004). On the other hand, these forest fragments harbor small mammals highly resilient to changes in habitat structure (e.g. marsupials and rodents) and can additionally act as corridors or óstepping-stonesô for large and medium-bodied mammals (Pardini et al., 2005), which in turn may explain the presence of dung beetles. Thus, differences in scat abundance and consequently in the frequency of coprophagous-specialist species represent one of the potential drivers for cross-habitat differences in terms of beetle abundance, species richness, taxonomic/ecological composition and the relationship we documented between fragment size and species richness, i.e. an indirect effect of patch size on dung beetle assemblages.

In addition to dung abundance, cross-habitat differences in terms of physical conditions may play a role as both matrix and forest edges are structurally different as compared to forest interior (Laurance, 2001). Soil texture and humidity content, for instance, can affect dung beetle reproduction by reducing their capacity to build nest in underground galleries (Fincher, 1973). As large dung beetle species require higher humidity content to excavate deeper galleries, small dung beetles are predominant in open habitats (Anduaga, 2004). Accordingly, the most abundant species in matrix habitats (i.e. *Canthon* sp. 2, *Canthon* aff. *piluliformis,* and *T. externepunctatum*) consisted of small-bodied species, which are widely recorded in anthropogenic environments (Korasaki et al., 2013). On the other hand, some large-bodied beetles (e.g. *Coprophanaeus dardanus*, and *Dichotomius mormon*) were restricted to forest interior or forest habitat (i.e. forest interior and edges). Apparently, some coprophagous-specialist and large-bodied species tend to be replaced by more generalists species (in terms of both feeding behavior or digging ability) from forest interior towards open habitats. However, such spatio-environmental replacement is not able to recover the full complement of species across disturbed habitats (edge-affected and open habitats). Obviously, we cannot disregard other driving forces such as low humidity and high temperatures causing higher mortality among dung beetle larvae in the soil (Fincher, 1973) of edge-effected and matrix habitats.

Despite reduced species richness at both sampling and habitat level, matrix habitats contributed to the total dung beetle diversity recorded in the Serra Grande landscape (i.e. 12 species restricted to this habitat) with some potential specialists in open habitats as mentioned previously. As almost any taxa inhabiting tropical forests, some beetle species are likely to benefit or are not negatively affected by the establishment of HMLs (i.e. winner species *sensu* Tabarelli et al., 2012), while many others are negatively affected by the creation of forest edges or habitat loss (see Ewers and Didham, 2006; Banks-Leite et al., 2010). It is likely that some forest-dependent beetles, such as *C. dardanus*, *Dichotomius* aff. *sericeus*, *Eurysternus hirtellus*, and *Oxysternon silenus*, may be eventually attracted by scattered dung deposited by native mammals using the matrix of sugar-cane plantation and pasture for different purposes (Fernandes 2003). These dung beetles are unlikely to be able to sustain viable populations if they remain isolated from forest populations (Barlow et al., 2010b; Korasaki et al., 2013). Open matrices may thus contribute to species persistence in HML by providing suitable habitats for generalist or disturbance-adapted species, but also by providing marginal or occasional habitat for forest-dependent species depending on matrix quality as previously suggested (Harvey et al., 2006).

4.2. Conclusions

We provide some evidence that the establishment of HMLs alters the structure of dung beetle assemblages, including their spatial organization, as habitat loss, creation of forest edges and the presence of open habitats operating as matrices impose disproportionate impacts on species of ecological groups associated with feeding behavior and digging ability. With a high number of forest-dependent or forest-interior specialist species, dung beetle persistence in HMLs is highly affected by the presence of forest interior patches, even assuming that extirpation of specialists can be, to some extent, numerically compensated by disturbance-adapted species inhabiting peculiar assemblages across edge-affected or open habitats. Unfortunately, in the Atlantic Forest, nearly half of the remaining forest is located less than 100 m from open areas, over 70% is located less than 250 m from open land (Ribeiro et al., 2009) and most forest fragments are currently defaunated in terms of mammals (Benchimol and Peres, 2013). Further studies should examine dung beetle responses to disturbance across several ecological groups, including their ability to persist in edge-affected habitats, since matrix specialists are likely to represent a small fraction of local fauna, particularly small-bodied species. This information is essential to permit a better prospect for dung beetle persistence in HMLs as they continue to move towards edge-dominated landscapes with intensively managed matrices (see Laurance et al., 2014).

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Appendix A. Attributes of Atlantic Forest fragments in Serra Grande landscape, northeast Brazil.

Forest fragments	Area (ha)	Core area $(m^2)^a$	TCAI [b]	Forest cover (%)	Soil type[c]	Vegetation type[d]
Encanamento	91.16	0	0	8.16	L	E
Val paraíso	79.64	0	0	17.13	L	S
Alto guzerá	86.63	2099.5	1.32	15.03	L	S
Usina	50.04	0	0	9.59	P	S
Aquidabã I	10.16	0	0	26.1	L	E
Taquara I	33.52	0	0	15.33	P	E
Taquara II	31.73	8188.2	3.66	24.13	P	E
Dois braços	16.86	0	0	8.97	P	E
Ibateguara	8.25	0	0	5.51	L	E
Aquidabã II	26.39	334.3	4.06	0	L	S
Coimbra	3500	1102029	36.09	6.67	P	E

[a] Core area (buffer 120 m).

[b] Total core area index (buffer 120 m).

[e] Latosols (L) and Podzols (P).

[d] Evergreen forest (E) and Semi-deciduos forest (S).

Appendix B. Species and number of individuals of dung beetles sampled in Serra Grande landscape, northeast Brazil.

Species	Coimbra forest interior	Coimbra forest edges	Coimbra sugar-cane matrix	Coimbra pasture matrix	Edges of small fragments	Fragment sugar-cane matrix
Agamopus convexus	1	0	0	0	42	0
Aphengium aff. *sordidum*	39	1	0	0	0	0
Ateuchus aff. *alipioi*	26	11	0	0	0	0
Ateuchus sp.	0	0	0	0	89	0
Canthidium sp.1	110	92	3	3	5	0
Canthidium sp.2	7	0	0	0	0	0
Canthidium sp.3	0	1	0	0	0	0
Canthidium sp.4	0	0	1	1	1	0
Canthidium sp.5	0	0	0	0	11	0
Canthon chalybaeus	0	0	3	0	0	0
Canthon oliverioi	0	1	0	0	2	0
Canthon mutabillis	0	0	1	0	0	0
Canthon nigripennis	1	3	0	0	8	0
Canthon aff. *piluliformis*	0	0	32	7	0	18
Canthon staigi	0	0	0	0	3	0
Canthon smaragdulus	1	1	0	0	0	0
Canthon sp.1	0	0	0	0	1	0
Canthon sp.2	0	0	34	10	0	5
Canthon sp.3	0	0	0	0	0	1
Canthonella aff. *silphoides*	10	3	0	0	9	0
Coprophanaeus acrisius	0	0	0	1	0	0
Coprophanaeus	0	0	0	0	1	0

cyanescens						
Coprophanaeus dardanus	25	1	2	0	0	0
Deltochilum calcaratum	2	2	0	0	0	0
Deltochilum irroratum	0	0	1	12	1	2
Diabroctis mimas	0	0	0	0	0	1
Dichotomius ascanius	2	1	0	0	0	0
Dichotomius nisus	0	0	5	5	0	2
Dichotomius aff. *sericeus*	736	370	2	0	862	2
Dichotomius depressicolis	1	1	0	0	2	0
Dichotomius mormon	18	1	0	0	1	0
Dichotomius sp.1	0	0	0	0	2	0
Dichotomius sp.2	0	0	0	0	1	0
Digitonthophagus gazella	0	0	0	0	0	1
Eurysternus hirtellus	12	50	0	10	84	0
Ontherus azteca	0	1	0	0	0	0
Ontherus aff. *erosus*	267	95	0	0	0	0
Onthophagus aff. *clypeatus*	300	29	0	0	0	0
Onthophagus sp.	0	0	0	1	0	0
Oxysternon silenus	5	2	1	0	1	0
Pseudocanthon aff. *xanthurus*	0	0	0	0	0	2
Sylvicanthon aff. *machadoi*	6	9	0	0	0	0

Trichilum externepunctatum	0	0	34	3	0	1
Uroxys aff. *batesi*	1	0	0	1	0	0
Uroxys sp.	0	0	0	0	638	1
Total	1570	675	119	54	1764	36

CAPÍTULO 2

Spatial turnover of Neotropical forest dung beetle assemblages in edge-dominated habitats: conservation implications for human-modified landscapes

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Spatial turnover of Neotropical forest dung beetle assemblages in edge-dominated habitats: conservation implications for human-modified landscapes

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ABSTRACT

Aim Understanding how landscape context and fragmentation-related effects govern species turnover can provide important insights into the processes driving species diversity in tropical forests. We ask whether anthropogenic land-use and fragmentation-related effects lead to a process of dung beetle homogenization (decreasing spatial turnover and increasing nested pattern) or dung beetle differentiation (increasing spatial turnover and decreasing nested pattern) in human-modified landscapes.

Location Atlantic Forest (Northeastern Brazil).

Methods We investigate the extent to which the beta diversity of dung beetle assemblages varies in edge-affected habitats at different spatial scales (i.e. traps according to the interior-exterior non-linear gradient, within and among habitats) using additive partitioning of diversity. We compare spatial turnover and nestedness of dung beetle assemblages using multiple dissimilarity measures accounting for compositional heterogeneity across forest (*i.e.*, forest edges and interiors of a primary forest and small fragments) and matrix habitats (*i.e.*, sugar cane plantations and pastures) as well as pairwise measures providing distance matrices accounting for the multivariate structure of dissimilarity.

Results There is a strong influence of fragmentation-related effects on dung beetle beta diversity with the spatial turnover increase in altered habitats (edge-affected and matrix habitats) promoting dung beetle differentiation. Although isolation distance among patches is a decisive predictor of spatial turnover, edge-effects augmented the spatial turnover at all scales. Lowest values of spatial turnover in interiors of primary forest suggest that dung beetle assemblages were not randomly distributed, with habitat quality necessarily leading to a strongly nested pattern of species composition.

Main conclusion We provide some evidence that the establishment of human modified landscape increases the spatial turnover of dung beetle assemblages, as habitat loss, creation of forest edges and the presence of open habitats operating as matrices promote dung beetle differentiation at habitat and landscape scale. These findings can help to implement conservation planning for dung beetles and other forest biodiversity persistence in severely deforested tropical landscapes.

Keywords: Atlantic Forest, edge-effects, land-use, nested pattern, species turnover, Scarabaeinae

INTRODUCTION

Beta diversity (ϐ) is a key component of species diversity originally introduced by Whittaker to describe changes in species composition and abundance across environmental continua (*e.g.*, gradients of elevation and moisture) and posteriorly also defined as species turnover or changes in species composition from one community to another (Whittaker, 1972; Veech, 2002). Spatial species turnover (*i.e.*, species replacement) and nestedness (*i.e.*, species loss or gain) of species assemblages are two different phenomena which ϐ-diversity is associated (Baselga, 2010). Spatial turnover implies the replacement of some species in one habitat by different species in the other habitat (Qian *et al*., 2005; Baselga, 2010). On the other hand, nestedness of species assemblages implies the elimination or addition of species in only one of the habitats with the poorest assemblage being a subsets of the biotas at richer habitats, reflecting a non-random process of species loss (or gain) (Baselga, 2010).

Analysis of spatial turnover and nestedness among sites, and in particular the relationships at different spatial scales, can provide important insights into the processes driving both local and regional patterns of species diversity (Rouquette *et al*., 2013). In this way, understanding the patterns of turnover and nestedness can be decisive to conservation implications. For instance, communities with high degree of nestedness in a landscape implies the need to prioritize a few high-diversity habitats in conservation planning, while communities with high spatial turnover suggests a regional approach focusing on multiple habitats (Wright & Reeves, 1992). This approach can be important in fragmented landscapes, where habitat loss and the consequent creation of artificial forest edges, have a pervasive and disruptive impact on biodiversity (Ewers & Didham, 2006). The long-term prospects of forest biodiversity and ecosystem services are thus inextricably linked to expanding human-modified landscapes that are often dominated by small forest fragments embedded within a harsh, open-habitat matrix (Melo *et al*., 2013). In the Brazilian Atlantic forest (one of the most diverse ecosystems in the world) (Silva & Tabrelli, 2000), nearly half of the remaining forest is located less than 100 m from open areas, over 70% is located less than 250 m from open land (Ribeiro *et al*., 2009).

With the expansion and consolidation of agricultural frontiers and the consequent reduction of pristine forests, few highly resilient species (ówinnersô) gradually come to dominate ecological communities at the expense of native species that cannot tolerate human-induced disturbances (ólosersô) (Tabarelli *et al*., 2012). This substitution of ólosersô by ówinnersô may result in a biotic homogenization, such species can even dominate communities, contributing to reduced ß-diversity across multiple spatial scales in response to the establishment of human-modified landscapes (Lôbo *et al*., 2011; Arroyo-Rodríguez *et al*., 2013). On the other hand, increases in ß-diversity (biotic differentiation) can also emerge in fragmented rain forest landscapes, as fragmentation limits interpatch dispersal patterns, and can therefore promote the compositional differentiation between forest patches and landscapes (Hubbell, 2001).

This understanding is particularly needed for dung beetle assemblages, as they are frequently used as indicators of natural or anthropogenic disturbance in tropical forests (Spector, 2006; Nichols *et al*., 2007; Gardner *et al*., 2008; Filgueiras *et al*., 2015). However, the value of altered habitats for dung beetle persistence is not a consensus. The influence of common limitations in sampling design, and differences in biogeographical and landscape context may explain why many studies about the response of dung beetles to habitat change have painted a more optimistic picture of the conservation value of anthropogenic habitats (Gardner *et al*., 2008). In this way, the spatial distribution and determinants for dung beetle ß-diversity have been rarely studied in human-modified landscapes, mainly the response of this component of species diversity to changes in landscape configuration. The use of turnover metrics can help to estimate the relative importance of changes in forest cover, landscape configuration and habitat quality as predictors of spatial patterns of variation in dung beetle assemblages in human-modified landscapes.

Here, we examine patterns of spatial turnover and nestedness in dung beetle assemblages across three spatial scales (among traps, among habitats, and among sampling arrays) in core areas and edges of a large tract of primary forest, small fragments, sugar-cane fields, and cattle pastures in a human-modified Atlantic Forest landscape of northeastern Brazil. We ask whether fragmentation-related effects lead dung beetle assemblages to a process of homogenization, with the spatial turnover within and among habitats decrease in altered habitats (*i.e.*, edge-affected and matrix habitats); or whether dung beetle assemblages are undergoing a process of differentiation, with the spatial turnover increase in altered habitats. To analyze these hypotheses the significance of species diversity at each habitat and the spatial turnover was evaluated with the additive partitioning of diversity (Veech *et al.*, 2002) and turnover metrics (Baselga & Orme, 2012), respectively. For this, we first investigate the extent to which the β-diversity of dung beetle assemblages varies in edge-affected habitats at different spatial scales according to additive partitioning of diversity. Second, we compare spatial turnover and nestedness using multiple dissimilarity measures accounting for compositional heterogeneity and pairwise measures providing distance matrices accounting for the multivariate structure of dissimilarity (Baselga & Orme, 2012) across several traps (in the interior-exterior non-linear gradient), within and among habitats. Third, we document levels of taxonomic similarity between habitats based on ordination analysis. Finally, we then discuss how additive partitioning of diversity and turnover metrics can be useful tools in improving sampling design of applied ecological studies.

METHODS

Study sites

The Serra Grande landscape is located within the Pernambuco Centre of Endemism, the most threatened ecoregion of the Brazilian Atlantic forest (Silva & Tabarelli, 2000). Annual precipitation is 2000 mm with a dry season (<60 mm/month) occurring from November to January and the wettest period between April and August (Pimentel & Tabarelli, 2004). The Serra Grande landscape (667 km^2) contain approximately 9000 ha of forest (9.2% of land cover) distributed across a total of 109 forest remnants, ranging from 1.67 to 3500 ha, all of which almost completely surrounded by sugar-cane fields (Silva & Tabarelli, 2000). The large Coimbra forest patch (3500 ha), the largest remnant of Atlantic forest in northeast Brazil, makes Serra Grande landscape an excellent scenario to understand the long-term effects of habitat fragmentation on plant (Oliveira *et al.*, 2004; Santos *et al.*, 2008) and animal communities (Filgueiras *et al.*, 2011; Leal *et al.*, 2012). The Coimbra forest is a primary forest fragment containing several large-seeded tree species and medium-sized frugivorous vertebrate, which have been almost completely extirpated in the entire region (Pimentel & Tabarelli, 2004). In addition to the dominant sugar-cane fields, the study landscape presents other matrix types, such as pastures and subsistence crops. However, the Coimbra forest is not fully representative of a vast tract of continuous forest, which constrains the comparative value of the best available baseline in our study design.

Survey effort was focused on 60 sampling units: 10 in core areas of the Coimbra forest remnant, 10 along forest edges, 10 in sugar-cane plantations and 10 in pastures, all of which adjacent to the Coimbra primary forest, 10 in small fragments, and 10 in their respective surrounding areas of sugar-cane plantations (Fig. 1). We selected 50 small forest fragments with little (< 9000 m^2) or no core area from which 10 fragments were drawn at random. We define core areas of forest interior as in previous studies (Santos *et al.*, 2008; Lopes *et al.*, 2009) beyond distances of 200m from the nearest forest edge. In this study, all study sites were spaced by at least 300m from each other (Mean ± SD: 2.91 ± 3.32), which minimized the lack of spatial independence between sites.

Patch and landscape metrics

Fragment area was quantified using two GIS packages (ArcView 3.2 and Erdas Imagine 8.4) on the basis of (1) three Landsat and Spot images (years 1989, 1998, 2003) and (2) a set of 160 aerial photos (1:8000) taken from helicopter overflights commissioned in April 2003 (and funded by Conservation International - Brasil). We measured the core area of each forest fragment to quantify the degree to which small patches used in this study were indeed edge-dominated. This was defined as the total remaining forest area once the 200-m buffer area had been subtracted (MacGarigal *et al.*, 2001).

Dung beetles sampling

Dung beetle surveys were carried out between October 2011 and February 2012. To avoid seasonality effects on dung beetle assemblages, trapping was carried out once at each site under comparable climatic conditions, avoiding rainy days (Estrada *et al.*, 1999). In the interior of the Coimbra forest, each sampling unit consisted of four pairs of pitfall traps, each of which 50 m apart and set along a linear transect. Paired traps within forest areas were set at distances of 15m, 30m, 60m and 120m away from the forest edge into core areas of the Coimbra forest; or at the geometric center of small fragments. Trapping within matrix habitats (cattle pasture and sugar-cane plantations) they were also set at 15m, 30m, 60m and 120m but away the nearest forest edge into the matrix (see Fig. S1). To avoid the lack of independence (Larsen & Forsyth, 2005), the trap-pairs along forest edges and matrix habitats were arranged according to an interior-exterior non-linear gradient (see Fig. S1). Sampling arrays in all habitats were located haphazardly but always ensuring a minimum distance from one another of 300 m. Pitfall traps consisted of plastic containers (15 cm in diameter and 13 cm in height) with a bait-holding recipient (3 cm in diameter by 4.8 cm in height) containing ~30 g of human feces. Dung beetle samples were collected 48 h after traps were installed, and taken to the Serra Grande field station, where the morphospecies were sorted. All dung beetles were then taken to the Insect Taxonomy and Ecology Laboratory at the Universidade Federal de Pernambuco for further identification and storage. Dung beetles were identified to species level at Universidade Federal de Pernambuco and Universidade Federal de Mato Grosso, Brazil, and voucher specimens of all species are deposited at both entomological collections.

Data analysis

We assessed the compositional completeness of each habitat using EstimateS 9.1 (Colwell, 2013) by calculating the number of observed species as a percentage of the total richness, which was estimated based on the average of three abundance-based nonparametric estimators: Bootstrap, Chao 1 and Jack 1. To describe patterns of β-diversity across the entire fragmented landscape, we used additive partitioning of the total diversity expressed as species richness. We calculated the average number of species absent from each site (ϐ-diversity) defined as ϐ = ɔ ï Ŭ, where ɔ is the total number of species sampled across the entire landscape (ɔ-diversity) and Ŭ is the average number of species occurring at any given site (Ŭ-diversity) (see Veech *et al,*. 2002). We also applied a hierarchical structure of these analyses across different spatial scales. In these terms, measures of Ŭ-diversity at the trap, forest interior-exterior gradient, and habitat levels are represented by the mean of 480 traps, 60 gradients, and six habitat types, respectively. ϐ-diversity among traps is then the difference between the Ŭ-diversity at the gradient scale and that of traps. Likewise, ϐ-diversity among gradient units is the difference between the habitat Ŭ-diversity and that of gradients, and so on.

To analyze patterns of spatial turnover and nestedness at multiple scales we used a species partitioning method (Baselga & Orme, 2012) that allows the total Sørensen dissimilarity (beta diversity, $ϐ_{sør}$) to be separated into components of dissimilarity due to species replacements (i.e. turnover; $ϐ_{sim}$) and dissimilarity due to nestedness ($ϐ_{sne}$). We used the $ϐ_{sim}$ (Simpson dissimilarity) (turnover component of Sørensen dissimilarity) and $ϐ_{sne}$ (the nestedness component of Sørensen dissimilarity) as in Baselga & Orme (2012):

$$ϐ_{sim} = b/b+a \text{ and } ϐ_{sne} = (c-b/a+b+c)(a/2b+a)$$

where *a* is the number of shared species between two cells, *b* the number of species unique to the poorest site, and *c* the number of species unique to the richest site. We analyze whether both turnover and nestedness differed according to distances along the interior-exterior non-linear gradient, between edge-dominated habitats (small fragments and forest edges along the large patch of primary forest), and the adjacent matrix (sugar cane plantation) using Kruskal-Wallis test. We also computed multiple-site dissimilarity measures of dung beetle assemblages from presence-absence tables for each pair of habitats and related to geographical distance using Mantel tests with 10,000 permutations.

To test whether dung beetle assemblages are taxonomically similar across the landscape, we used Non-metric Multidimensional Scaling (NMDS) ordination of all 60 habitats using their Bray-Curtis dissimilarity matrix with 1000 random restarts. Finally, we used analysis of similarities (ANOSIM - Clarke and Gorley, 2001) to test for significant differences in dung beetle assemblages in the landscape. NMDS ordinations and ANOSIM were carried out in PRIMER (Clarke and Gorley, 2001). Estimates of ϐ-diversity and Mantel tests were carried out using the *betapart* and *ecodist* packages, respectively, in R version 3.1.0 (R Core Team 2014).

RESULTS

Dung beetle species distribution

We captured a total of 4,218 dung beetles belonging to 45 species and 19 genera. Comparisons of full estimates of species richness with numbers of species that were actually observed indicated that on average we detected 78% of all species present at each site (range = 73 - 84%) (Table S1). As expected, the number of species varied among habitats, being higher in forest sites (forest interior, forest edge and small fragments, 20 species) than in matrix habitats (pastures around the Coimbra forest and sugar-cane plantations around small fragments, 11 species) (Fig. 1A). The highest proportion of rare (species with one individual) (9 species, 45%) and restricted species (7 species, 35%) was found in forest edges and small fragments, respectively (see Fig. 1A). Additive partitioning of diversity indicated that Ŭ-diversity of forest environments (i.e. forest edges, small fragments and core primary forest) comprised 64% of the total species richness across all sites. Beta diversity contributed to 19%, 19% and 18% of the total diversity for the sugar-cane matrix of small fragments, pasture, and sugar-cane matrix of primary forest, respectively (see Fig. 1B). In terms of the overall spatial hierarchy, ϐ-diversity contributed to 68% and 7% of total dung beetle diversity at the habitat and trap levels, respectively (Fig. 1B).

Patterns of spatial turnover and nestedness across spatial scales

The percentage of shared species ranged from 20% between the Coimbra forest interior and small fragments, and between forest edges and small fragments, to 38% between forest interior sites and forest edges (Table 1). In terms of matrix habitats, sugar-cane plantations and pastures around the Coimbra forest shared the highest percentage of species (see Table 1).

As expected, spatial turnover was much higher within and among habitats than across traps (Table 2). At both the trap and habitat scales, forest interior showed lower spatial turnover in dung beetle species. In general, edge-affected habitats and adjacent matrix increase the spatial turnover and decrease nested pattern of dung beetle assemblages (see Table 2). In terms of the interior-exterior non-linear gradient (forest edges + pastures + sugar cane), there was only significant differences in nestedness (K-W-test $H= 4.74$, d.f.=1, $P< 0.05$) while for species turnover (K-W-test $H= 2.1$, d.f.=1, $P> 0.05$) there was no difference among habitats (Fig. 2A-B). Small fragments and sugar cane plantations did not exhibit any differences in both species turnover (K-W-test $H= 2.08$, d.f.=1, $P > 0.05$) and nestedness (K-W-test $H= 3.5$, d.f.=1, $P > 0.05$) (Fig. 2C-D). In addition, when we calculated pairwise ϐ-diversity between sampling arrays using $ϐ_{sim}$, forest environments and matrix habitats resulted in two clearly segregated clusters (Fig.3A-B). However, for forest edge and core primary forest as well as sugar-cane plantation and pastures, the pattern of ϐ-diversity aggregation was unclear (Fig. 3C-D).

Mantel tests failed to uncover any spatial effects on species turnover and nested pattern (see Fig. S2). At both within and among habitats, dung beetle turnover and nestedness were not correlated with geographical distance (Fig. S2), whereby neighbouring sites were not necessarily more similar in their community composition (Table S2). In general, species turnover was most closely aligned with distance along forest edges and between forest edges + forest interiors of primary forest (Fig. S2). This was confirmed by NMDS ordination of sampling units based on species composition and abundance resulted in consistent and segregated clusters as follow: (a) one formed by forest edges, core areas of Coimbra forest and small fragments (Fig. 4A), and (b) one cluster formed by forest edges and core areas and another cluster formed by small fragments (Fig. 4B). This clear taxonomic segregation in dung beetle assemblages across the landscape, particularly in both abundance ($R = 0.67$, $p < 0.01$) and species composition ($R = 0.68$, $p < 0.01$) were supported by ANOSIM tests.

DISCUSSION

The relationship between species turnover and habitat configuration is highly relevant to the potential conservation value of human-modified tropical forest landscapes (Arroyo-Rodríguez *et al.*, 2013). Our results suggest that dung beetle assemblages showed a highest spatial turnover in edge-dominated habitats, corroborating the hyphothesis of differentiation these beetles in human-modified landscapes. More specifically, we found that (1) there is a strong influence of fragmentation-related effects on dung beetle β-diversity with the spatial turnover increase in altered habitats (edge-affected and matrix habitats) in all spatial scales; (2) although isolation distance among patches is a decisive predictor of spatial turnover, edge-effects augmented the spatial turnover; (3) dung beetle assemblages in forest interiors of primary forest were not randomly distributed (lowest value of turnover), with habitat quality necessarily leading to a strongly nested pattern of species composition, and (4) dung beetle turnover and nestedness were not correlated with geographical distance, whereby neighboring sites were not necessarily more similar in their community composition.

The increase of species turnover in edge-affected and matrix habitats corroborate the hypothesis of dung beetle differentiation suggests that human-modified landscapes are able to retain a significant proportion of dung beetle fauna, although forest interior represents an irreplaceable habitat (Gardner *et al.*, 2008; Filgueiras *et al.*, in press). The spatial distribution of small fragments (*i.e.*, edge-dominated habitats) had an important role in spatial turnover even though small fragments had limited habitat availability and contained less resources, inflating species niche overlap and local extinction risk (Fahrig, 2003; Banks-Leite *et al.*, 2010). The landscape-scale composition and spatial configuration of habitats can be decisive to the dispersal ability and landscape connectivity of isolated populations (Prevedello & Vieira, 2010). For instance, the configuration of habitat patches within the overall landscape matrix has a decisive effect on the species similarity of dung beetle assemblages in a Mediterranean system (Numa *et al.*, 2009). In the Atlantic Forest, low structural connectivity through greater distances between forest fragments may impose severe limitations on matrix dispersal (Filgueiras *et al.*, 2011). This spatial limitation among patches can therefore explain in part the compositional differentiation of dung beetle assemblages between forest patches. Additionally, the effect of patch isolation is also correlated with the type and composition of the matrix, the degree of contrast between forest and the adjacent matrix (Ewers & Didham, 2006), and the ability of different species to traverse habitat edges (Uezu *et al.*, 2008; Uezu & Metzger, 2011). Matrix quality is therefore a critical determinant of the persistence of forest species in human-modified landscapes (Perfecto & Vandermeer, 2002).

In our study we corroborated the hypothesis that forest species from small patches show weaker patterns of response to edge-effects to those previously reported for primary forest (Fletcher *et al*., 2007). In fact, small fragments and their adjacent matrix exhibit a lower dung beetle turnover than a comparable gradient between forest edges along large areas of primary forest and their adjacent matrix. Multiple edges profoundly influence ecological patterns and processes within small forest patches (Malcolm, 1994; Fletcher *et al*., 2007), and theoretical models consistently predict that edge effects should occur on both sides of the habitat boundary (*i.e.*, forest + matrix) (Ewers & Didham, 2006). We surmise that the mass effect of matrix dynamics is stronger in small forest fragments, where species persistence tends to be associated with a preference for edge habitats.

On the other hand, the small difference in species turnover among matrix habitats reflects a drastic biotic homogenization of dung beetle assemblages compared to forest environment (*i.e.*, edges of primary forest and small fragments), then thus contributing with a small position of the overall diversity across the entire landscape. The configuration and dispersion of matrix habitats may either reduce or increase landscape connectivity (Kindlmann & Burel, 2008). At Serra Grande, small fragments are entirely surrounded by an uniform and inhospitable matrix of sugar-cane monoculture (Santos *et al*., 2008) that are periodically subjected to hostile cropland treatments, including burning and use of pesticides, making it uninhabitable to most forest dung beetles (BKCF pers. obs.). Even with the presence of cattle pastures around the Coimbra primary forest, which can be an attractive food source for forest dung beetles (Halffter & Arellano, 2002), structural differences between open and forest habitats can largely explain the divergence in community structure (Hanski & Cambefort, 1991). On the other hand, the presence of a few forest species within the matrix (*e.g.*, *Dichotomius* aff. *sericeus*, *Coprophanaeus dardanus*, *Oxysternon silenus*) supports the habitat supplementation hypothesis, which posits that species typical of a habitat type may be supplement their metabolic requirements with resources from an adjacent habitat type (Brotons *et al.*, 2005). In these terms, edge-dominated and matrix habitats can be regarded as suitable only for a limited subset of generalists forest species (Wright & Muller-Landau, 2006). In fact, dung beetle species sensitivity to landscape structure can be observed across the varying species responses to landscape matrix type (Numa *et al.*, 2009) altering the spatial turnover of human-modified landscapes.

The greatest number of shared species between forest edges and core areas of Coimbra forest supports geometrical propositions asserting that edge-dominated areas often receive individuals from central patch areas (Peyras *et al.*, 2013; Prevedello *et al.*, 2013). If so, larger patches promote higher edge colonization rates than smaller patches (Prevedello *et al.*, 2013). This low species turnover can be explained by the wider spectrum of habitats exploited by dung beetles in primary forest. Nonetheless, the structural differences between forest edge and interior, such as lower canopy cover, reduced vertical stratification, and drier microclimatic conditions near edges (Laurance, 2001), are far less limiting for dung beetles than the drastic environmental conditions of matrix habitats. The Coimbra forest still retains a virtually complete set of medium and large-bodied mammal species (*e.g.*, agoutis, *Dasyprocta* sp.; paca, *Cuniculus paca*; coati, *Nasua nasua*; peccary, *Tayassu tajacu*; cats, *Herpailurus yaguarondi*, *Leopardus tigrinus* and *Leopardus pardalis*) (Pimentel & Tabarelli, 2004), which produce high-quantity fecal resources for dung beetles, thereby partly explaining the greater number of species shared along the forest edge-interior gradient of the Coimbra forest. In fact, more evenly distributed dung beetle assemblages rely on maintaining a large mammal biomass (Culot *et al.,* 2013; Nichols *et al.,* 2013). On the other hand, habitats that were closer together did not necessarily exhibit a similar nested pattern, highlighting the role of configuration in habitat heterogeneity in boosting species turnover in human-modified landscapes. For example, the species turnover of small fragments P_{31} and P_{45}, which are 16.5 km apart, was identical to that of E_6 (forest edge 6) and I_{10} (forest interior 10), which are only 0.3 km apart (see Table S2).

In conclusion, we showed that differences in spatial turnover are strongly influenced by habitat configuration. Variation in β-diversity increase in altered habitats (*i.e.*, edge-affected and matrix habitats) corroborating the hypothesis of dung beetle differentiation. In this way, the use of turnover metrics to understand the importance of ecological boundaries gained new insights into the relative importance of spatial turnover to dung beetle persistence in human-modified landscapes. To implement conservation planning in these landscapes, knowledge of spatial turnover will be of indispensable value to characterize the conservation potential of tropical forest species. Although most conservation efforts prioritize remaining core areas of continuous forest, the importance of preserving all components of hyper-fragmented landscapes cannot be neglected. Our study demonstrates that although core forest areas contain a substantial component of the native forest dung beetle fauna, edge-affected habitats (*i.e.*, edges of primary forest and small fragments) played a contribution to the overall diversity of the entire landscape, and can be considered targets of conservation management. In fact, heterogeneous mosaics are able to retain high levels of biodiversity (Wright & Muller-Landau, 2006) and could additionally act as corridors or óstepping-stonesô for different organisms (Pardini *et al.*, 2005). However, we collected 20 dung beetle species within 3.24 km of forest interior and 20 species along 5.05 km of forest edges of primary forest. On the other hand, we also collected 20 dung beetle species in small fragments, but spanning a much wider range of 12.47 km. In this way, the conservation planning to maximize the number of dung beetle species should focus on different elements of the landscape (including edge-affected habitats), but prioritizing forest environments containing high-habitat quality.

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Table 1. Matrix table describing the percentages of species shared between habitat types sampled across the Serra Grande landscape, Alagoas, Brazil. FI: Forest Interior; FE: Forest Edge; MC: Sugar-cane matrix of the Coimbra Forest; MP: Pasture matrix of Coimbra Forest; SF: small forest fragments; MSF: Sugar-cane matrix of small fragments.

Locality (species richness)	FE (%)	MC (%)	MP (%)	SF (%)	MSF (%)
FI (20)	38	9	7	20	2
FE (20)		9	4	20	2
MC (12)			16	11	13
MP (11)				9	11
SF (20)					7

Table 2. Mean ± SD of species turnover (β_{sim}), nestedness (β_{sne}) and Sørensen dissimilarity ($\beta_{sør}$) of dung beetle assemblages among pitfall traps, habitat types and sampling arrays across the entire Serra Grande landscape, Alagoas, Brazil.

	Sites	β_{sim} [a]	β_{sne} [b]	$\beta_{sør}$ [c]
Traps	Forest interiors (N=80)	0.17(0.05)	0.09(0.02)	0.26(0.03)
	Forest edges (N=80)	0.29(0.04)	0.16(0.04)	0.45(0.02)
	Matrix of primary forest (sugar-cane) (N=80)	0.38(0.06)	0.09(0.04)	0.47(0.03)
	Matrix of primary forest (pastures) (N=80)	0.23(0.10)	0.17(0.05)	0.4(0.07)
	Small fragments (N=80)	0.33(0.03)	0.02(0.001)	0.35(0.03)
	Matrix of small fragments (sugar-cane) (N=80)	0.66(0.07)	0.07(0.01)	0.73(0.05)
Within habitats	Forest interiors (N=10)	0.44(0.01)	0.16(0.01)	0.60(0.01)
	Forest edges (N=10)	0.52(0.03)	0.16(0.02)	0.67(0.01)
	Matrix of primary forest (sugar-cane) (N=10)	0.47(0.04)	0.20(0.02)	0.67(0.02)
	Matrix of primary forest (pastures) (N=10)	0.66(0.04)	0.09(0.02)	0.75(0.02)
	Small fragments (N=10)	0.69(0.02)	0.10(0.01)	0.79(0.01)
	Matrix of small fragments (sugar-cane) (N=10)	0.77(0.02)	0.07(0.01)	0.84(0.01)
Among habitats	Forest interiors + forest edges (N=20)	0.66(0.01)	0.13(0.05)	0.79(0.03)
	Forest edges + small fragments (N=20)	0.81(0.05)	0.06(0.03)	0.87(0.02)
	Forest edges + sugar-cane (N=20)	0.82(0.05)	0.06(0.03)	0.88(0.01)
	Forest edges + pasture (N=20)	0.83(0.04)	0.06(0.03)	0.89(0.01)
	Forest edges + sugar-cane + pasture (N=30)	0.86(0.01)	0.04(0.01)	0.90(0.10)

Forest edge + forest interior + sugar cane + pasture (N=40)	0.88(0.01)	0.04(0.01)	0.92(0.05)
Small fragments + sugar-cane (N=20)	0.85(0.06)	0.05(0.004)	0.90(0.03)
Matrix of primary forest sugar-cane + pastures (N=20)	0.75(0.01)	0.08(0.008)	0.83(0.006)

[a] ɓ$_{sim}$ (Simpson dissimilarity) (turnover component of Sørensen dissimilarity).

[b] ɓ$_{sne}$ (the nestedness component of Sørensen dissimilarity).

[c] ɓ$_{sør}$ (Sørensen dissimilarity) = ɓ$_{sim}$ + ɓ$_{sne}$.

Figure Labels

Figure 1. Total species richness, number of species rare and restricted in all habitats sampled (A). Additive partitioning of dung beetles (β diversity) in all habitats sampled and in a hierarchy of different spatial scales (B). Additive partitioning of dung beetles (α + β diversity) among habitats: S1 (small fragments + sugar cane plantation) and S2 (forest interior + forest edge + sugar cane plantation + pasture) (B). FI= forest interior, FE= forest edge, ME= matrix (sugar-cane plantation) of Coimbra forest, MP= = matrix (pasture) of Coimbra forest, SF= small fragments, MSF= = matrix (sugar-cane plantation) of small fragments. β_1=trap scale, β_2=non-linear gradient scale and β_3=habitat scale. β_I= β-diversity of forest interiors of primary forest, β_E= β-diversity of forest edges of primary forest, β_{SF}= β-diversity of small fragments, β_{MSF}= β-diversity of matrix (sugar-cane plantation) of small fragments, β_P = β-diversity of matrix (pastures) of primary forest, β_{ME}= β-diversity of matrix (sugar-cane plantation) of primary forest.

Figure 2. Species turnover (β_{sim}) and nestedness (β_{sne}) of dung beetle assemblages according to different distances in a non-linear gradient sampled in Serra Grande landscape, Alagoas, Brazil. (A) and (B) forest edge of primary forest (negative distance) + matrix (pastures and sugar-cane plantations) (positive distance), (C) and (D) small fragments (negative distance) + matrix (sugar-cane plantation) (positive distance).

Figure 3. Clustering using average linkage of the β_{sim} components of species dissimilarity between: (A) small fragments (P31, P36, P38, P44, P45, P47, P48, P57, PDB, PIB) + matrix (MP31-MPIB), (B) forest edges of primary forest (E1-E10) + matrix (M1-M10), (C) forest edges (E1-E10) + forest interiors (I1-I10) of primary forest

and (D) sugar-cane plantation (M1-M10) + pastures (P1-P10) of primary forest sampled in Serra Grande landscape, Alagoas, Brazil.

Figure 4. NMDS based on dung beetle community structure in terms of abundance (A) and species composition (B) across forest and matrix habitats. Forest edges (open squares) and sugar-cane plantation (dark shaded squares) of small forest fragments, forest edge (dark shaded trianlges), interior forest areas (open triangles), sugar-cane plantation (open circles) and pastures (dark shaded circles) of Coimbra forest (primary forest).

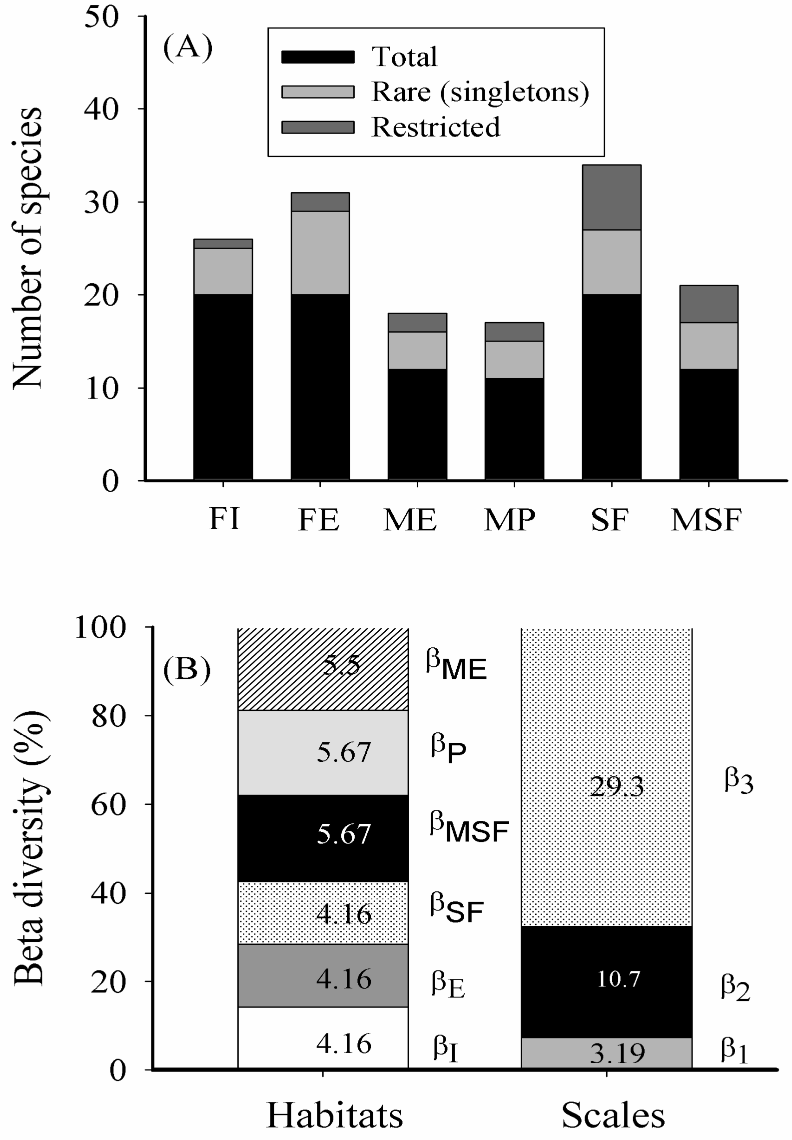

(A)
Number of species
0
10
20
30
40
50
Total
Rare (singletons)
Restricted
FI
FE
ME
MP
SF
MSF
(B)
Beta diversity (%)
0
20
40
60
80
100
5.5
β_{ME}
5.67
β_P
5.67
β_{MSF}
4.16
β_{SF}
4.16
β_E
4.16
β_I
29.3
β_3
10.7
β_2
3.19
β_1
Habitats
Scales

Fig. 1

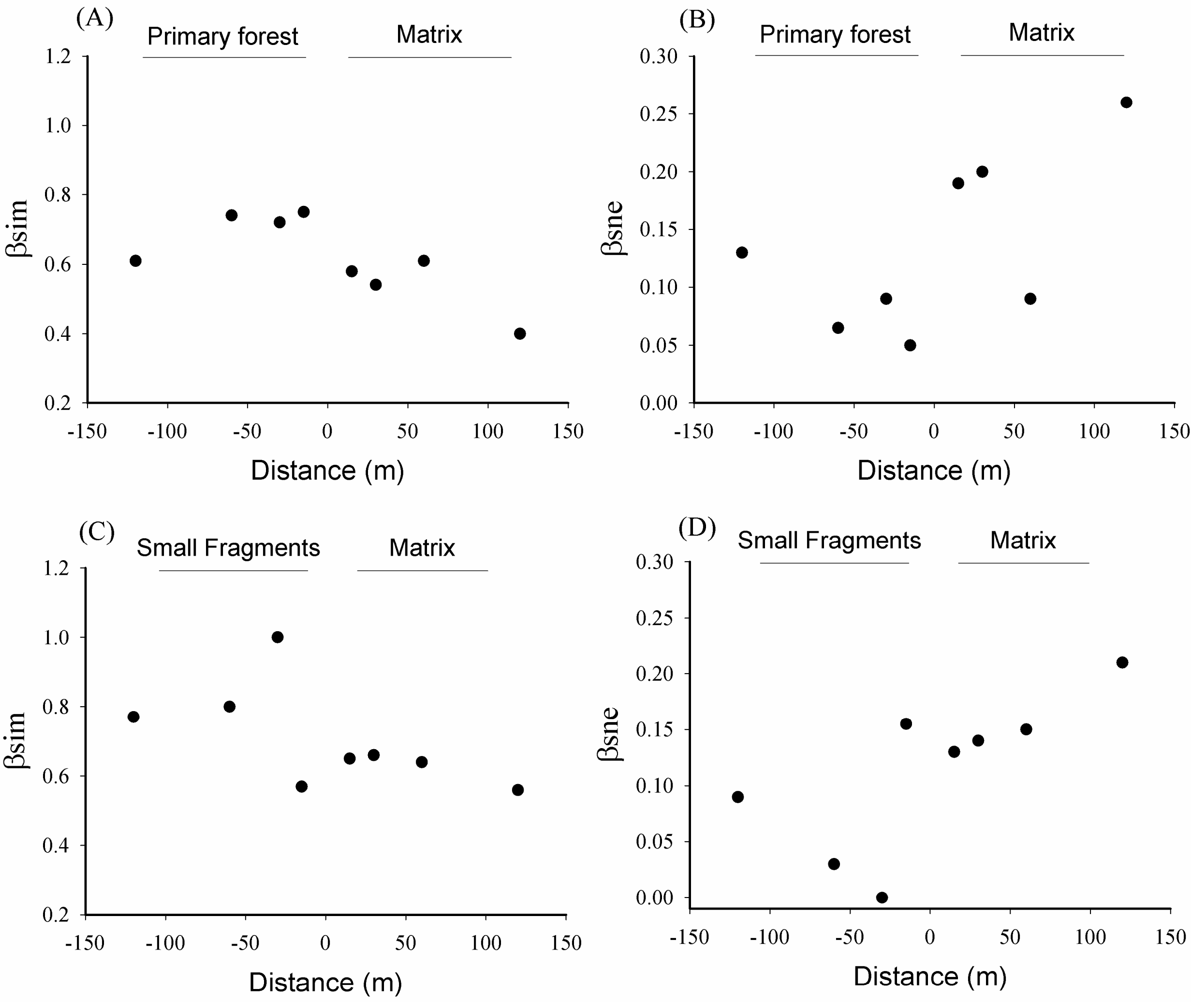

(A)
Primary forest
Matrix
βsim
1.2
1.0
0.8
0.6
0.4
0.2
-150
-100
-50
0
50
100
150
Distance (m)
(B)
Primary forest
Matrix
βsne
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-150
-100
-50
0
50
100
150
Distance (m)
(C)
Small Fragments
Matrix
βsim
1.2
1.0
0.8
0.6
0.4
0.2
-150
-100
-50
0
50
100
150
Distance (m)
(D)
Small Fragments
Matrix
βsne
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-150
-100
-50
0
50
100
150
Distance (m)

Fig.2

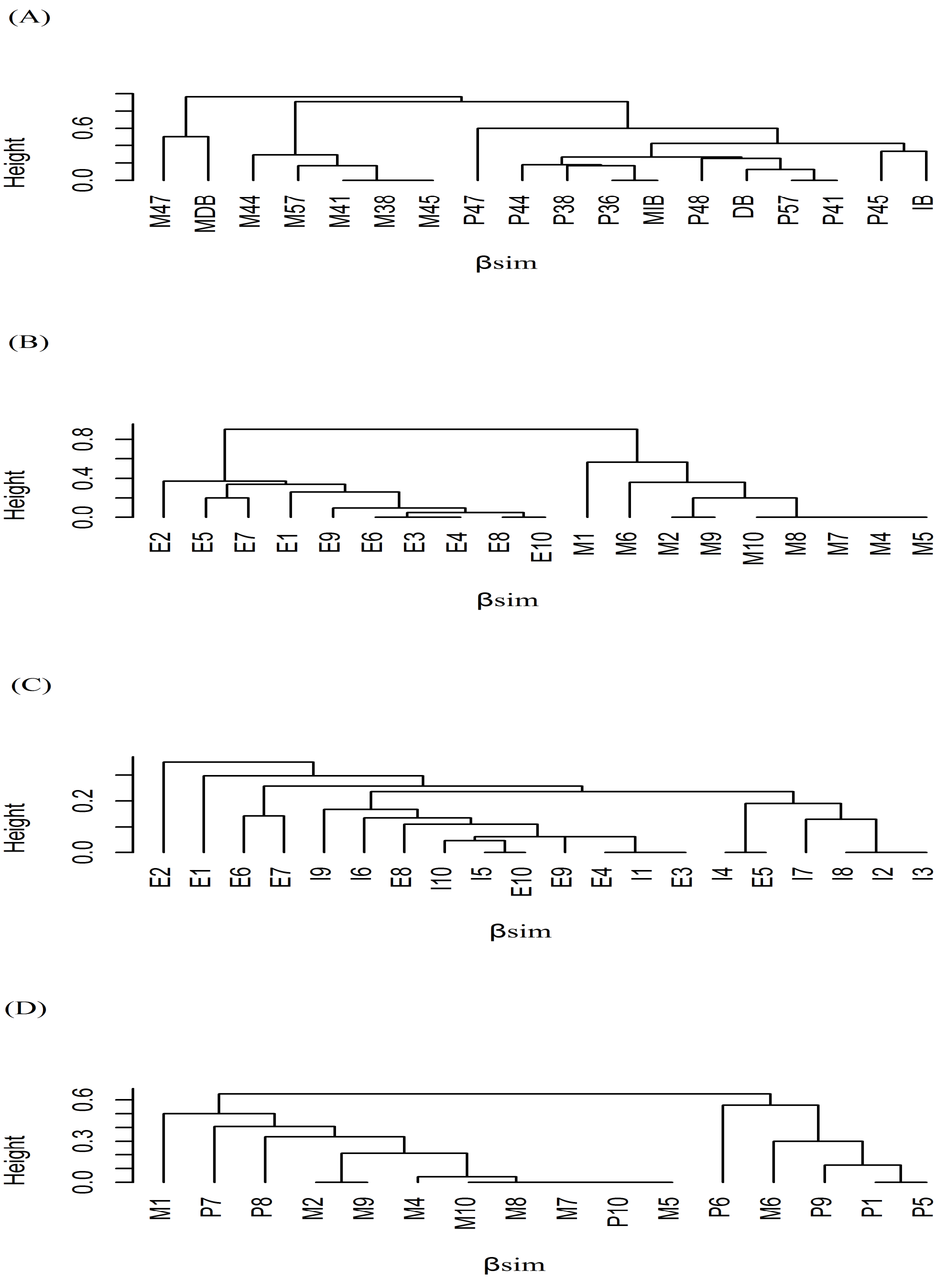

(A)
Height
0.0
0.6
M47
MDB
M44
M57
M41
M38
M45
P47
P44
P38
P36
MIB
P48
DB
P57
P41
P45
IB
βsim
(B)
Height
0.0
0.4
0.8
E2
E5
E7
E1
E9
E6
E3
E4
E8
E10
M1
M6
M2
M9
M10
M8
M7
M4
M5
βsim
(C)
Height
0.0
0.2
E2
E1
E6
E7
I9
I6
E8
I10
I5
E10
E9
E4
I1
E3
I4
E5
I7
I8
I2
I3
βsim
(D)
Height
0.0
0.3
0.6
M1
P7
P8
M2
M9
M4
M10
M8
M7
P10
M5
P6
M6
P9
P1
P5
βsim

Fig. 3

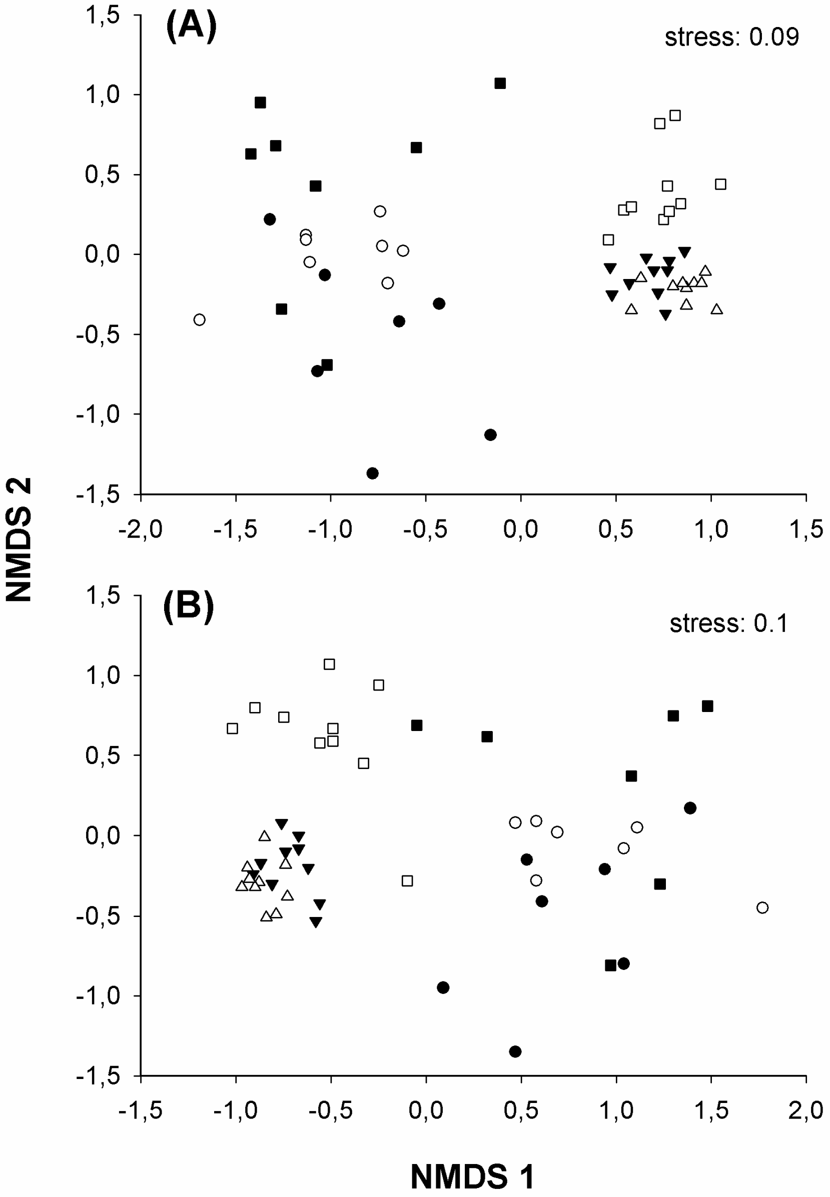

(A)
stress: 0.09
(B)
stress: 0.1
NMDS 2
NMDS 1
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-2,0
-1,5
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0

Fig. 4

Table S1. Species richness, completeness and abundance for dung beetles sampled in Atlantic forest, Alagoas, north-eastern Brazil.

Habitats			Completeness[a]			
	Richness	Abundance	Chao1	Jack1	Bootstrap	Mean±SD
Forest interiors (Coimbra forest)						
1	12	107	12	14.5	12.7	13.06 ±0.74
2	11	150	14	14.5	12.6	13.7 ±0.56
3	9	477	10	10.88	10.67	10.51 ±0.26
4	9	187	10	11.63	10.28	10.63 ±0.5
5	12	245	12	12.88	12.99	12.62 ±0.31
6	7	116	7	7.88	7.49	7.45 ±0.25
7	8	103	12	12.5	10.52	11.67 ±0.59
8	6	24	6	6.88	6.67	6.51 ±0.26
9	7	50	7	7.75	6.73	7.16 ±0.3
10	11	109	11.25	13.63	12.35	12.41 ±0.68

Forest edges (Coimbra forest)						
1	6	30	6.5	8.63	7.13	7.42 ±0.63
2	6	47	5.5	6.75	5.79	6.01 ±0.37
3	5	27	5	6.75	5.89	5.88 ±0.5
4	6	64	6	6.88	6.37	6.41 ±0.25
5	5	59	5	5.88	5.47	5.45 ±0.25
6	11	102	16	15.38	12.83	14.73 ±0.97
7	7	92	10	9.63	8.04	9.22 ±0.6
8	9	118	12	13.38	10.94	12.11 ±0.7
9	11	83	32	17.13	13.51	20.88 ±5.65
10	5	55	5	5.88	5.41	5.43 ±0.25
Matrix of Coimbra forest (sugar-cane)						
1	2	10				NE

2	3	3	6	5.63	4.03	5.22 ±0.36
3	0	0				NE
4	6	13	7	9.5	7.5	8 ±1.34
5	3	12	3	3	3.22	3.07 ±0.31
6	5	8	11	8.5	6.47	8.65 ±0.25
7	3	13	3	3	3.22	3.07 ±0.64
8	4	19	8.75	11.5	9.58	9.94 ±0.56
9	8	32	8.75	11.5	9.58	9.94 ±0.81
10	3	9	3	4.75	3.71	3.82 ±0.5
Matrix of Coimbra forest (pastures)						
1	5	10	5.5	6.75	5.99	6.08 ±0.36
2	0	0				NE
3	0	0				NE
4	0	0				NE

5	1	3				NE
6	4	4	10	7.5	5.37	7.62 ±1.38
7	3	11	4	4.75	3.71	4.15 ±0.31
8	3	7	3	3.88	3.47	3.45 ±0.25
9	4	10	4.5	6.63	5.03	5.38 ±0.64
10	5	9	8	7.63	6.15	7.26 ±0.56
Forest edges of small fragments						
P36	3	69	3	3.88	3.34	3.41 ± 0.25
P38	8	323	12	12.5	10.5	11.67± 0.6
P44	5	452	7	8.75	7.81	7.85±0.5
P45	3	75	5	5.88	5.39	5.42 ±0.25
P47	3	62	3	3.88	3.44	3.44 ±0.25
P48	4	165	4	4.75	3.69	4.14 ±0.31
P57	4	116	4	4.88	4.32	4.4 ±0.25

P54	4	44	4	4.88	4.44	4.44 ±0.25
PIB	6	62	4	4	4.1	6.68 ±0.03
P31	7	395	6	6.88	6.49	7.85 ±0.25
Matrix of small fragments (sugar-cane)						
Matrix P36	0	0				NE
Matrix P38	3	3	3.5	4.75	3.79	4.01 ±0.37
Matrix P44	3	4	2	2.88	2.44	4.65 ±0.25
Matrix P45	1	3				NE
Matrix P47	4	8	6	5.63	4.03	5.22 ±0.6
Matrix P48	0	0				NE
Matrix P57	2	2	4	5.75	4.89	4.88 ±0.5
Matrix PDB	2	3	3	3.75	2.69	3.14 ±0.31
Matrix PIB	1	1				NE
Matrix P31	1	11				NE

[a] Estimated species richness based on three abundance-based richness estimators,Chao 1, Jack 1 and Bootstrap (see Colwell 2013).

Table S2. Pairwise Beta diversity (β_{sim}) of dung beetles and linear distances (km) for small forest fragments (A), forest edge and forest interior (B) and adjacent matrices (C). Linear distances (km) are shown above the diagonal line for (A), and in parentheses for (B) and (C).

						Habitat types					
(A)						Fragments					
		p36	p38	p44	p45	p47	p48	p57	pDB	pIB	p31
Fragments	p36		6.05	6.9	4.62	13.67	5.6	4.8	9.38	9.1	12.23
	p38	0.33		1.36	9.9	9.23	9.63	10.04	8.82	5.79	7.3
	p44	0.33	0.2		10.55	8.67	10.45	10.88	9.52	5.78	6.96
	p45	0.66	0.33	0.66		18.2	7.83	6.92	13.02	13.33	16.53
	p47	0.66	0.66	0.66	0.66		14.63	15.63	9.43	5.6	1.89
	p48	0.33	0.25	0.5	0.33	0.66		1.34	6.41	9.15	13.1
	p57	0.33	0.25	0.5	0.33	0.66	0.25		7.7	10.16	14
	pDB	0.33	0.25	0.5	0.33	0.66	0.25	0.25		4.73	8.44
	pIB	0.66	0.5	0.6	0.33	0.66	0.5	0.5	0.5		4.06
	P31	0.33	0.28	0.4	0.33	0.66	0.25	0	0	0	
(B)						Interiors					
		I1	I2	I3	I4	I5	I6	I7	I8	I9	I10
Edges	E1	0.16 (1.58)	0.16(1.2)	0.16(1.66)	0.5(3.67)	0.16(3.43)	0.33(1.76)	0.33(1.7)	0.33(1.87)	0.33(2.12)	0.16(2.1)
	E2	0.33(3.66)	0.33(2.52)	0.33(2.81)	0.33(5.88)	0.33(5.69)	0.33(3.78)	0.33(3.72)	0.33(3.68)	0.33(3.99)	0.33(4.2)
	E3	0(0.54)	0.2(1.35)	0.2(1.6)	0.4(2.51)	0(2.28)	0.2(0.78)	0.4(0.88)	0.4(1.08)	0.2(1.19)	0(0.98)
	E4	0(0.49)	0.16(0.87)	0.16(1.03)	0.33(2.74)	0(2.61)	0.16(0.61)	0.44(0.91)	0.33(0.67)	0.16(0.94)	0(1.06)
	E5	0.2(0.31)	0.2(1.2)	0.2(1.3)	0(2.39)	0.2(2.21)	0.2(0.34)	0.2(0.58)	0.2(0.61)	0.4(0.75)	0.2(0.73)
	E6	0.27(0.38)	0.27(1.63)	0.27(1.65)	0.33(1.88)	0.27(1.78)	0.14(0.31)	0.22(0.32)	0.16(0.49)	0.28(0.56)	0.36(0.3)

E7	0.28(0.85)	0.28(2.03)	0.28(2.18)	0.42(1.95)	0.28(1.65)	0.28(0.96)	0.42(1.13)	0.33(1.37)	0.42(1.33)	0.28(0.82)
E8	0.22(1.06)	0.33(2.31)	0.33(2.45)	0.44(1.57)	0.22(1.27)	0.14(1.09)	0.44(1.15)	0.16(1.54)	0.28(1.4)	0.11(0.84)
E9	0.18(1.68)	0.09(3.02)	0.09(3.06)	0.33(0.86)	0.09(0.51)	0.14(1.69)	0.22(1.85)	0(2.01)	0.14(1.79)	0.09(1.28)
E10	0(1.9)	0(3.21)	0(3.3)	0.2(1.03)	0(0.64)	0(1.92)	0.2(2.1)	0.2(2.3)	0(2.08)	0(1.51)

(C)		Pastures					
		P5	P6	P7	P8	P9	P10
Sugar-cane	M1	0.5(1.58)	1.0(0.84)	1.0(0.91)	0.5(1.07)	0.5(1.2)	0.5(1.54)
	M2	0.33(2.94)	1.0(2.35)	1.0(2.29)	0.66(2.56)	0.33(2.59)	0.66(2.77)
	M4	0.4(3.6)	1.0(3.47)	0.75(3.4)	0.33(3.57)	0.33(3.32)	0.5(4.01)
	M5	0.33(2.82)	1.0(2.49)	1.0(2.42)	0.33(2.61)	0.33(2.51)	0.66(2.99)
	M6	0.4(2.87)	0(2.39)	0.75(2.33)	0.66(2.55)	0.66(2.54)	0.5(2.18)
	M7	0.33(2.3)	1.0(1.66)	1.0(1.62)	0.33(1.89)	0.33(1.97)	0.66(2.06)
	M8	0.25(2.02)	1.0(1.01)	1.0(1.05)	0.33(1.28)	0.33(1.62)	0.5(1.33)
	M9	0.2(2.21)	1.0(1.06)	1.0(1.1)	0.33(1.4)	0.33(1.81)	0.5(1.07)
	M10	0.33(2.49)	1.0(0.31)	1.0(0.35)	0.33(0.61)	0.33(1.11)	0.66(0.94)

Figure S1. Map of Serra Grande landscape of northeastern Brazil (A) showing the 60 sampling sites in Atlantic forest (B). Schematic figure showing an example of the sampling design used to assess dung beetle communities in interior-exterior non-linear gradient in forest edges and matrix habitats. Pitfall traps (dark shaded circles) (C). The forest fragments sampled are represented by black circles. Light-shaded areas represent remaining Atlantic forest remnants that were not sampled. Blank spaces represent uniform matrix of sugar-cane monoculture and pastures.

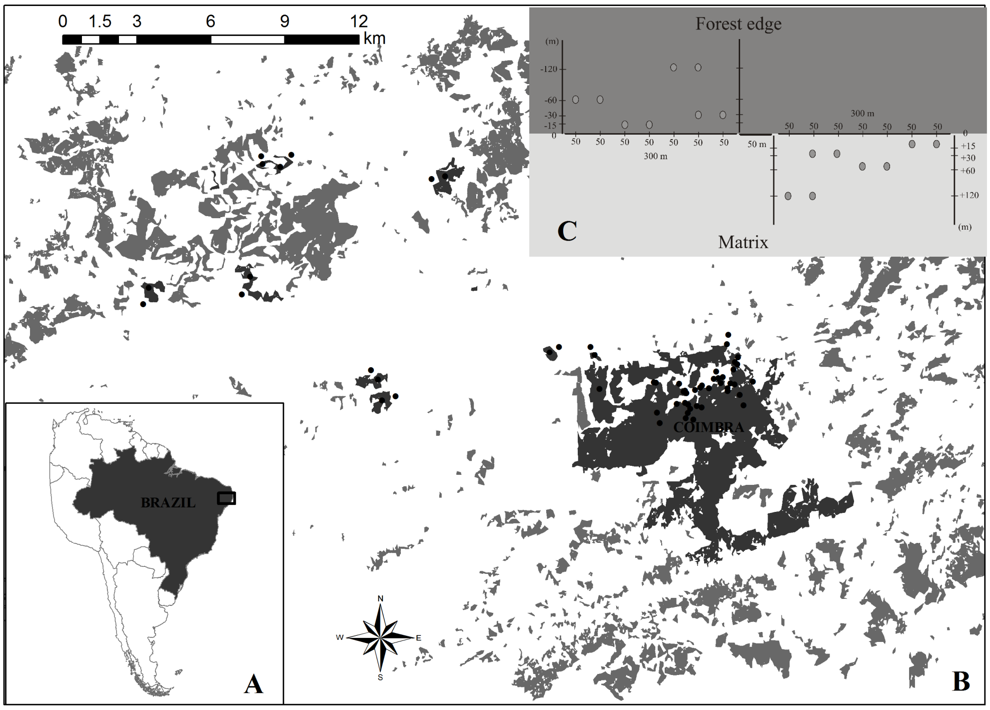
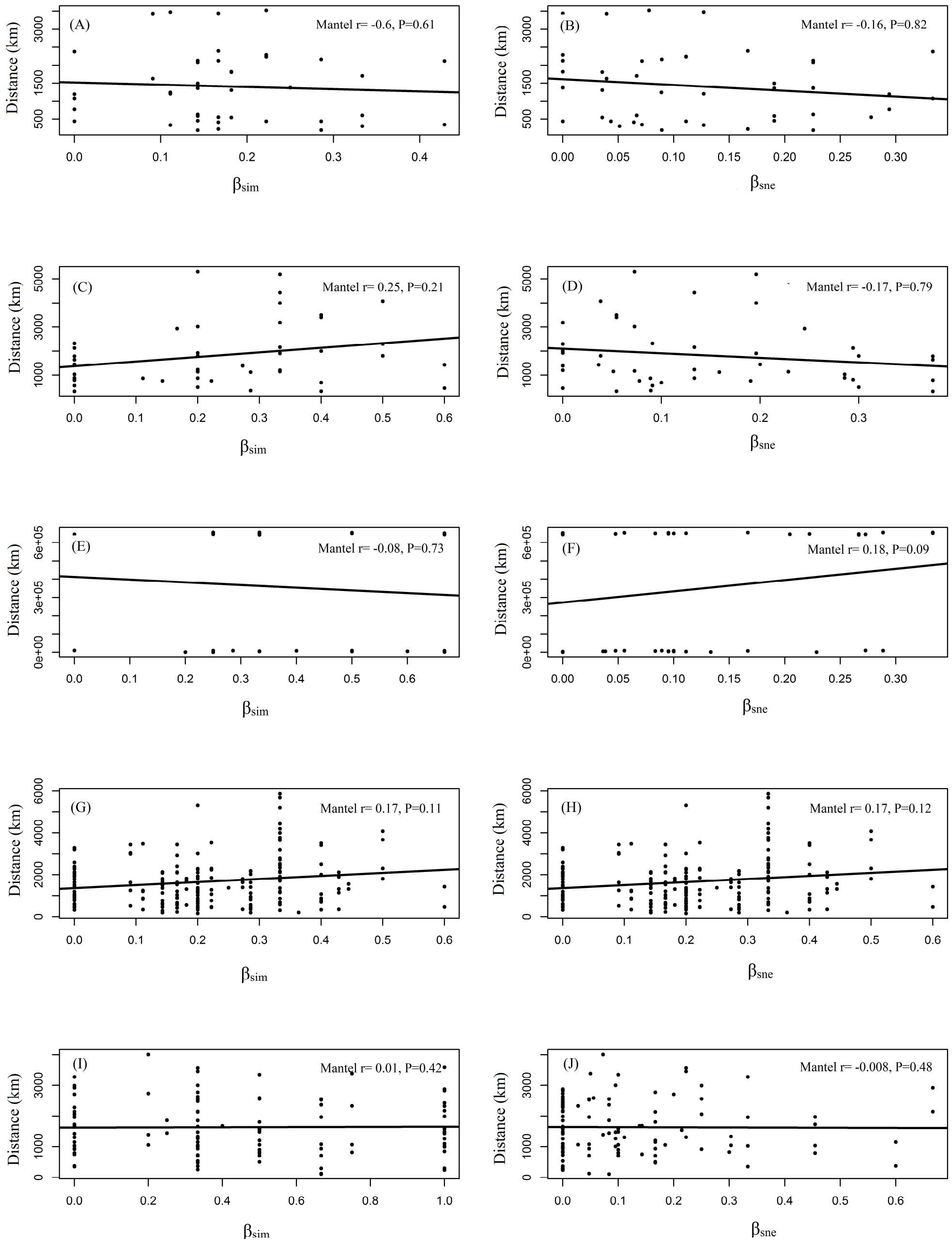


Fig.S2. Results of Mantel test showed the correlation between turnover (β_{sim}) and nestedness (β_{sne}) of dung beetle assemblages with linear distances (m) for forest interiors (A,B), forest edges (C,D), small fragments (E,F), forest edges + forest interiors (G,H) and pastures + sugar-cane plantation (I,J) of Serra Grande landscape, Alagoas, Brazil.



CAPÍTULO 3

The Value of Edge-Dominated Habitats for Fruit-Feeding Butterfly Persistence in a Human-Modified Atlantic Forest Landscape

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The Value of Edge-Dominated Habitats for Fruit-Feeding Butterfly Persistence in a Human-Modified Atlantic forest Landscape

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Abstract

As primary forests decline, the challenge of most tropical forest species is to persist in small forest fragments (i.e. edge-dominated habitats) embedded within predominantly harsh and open-habitat matrices. Here, we analyse the role played by edge-dominated habitats on fruit-feeding butterfly persistence, quantifying the effects of fragmentation metrics and tree attributes. We test the hypothesis that the consequences of habitat fragmentation can interact and cause cascading ecosystem changes with the pervasive simplification and striking convergence of tree assemblages inhabiting edge-dominated habitats altering fruit-feeding butterfly persistence. For this, portable traps were distribute in eight small forest fragments, eight forest edges and eight forest interiors of a human-modified Atlantic forest landscape. We capture more species and individuals in edge-dominated habitats (i.e. small fragments) than in forest edge and interiors of primary forest. Model selection for landscape revealed strong support for the influence of fragment area, tree density and pioneer trees on species richness. In terms of species composition, the environmental variables that best explained this variation were fragment area, forest cover and the proportion of pioneer trees. The data reported indicate that small and isolated remnants with high proportion of pioneer trees are important habitats for persistence of fruit-feeding butterflies mainly edge species more tolerant to sunlight in fragmented landscapes. Thus, the elevated presence of edge-adapted species in Atlantic forest fragments makes a substantial contribution to regional diversity of fruit-feeding butterflies.

Key words: butterfly diversity; edge habitats; Nymphalidae; pioneer trees; small fragments.

Introduction

The expansion of human-modified landscapes reduces habitat size and quality of tropical forests, increases isolation and creates ecological boundaries that differ significantly from true core habitat (Wright & Muller-Landau 2006). As consequence, highly-fragmented landscapes with forest fragments immersed in hostile matrices (e.g. croplands, pastures and urban areas) are predominant in aging tropical deforestation frontiers (Melo *et al.* 2013). The conversion of old-growth tropical forest in small forest fragments embedded within predominantly harsh and open-habitat matrices is in fact a pervasive phenomenon that poses enormous threats to forest biotas (Tabarelli *et al.* 2010). Identifying the potential for biodiversity persistence in altered habitats (e.g. small forest fragments ï edge-dominated habitats) have become an urgent task and knowledge about this sort of conservation service must be translated into practical guidelines relative to land-use regulation and habitat management in human-modified landscapes (Harvey *et al.* 2006, Gardner *et al.* 2009). Although the future of tropical forest biodiversity and provision of forest ecosystem services are inextricably tied to our ability to understand the changes triggered by human disturbances and the conservation value of human-modified landscapes (Tabarelli *et al.* 2010), our understanding about biodiversity persistence in these landscapes remains unclear.

Relative to biodiversity persistence in human-modified landscapes, tropical biodiversity has been roughly assigned into two mutually excluding groups: forest-dependent species as those with persistence depending on the presence of old-growth forest stands (Melo *et al.* 2013), and disturbance-adapted species as those able to persist or even proliferate in human-modified landscapes dominated by edge-affected habitats (Tabarelli *et al.* 2010). Several studies in human-modified landscapes showed that small forest fragments are able to retain high species richness of vascular plants (Norden *et al.*

2009), birds (Thornton *et al*. 2011) and mammals (Hawes *et al*. 2008). However, habitat fragmentation and its edge effects typically drive changes in both the taxonomic and functional composition of tree assemblages (Laurance *et al*. 2002, Lopes *et al*. 2009). In general, forest edges and small forest fragments are expected to exhibit species-poor tree communities and may be impoverished in terms of emergent (Laurance *et al*. 2000), understorey (Tabarelli *et al*. 1999), and hardwood or old-growth tree species (Michalski *et al*. 2007). On the other hand, the elevated abundance and richness of fast-growing pioneer species is one of the most conspicuous features of tree assemblages along hyper-fragmented landscapes (Oliveira *et al*. 2004, Santos *et al*. 2008).

The consequences of habitat fragmentation can interact and cause cascading ecosystem changes and regime shifts in species plant-dependent (Laurance *et al*. 2002, Leal *et al*. 2014). Fruit-feeding butterflies are frequently used as indicators of habitat change and the conservation value of forest habitats (Uehara *et al*. 2007). Previous studies indicated that the diversity and composition of butterfly communities can be altered in human-modified landscapes (Horner-Devine *et al*. 2003, Uehara-Prado *et al*. 2007, Collier *et al*. 2010, SantôAnna *et al*. 2014). Some studies relate that fruit-feeding butterfly diversity decreases along a coarse gradient from pristine forest to agroforestry, plantations and secondary forest (Barlow *et al*. 2007, Nyafmno *et al*. 2014). Other studies have reported that small forest patches are able to retain butterfly diversity with most abundant species typical of forest edges, clearing and disturbed areas (Brown &Hutchings 1997, Bobo *et al*. 2006, Ribeiro *et al*. 2012). The high abundance of several species of fruit-feeding butterflies in forest fragments can be linked with the use of host plants, which are abundant in edge-dominated habitats (e.g. pioneer shrubs and trees) (Uehara-Prado *et al*. 2007).

Here, we used a hyper-fragmented Atlantic forest landscape to assess the importance of edge-dominated habitats for fruit-feeding butterfly persistence on the potential conservation value of human-modified landscapes. We test the hypothesis that the proliferation of a small set of pioneer trees and the simplification of forest vertical stratification in edge-dominated habitats affect fruit-feeding butterfly assemblages. In this way, we test (1) whether due to the functional convergence of tree assemblages promoted by habitat fragmentation, there is high similarity of fruit-feeding butterflies between small fragments and forest edges of primary forest differing from those found in forest interiors, and (2) whether independently of fragment area and isolation distance the pervasive simplification and striking convergence of tree assemblages inhabiting forest edges affect butterfly persistence. We expect that small fragments and forest edges, both with low tree species richness as well as high proportion of pioneer trees, exhibits similar patterns of abundance, diversity and species richness of fruit-feeding butterflies. Additionally, as forest interior and forest edge are contrasting habitats in terms of ecological and taxonomic composition of trees (e.g., forest edge exhibits high proportion of pioneer trees and consequent edge-induced microclimatic changes) (Oliveira *et al.* 2004, Laurance *et al.* 2006), we believe that fruit-feeding butterflies show different species richness and composition in these habitats.

Methods

Study sites

The study was carried out at Usina Serra Grande, a large private sugar-cane landholding in the State of Alagoas in northeastern Brazil (8°30ôS, 35°50ôW) (Fig. S1). The Serra Grande landscape is located within the most threatened region of the Brazilian Atlantic forest (Silva & Tabarelli 2000, Lopes *et al.* 2009). Field work was carried out in a fragmented landscape (667 km^2; 9.2% of forest cover), containing 109 forest remnants (ranging in size from 1.67 to 3500 ha) inside a uniform matrix of sugar-cane monoculture (Silva & Tabarelli 2000, Santos *et al.* 2008). The Coimbra Forest is the largest forest fragment in this landscape (3500 ha) and the best preserved forest in the region. This fragment still support important ecological groups believed to be typical of continuous and undisturbed tracts of Atlantic forest, such as large-seeded trees and frugivorous vertebrates (Santos *et al.* 2008). This landscape is therefore a useful scenario for assessing persistent and long-term effects of habitat loss and fragmentation as reflected by a number of published studies (e.g., Oliveira *et al.* 2004, Girão *et al.* 2007, Santos *et al.* 2008, Lopes *et al.* 2009).

The Serra Grande landscape is situated on a low altitude plateau (300-400 m above sea level) covered by two similar classes of dystrophic and clay-laden soils: yellow-red latosols and yellow-red podzols according to the Brazilian system of soil classification (IBGE 1985). The vegetation consists of lower montane rain forest, with Leguminosae, Lauraceae, Sapotaceae, Euphorbiaceae, Chrysobalanaceae and Lecythidaceae as the richest families in terms of tree species (Grillo *et al.* 2006). Annual rainfall is about 2000 mm, with a dry season (< 60 mm/month) occurring from November to January (Oliveira *et al.* 2004) and with the wettest period between April and August (Pimentel & Tabarelli 2004).

Attributes of fragments and landscape

We estimated the amount of forest cover retained in the surrounding landscape as a measure of patch isolation (Gorresen & Willig 2004). It was defined as the percentage of forest within 1-km of the fragment perimeter. The area of fragments and the amount of forest cover retained in the surrounding landscape were quantified using two GIS packages (ArcView 3.2 and Erdas Imagine 8.4) on the basis of: (1) three Landsat and Spot images (years 1989, 1998, 2003) and (2) a set of 160 aerial photos (1:8000) taken from helicopter overflights commissioned in April 2003 (provided by Conservation International do Brasil).

Tree community attributes

The tree database available to us was obtained from several studies carried out by Oliveira *et al.* (2004); Girão *et al.* (2007); Santos *et al.* (2008) and Lopes *et al.* (2009) between 2002 and 2009 based on permanent plots of 0.1 ha (10 m x 100 m) disposed in the centre of small fragments and forest edges and interiors of Coimbra forest to characterize the tree communities in Serra Grande landscape. Fragment surveys included trees with a diameter at breast height bigger than 10 cm, which were classified with regard to regeneration strategy (pioneer, and shade-tolerant trees) and forest vertical stratification (understory, canopy, and emergent trees) (see Santos *et al.* 2008). In addition, we used tree density and tree richness as tree community attributes (Table S1). The percentage of pioneer trees was used as indicator of habitat degradation, because this ecological group have been consistently reported as positively affected by habitat fragmentation in the Atlantic forest in north-eastern Brazil (*e.g.*, Oliveira *et al.* 2004; Santos *et al.* 2008). Further details about tree community attributes are available in the above-cited papers.

Fruit-feeding butterflies sampling

Sampling of fruit-feeding butterflies was carried out monthly between November 2012 and January 2013 (hot season) with four consecutive trap days each month. Although not exhaustive, sampling during three consecutive months during the hot season in Atlantic Forest is considered enough to produce a sample representative of a fruit-feeding butterfly community (Ribeiro *et al*. 2010). The study was carried out in 24 sites in three habitat types: (1) eight small forest fragments, ranging from 8 to 126 ha (hereafter fragments), (2) the edge (< 50 m from forest border) of the Coimbra forest (3,500 ha) (hereafter forest edge), and (3) the interior (> 200 m from forest border) of the same fragment (hereafter forest interior) used here as control area. Each one of the eight fragments received one sample unit (hereafter SU) consisting of five portable traps in its interior, totaling 40 traps in eight SUs. In the control area, eight SUs were installed in forest edge and eight in the interior, totaling 80 traps in 16 SUs.

Bait traps consisted of tubes 110 cm high × 35 cm diameter made with netting, with an internal funnel (30 cm high and 22 cm wide at the opening) to prevent butterflies from escaping. The tube was attached ca. 4 cm above a plastic platform, on which the bait was placed. The traps were disposed linearly, suspended 1.0-1.5 m above the ground and distant ca. 30 m of each other, and baited with a standard mixture of mashed banana with sugar cane juice, fermented for at least 48 h. All SUs were distant at least 300 m from each other. However, there was not spatial independence between forest edge and forest interior of Coimbra forest (Mantel test **Ɉ** = 0.2, $P = 0.02$) when we correlate the compositional similarity among plots (Bray-Curtis index) with the inter-plot isolation distances using the package ǿecodistô for R version 3.1.0 (R Core Team 2014).

We classified fruit-feeding butterfly assemblages into three categories of habitat preference: Forest, Edge and Open habitat. Our measurement of habitat specificity categorized species according to their ability to utilize different habitats. Categories of habitat preference were based on Brown (1992) and SantôAnna et al. (2014).

Data analysis

We assessed the completeness of each habitat in EstimateS 9.1 (Colwell 2013) by calculating the number of observed species as a percentage of the total richness, which was estimated based on the average of three abundance-based nonparametric estimators- Bootstraps, Chao 1 and jack 1. Comparisons of species richness among habitat types were made by visual assessment of overlapping 95% confidence intervals on individual-based rarefaction curves (Gotelli & Colwell 2001). To evaluate the efficiency of our survey relative to the sampling effort we also used time-based accumulation curves and its standard deviation from random permutations of the data (Gotelli & Colwell 2001). We used SIMPER (Primer v.6, Clarke & Gorley 2001) to determine the contribution that individual species made toward distinguishing differences in quantitative community structure among forest edges of small fragments and forest edges and interiors of primary forest.

Generalized Linear Mixed-Effects Models (GLMM) were used to test the effects of explanatory variables (i.e. fragment area, forest cover, the proportion of pioneer trees, shade-tolerant, emergent trees, canopy trees, understorey trees, tree density and tree richness) on abundance, species richness and adjusted species richness of fruit-feeding butterflies. Mixed-effects models were used to account for óhabitatô, entered as a random factor and tree attributes and fragmentation metrics as fixed factor. To fit GLMM we used Poissonôs error structure for count data. The performance of GLMM was assessed using Akaikeôs Information Criterion (AIC). We used three measures associated with the AIC to determine the optimal model given the data: the φAIC ranks alternative models according to their AIC values; the AIC for each model (rescaled based on the best model) and wAICc ï chance for the model to be selected, which varies from 0 to 1 (Burnham & Anderson 1998). To test whether our independent variables in multivariate analysis are correlated, we used the variance inflation factors (VIF). For all models VIF < 7.4 showed that collinearity is not a problem.

Finally, to determine whether the local habitat structure variables (i.e. tree attributes and fragmentation metrics) explained the variation in species composition and whether any species were associated with any of these environmental variables, a canonical correspondence analysis (CCA) was conducted with a *stepwise forward* selection in which only significant ($P < 0.05$) environmental variables were included in the final ordination. The effects of constraints variables on the composition of fruit-feeding butterflies were tested with the function *anova.cca* in R. GLMM and CCA were performed in R environment (R Development Core Team 2014).

Results

We captured a total of 833 individuals representing 61 species of fruit-feeding butterflies, with 608 individuals (48 species) in fragments, 128 individuals (34 species) in forest edge and 97 individuals (24 species) in forest interior (Table S2). Habitats largely differed in terms of assemblage structure as follows: small fragments exhibited higher abundance, observed and estimated species richness than all the other habitats (Fig.1). We refer to a Ó40%-reduction in observed species richness from fragments (mean ± SE: 18.62 ± 2.29 species/sampling unit) to forest edge (mean ± SE: 9.62 ± 0.73 species/sampling unit) or forest interior (mean ± SE: 7.62 ± 0.96 species/sampling unit) (Fig. 1). In this way, small fragments exhibited the highest scores of species completeness (mean ± SE: 29.25 ± 3.86) as compared to other habitats. However, the three habitat types, forest edge, forest interior and fragments, showed similar patterns of species coverage (i.e. number of species observed as a percentage of the average estimated richness) (Fig.1). Additionally, when the rarefaction curves of these habitats were compared, total species richness was not significantly different between them (Fig. S2). The time-based accumulation curves showed asymptotic trends in all habitats with the total observed richness increased with the number of days sampled (Fig. S2).

The proportion of butterfly species classified as forest interior, edge and open habitat, showed a similar pattern to both abundance and species richness (Fig.2). The proportion of forest species was markedly higher in all habitat types, while the proportions of open habitats and edge butterflies species were higher in forest edge and fragments, respectively (Fig.2). The average dissimilarity for differentiation between habitat types varied from 45.3% to 64.1% (Table 1). This differentiation was more pronounced when we compared forest interior with fragments (Table 1). The SIMPER analysis illustrated that the community structure of fruit-feeding butterflies in forest forest interior was distinct from that of fragments due to high presence of edge-specialist species in fragments (*e.g.*, *Pareuptychia* sp., *Pharneuptychia* sp., *T. laches* and *Yphthimoides renata*) rarely found in core areas.

Model selection for landscape revealed support for the influence of fragment area, forest cover, tree density and pioneer trees on species richness (Table 2). In terms of abundance, fragment area and forest cover affected fruit-feeding butterflies. To analyse the effects of tree assemblages on fruit-feeding butterflies in forest edges and interiors of Coimbra forest, we detected the influence of tree richness, the proportion of canopy, pioneer and understory trees on species richness and abundance (Table 2). In terms of species composition, the first two axes of CCA explained 58.7% of the variation in species composition. The final model was significant (F= 3.24; n = 199, P = 0.01) and the environmental variables that best explained this variation were fragment area, forest cover and the proportion of pioneer trees (Fig. 3). CCA axis-1 was negatively correlated with fragment area, forest cover and tree density. CCA axis-2 was negatively correlated with the proportion of canopy trees and fragment area and positively correlated with the proportion of pioneer trees. Four species, *Chloreuptychia herseis*, *Hermeuptychia gisella*, *Pareuptychia* sp. and *Taygetis laches* exhibited a stronger association with pioneer and understorey trees, while *Archaeoprepona demophon thalpius*, *Colobura dirce*, *Myscelia orsis* and *Taygetis sosis* were associated with the area of the fragment (Fig. 3).

Discussion

Our results reveal that small isolated forest fragments with high proportion of pioneer tress provide an important refuge for fruit-feeding butterflies in human-modified landscapes. The hypothesis that, due to the functional convergence of tree assemblages promoted by habitat fragmentation, fruit-feeding butterflies in small fragments and forest edges are much more similar to each other than to those in forest interiors was not accepted in this study. On the other hand, we capture significantly more individuals in small fragments than in forest edges and forest interior, which were indistinguishable from each other in terms of both abundance and species richness, suggesting that fragmentation is acting in different ways than only promoting more edge habitats.

Butterfly communities in the studied landscape had high abundance of species associated with high light environments, such as clearings (*e.g.*, *C. dirce* and *T. laches*) and low proportion of shade-dwelling species associated with closed canopy forest (*e.g.*, *Morpho helenor anakreon*). According to Leidner *et al.* (2010) there is a pattern in fragmented landscapes where species typical of edge-affected habitats are predominant. The loss of forest adapted species is probably offset by colonization of widespread and sun-loving species in fragmented landscapes (Brown & Hutchings 1997; Leidner *et al*. 2010). In contrast, the sensitivity of closed-canopy specialist species to disturbance as well as their specialization to scarce host-plant (Leidner *et al.* 2010) can help to understand the low species richness of fruit-feeding butterflies in forest interior in comparison to edge-affected habitats.

A similar pattern has been observed for tree assemblages in hyper-fragmented landscapes. Tree assemblages are undergoing a drastic reduction in species richness and functional groups as a result of habitat loss and fragmentation (Oliveira *et al.* 2004, Santos *et al.* 2008, Lopes *et al.* 2009). Forest fragmentation and its edge effects reduce plant recruitment due to habitat desiccation and seedling damage caused by litterfall and treefall near forest edges (Laurance *et al.* 2000). Thus, the abundant light provided by treefall gaps and forest edges (Hartshorn 1978) favour the elevated abundance and richness of fast-growing pioneer species in fragmented landscapes. In fact, pioneer species account for over 70% of all tree species and individuals occurring in Atlantic forest fragments (Santos *et al.* 2008). We believe that these edge-affected habitats with high proportion of pioneer trees as well as others plants common in altered habitats (*e.g.*, saplings, shrubs and herbs) and consequent adverse microclimatic conditions (*i.e.*, low humidity and high temperature) favour species which are more tolerant to sunlight and drought. For example, the species affected positively by the proportion of pioneer trees, like *Chloreuptychia herseis*, *H. gisella*, *Pareuptychia* sp. and *T. laches* (all Satyrinae species) feed on grasses (*e.g.*, poaceae) in larval stage (AVLF pers. obs.). Thus, the high density of edge-dependent host-plants favoured by habitat fragmentation affects positively fruit-feeding butterflies typical of forest edges, providing suitable breeding and feeding sites. In addition, the immediate surroundings of forest edges and fragments are also important and could also explain this high abundance of Satyrinae on forest edges and fragments (Ribeiro & Freitas 2012). On the other hand, species with narrow ecological niches are less able to adapt to rapid changes in environmental conditions, such as those associated with fragmented landscapes (Koh *et al.* 2004, Benedick *et al.* 2006).

The differences between small fragments and forest edges in terms of the number of species and species composition can be explain for three possible explanations. First, forest stratification is distinct between the forest edges and the fragments (see Table S1), resulting in different microclimatic conditions and resource availability. To exemplify, forest edges have more canopy trees such as pioneer species occurring in subcanopy and canopy (*e.g.*, *Tapirira guianensis* and *Schefflera morototoni*) than fragments. Second, the immediate surroundings of the habitat types are affecting not only abundance (as discussed above), but also species composition. Finally, since intensity and magnitude of fragmentation-induced changes are greatly modulated by the spatial arrangement of forest fragments (landscape configuration) (Tabarelli *et al.* 2008), edge effects trigger an extensive suite of processes in fragments, benefiting edge-adapted butterflies. In fact, small fragments have high perimeter/area ratios and the centres of those patches are consequently affected by multiple edges in such a way that they do not have a true interior (Malcolm 1994). Thus, the community composition of trees and consequent adverse microclimatic conditions are present in all habitats in the small fragments, which implies a great availability of resources for butterflies associated to edge-dominated habitats and open sites.

Overall, our study demonstrated that the characteristics found in edge-dominated habitats represent a set of interrelated processes that affect directly the community structure of fruit-feeding butterflies in Atlantic forest. The arrangement of small fragments and local tree species composition are effective predictor of fruit-feeding butterfly diversity benefited sun-loving species in fragmented landscapes. As species-specific responses related to dispersal ability, behaviour and host-plant distribution might be the cause of distinct responses to habitat fragmentation (Shahabuddin & Terborgh 1999; Uehara-Prado *et al.* 2007), we need many more studies with well-established sampling protocols to understand the dynamic of fruit-feeding butterflies in hyper-fragmented landscapes.

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Table 1. Pairwise dissimilarities among groups of habitats in Atlantic forest. FICF: forest interiors of Coimbra forest (primary forest); ECF (habitat edges of Coimbra forest); and SF: small fragments in Serra Grande Landscape, Alagoas, northeastern Brazil.

Comparison	Av. diss (overall)	Species	Av.Abund		Av.Diss	Con%	Cum.%
SF x ECF	54.4		SFF	ECF			
		Pharneuptychia sp.	8.37	0	4.3	7.9	7.9
		Pareuptychia sp.	10.49	3.61	3.53	6.5	14.39
		Yphthimoides renata	6.86	0	3.52	6.47	20.87
		Taygetis laches	7.55	2.83	2.42	4.46	25.32
		Cissia palladia	4.58	1	1.84	3.38	28.7
		Cissia terrestris	6.63	3.87	1.42	2.61	31.31
		Cissia myncea	4.12	1.41	1.39	2.56	33.87
		Yphthimoides manasses	2.65	0	1.36	2.5	36.36
		Archaeoprepona demophoon antimache	2.45	0	1.26	2.31	38.68
		Historis odius dious	2.45	0	1.26	2.31	40.99
		Paryphthimoides poltys	2.45	0	1.26	2.31	43.3
		Colobura dirce	6.24	3.87	1.22	2.24	45.54
		Callicore astarte	3.32	1	1.19	2.19	47.73
		Caligo illioneus illioneus	2.24	0	1.15	2.11	49.84
SF x FICF	64,12		SFF	FICF			
		Pareuptychia sp.	10.49	1.41	4.97	7.76	7.76
		Pharneuptychia sp.	8.37	0	4.59	7.15	14.91
		Yphthimoides renata	6.86	1	3.21	5.01	19.92
		Taygetis laches	7.55	1.73	3.19	4.97	24.89

		Hermeuptychia atalanta	5.1	0	2.8	4.36	29.25
		Cissia terrestris	6.63	2	2.54	3.96	33.21
		Cissia myncea	4.12	0	2.26	3.53	36.74
		Cissia palladia	4.58	1	1.96	3.06	39.8
		Callicore astarte	3.32	0	1.82	2.84	42.64
		Hermeuptychia gisella	3.32	0	1.82	2.84	45.47
		Eryphanis automedon	2.83	0	1.55	2.42	47.89
		Yphthimoides manasses	2.65	0	1.45	2.26	50.15
		Archaeoprepona demophoon antimache	2.45	0	1.34	2.09	52.25
		Historis odius dious	2.45	0	1.34	2.09	54.34
		Opsiphanes invirae remoliatus	2.45	0	1.34	2.09	56.44
		Paryphthimoides poltys	2.45	0	1.34	2.09	58.53
ECF X FICF	45,26		ECF	FICF			
		Hermeuptychia atalanta	3	0	3	6.62	6.62
		Pseudodebis sp.	0	2.24	2.23	4.94	11.56
		Pareuptychia sp.	3.61	1.41	2.19	4.84	16.4
		Hermeuptychia gisella	2	0	2	4.42	20.82
		Cissia terrestris	3.87	2	1.87	4.14	24.95
		Caligo brasiliensis brasiliensis	0	1.73	1.73	3.82	28.78
		Memphis acidalia	1.73	0	1.73	3.82	32.6
		Archaeoprepona demophon thalpius	2	3.46	1.46	3.23	35.83
		Cissia myncea	1.41	0	1.41	3.12	38.96
		Taygetis sosis	1.41	2.83	1.41	3.12	42.08
		Taygetis virgilia	1.41	0	1.41	3.12	45.2
		Taygetis laches	2.83	1.73	1.1	2.42	47.62

Table 2. Results of the Generalized Linear Mixed Models for the effects of tree attributes and fragmentation metrics on total observed richness, total estimated richness and abundance of fruit-feeding butterflies in Atlantic forest fragments in Serra Grande Landscape, Alagoas, north-eastern Brazil. Models are ranked from best to worst according to model φAICc. AREA=Fragment Area, FC=Forest Cover, PT=% Pioneer tree, CT= % Canopy tree, TD= Tree density, TR= Tree richness, UT=% Understorey tree.

	Small fragments and Coimbra forest (edge + interior)					Coimbra Forest (edge + interior)				
Response variables	Models	φ AICc[a]	AICc[b]	K[c]	wi[d]	Models	φ AICc[a]	AICc[b]	K[c]	wi[d]
Total observed richness	AREA + TD	0	127.15	3	0.32	TR	0	87.3	4	0.26
	AREA + PT	1.51	128.65	3	0.15	CT	0.75	88.05	4	0.18
	AREA + TR	2.12	129.27	3	0.11	UT	0.78	88.08	4	0.18
	AREA	2.3	129.44	2	0.1	PT	0.81	88.11	4	0.17
Total estimated richnessÀ	AREA + FC	0	161.65	5	0.51	TR	0	112.96	4	0.26
	FC	1.35	163	4	0.26	UT	1.51	113.13	4	0.24
	AREA	2.32	163.96	4	0.16	CT	2.12	113.37	4	0.21
	AREA + CT	6.19	167.84	5	0.02	PT	2.3	114.72	4	0.11
Abundance	AREA + FC	0	218.97	5	0.41	TR	0	103.6	4	0.27
	AREA + TD	3.01	221.98	4	0.09	UT	1.51	104.23	4	0.19
	AREA + FC + CT + PT	3.09	222.06	7	0.09	CT	2.12	104.3	4	0.19
	AREA + FC + PT + TR	3.1	222.07	7	0.09	PT	2.3	104.75	4	0.15

ÀEstimated species richness based on the average of three abundance-based richness estimators, Bootstrap, Chao 1 and Jack 1 (Colwell 2009).

[a] ȹ AICc relative difference to the value of AICc of the best model.

[b] AICc the model distance to the real model.

[c] K (number of estimated parameters).

[d] *wi* (AICc weight) which is the chance for the model to be selected.

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Figure 1. Mean ± SE of abundance (A), species richness (B), estimated richness based on the average of three abundance-based richness estimators, Bootstrap, Chao 1 and Jack 1 (C), diversity (Shannon index) (D), completeness (number of species observed as a percentage of the landscape total) (E) and coverage (number of species observed as a percentage of the average estimated richness) (Mean ± SE) of fruit-feeding butterflies sampled in Atlantic forest, Alagoas, north-eastern Brazil. White bars (FI-Forest Interior), gray bars (FE- Forest Edge) and black bars (SF- Small Fragments).

Figure 2. Proportion of individuals (top) and species (bottom) of fruit-feeding butterflies sampled in Atlantic forest, Alagoas, north-eastern Brazil, classified in the three habitat categories (Forest, Edge, and Open habitats) in each site: Forest Interior (FI), Forest Edge (FE), and Small Fragments (SF).

Figure 3. Biplots of the first and second axes of the Canonical Correspondence Analysis based on fruit-feeding butterflies species composition. Explanatory variables: AR =fragment area, CT =canopy trees, FC=forest cover, DT=density of trees, PT=pioneer trees), RT=richness of trees and UT=undersorey trees; habitats: I1-I8= forest interiors, B1-B8= edge habitats; Small fragments: AG=alto guzerá, AQUI=aquidaba I, AQUII=aquidaba II, DOISBI=dois braços I, DOISBII=dois braços II, ENCA=encanamento, MATAP=mata dos pintos and USINA. Species: Archa=*Archaeoprepona demophon thalpius*, Calli=*Callicore astarte*, Chlo=*Chloreuptychia herseis*, Cissm=*Cissia myncea*, Cisst=*Cissia terrestris*, Colod=*Colobura dirce*, Fount= *Fountainea ryphea phidile*, Herma=*Hermeuptychia atalanta*, Hermg=*Hermeuptychia gisella*, Morph= *Morpho helenor anakreon*,

Mysce=*Myscelia orsis*, Pareu=*Pareuptychia* sp., Pharn=*Pharneuptychia* sp., Taygl=*Taygetis laches*, Taygs=*Taygetis sosis* and Yphtr=*Yphthimoides Renata*.

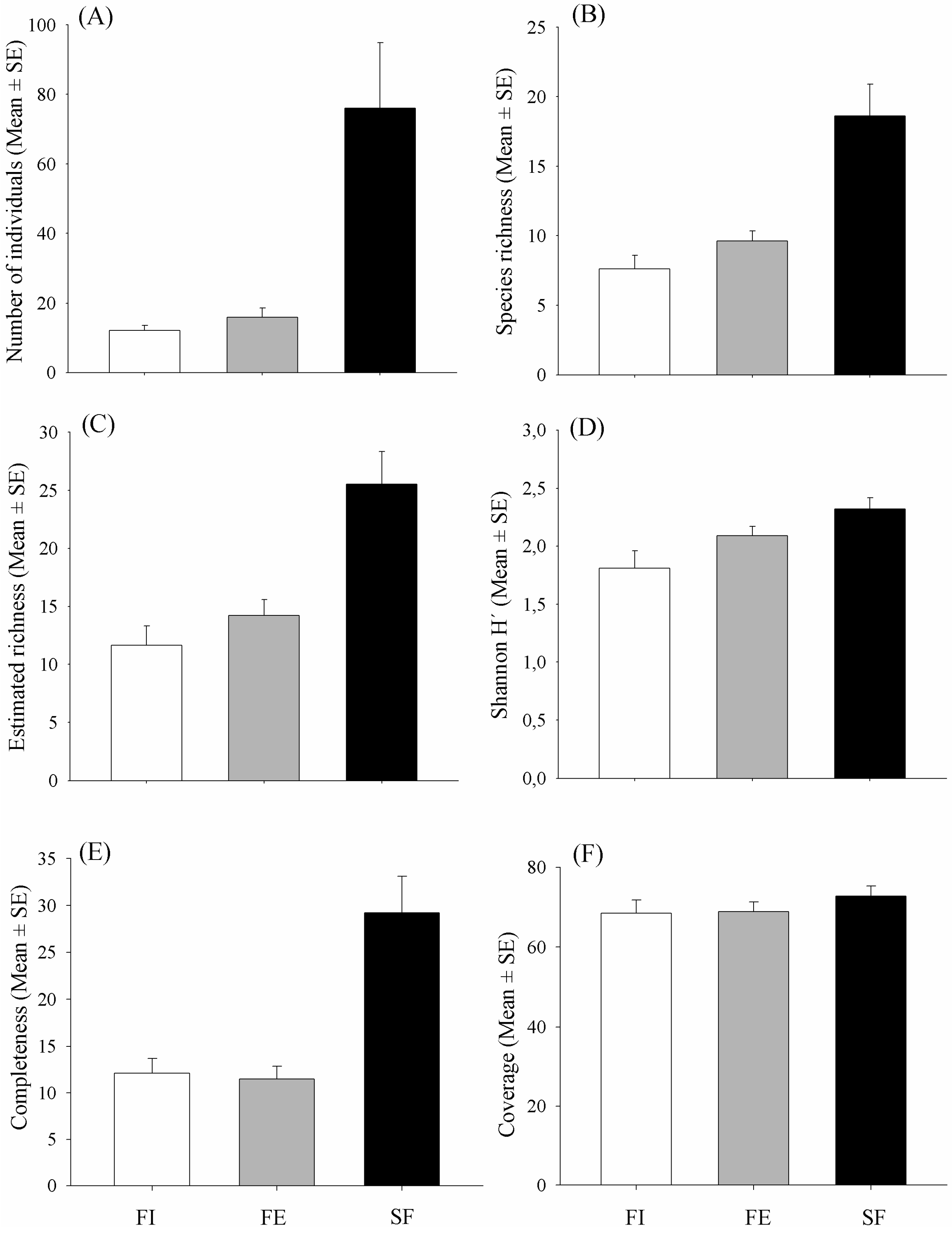

(A)
Number of individuals (Mean ± SE)
0
20
40
60
80
100
(B)
Species richness (Mean ± SE)
0
5
10
15
20
25
(C)
Estimated richness (Mean ± SE)
0
5
10
15
20
25
30
(D)
Shannon H´ (Mean ± SE)
0,0
0,5
1,0
1,5
2,0
2,5
3,0
(E)
Completeness (Mean ± SE)
0
5
10
15
20
25
30
35
(F)
Coverage (Mean ± SE)
0
20
40
60
80
FI
FE
SF
FI
FE
SF

Fig. 1

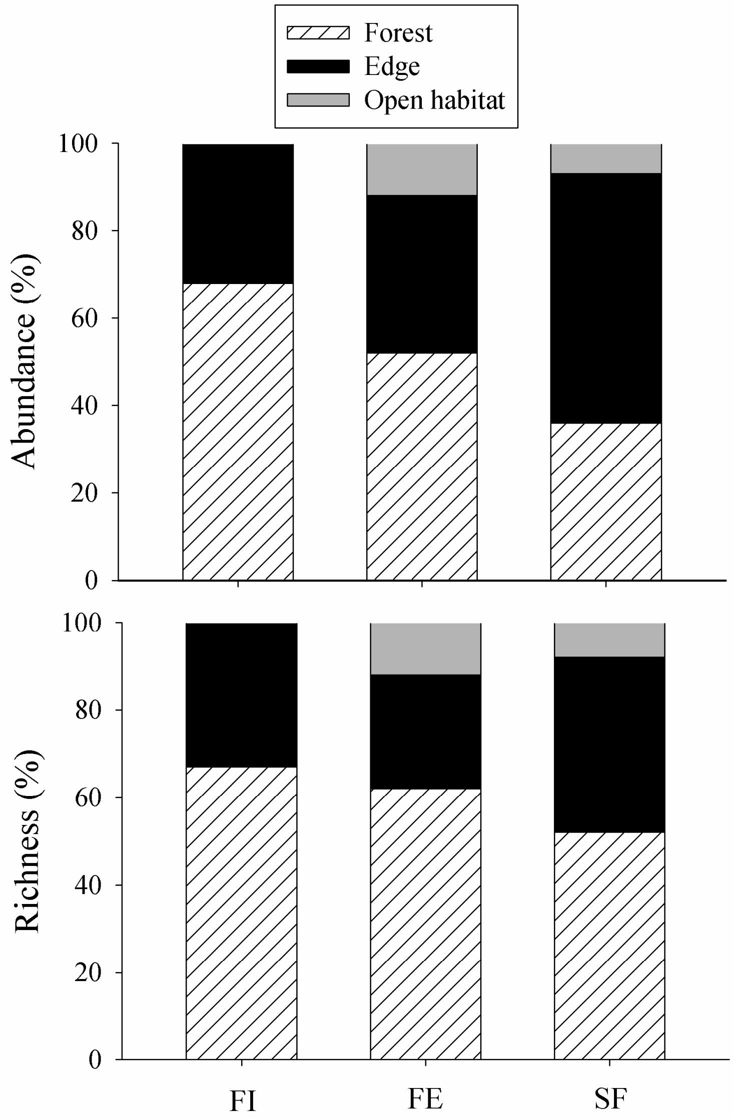

Forest
Edge
Open habitat
Abundance (%)
100
80
60
40
20
0
Richness (%)
100
80
60
40
20
0
FI
FE
SF

Fig. 2

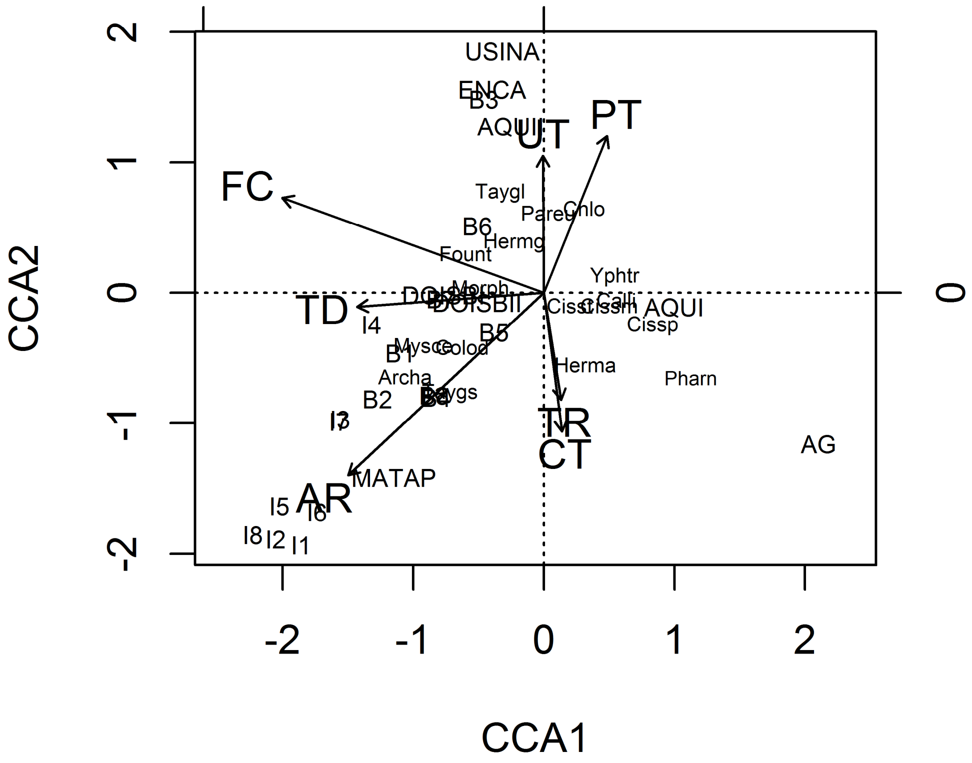

USINA
ENCA
B3
AQUI
UT
PT
FC
Taygl
Chlo
Pareu
B6
Hermg
Fount
Yphtr
Morph
TD
DOISBII
Cissi
Cissm
Cali
AQUI
I4
Cissp
B5
Mysce
Colod
B1
Herma
Archa
Pharn
Baygs
B4
B2
I3
I7
TR
CT
AG
MATAP
AR
I5
I6
I8
I2
I1
CCA2
CCA1
2
1
0
-1
-2
-2
-1
0
1
2
0

Fig. 3

Table S1. Mean ± SE of attributes of Atlantic forest fragments in Serra Grande Landscape, Alagoas, north-eastern Brazil. Tukey posthoc tests were used for pairwise comparisons of means. FI=forest interiors, FE=forest edges and SF=small fragments. **P* < 0·05; ***P* < 0·01; ****P* < 0·001, NS=non significant.

Variables	FI (n=8)	FE (n=8)	SF (n=8)	Interhabitat differences (ANOVA)	Significant pairwise comparison at P<0.05
Fragment area (ha)	3500	3500	1.67±0.15	F_2=143.55***	(FI) vs. (SF) and (FE) vs. (SF)
Forest cover (%)	6.65	6.65	12.5±2.56	F_2=5.2*	(FI) vs. (SF) and (FE) vs. (SF)
Pioneer tress (%)	14.37±2.33	89.16±2.88	52.3±7.29	F_2=62.61***	all
Shade-tolerant tress (%)	85.63±2.33	10.83±2.88	47.69±7.29	F_2=62***	all
Emergent trees (%)	5.45±0.92	8.65±2.02	15±6.83	F_2=1.37	NS
Canopy trees (%)	48.36±4.24	81.98±2.54	33.77±7.46	F_2=22.88***	(FI) vs. (FE) and (FE) vs. (SF)
Understorey trees (%)	46.18±4.12	9.36±2.14	51.22±7.36	F_2=20.65***	(FI) vs. (FE) and (FE) vs. (SF)
Tree density	116.75±9.59	58.75±2.88	95.75±13.95	F_2=8.76**	(FI) vs. (FE) and (FE) vs. (SF)
Tree richness	39±3.16	18.37±1.79	28.25±5.25	F_2=7.81**	(FI) vs. (FE)

Table S2. Species, habitat preference (F=forest interior, E=forest edge, O=open habitat) and number of individuals of fruit-feeding butterflies sampled in Atlantic forest, Alagoas, north-eastern Brazil.

Species	Habitat preference	Edges of Coimbra forest	Interiors of Coimbra forest	Small fragments
Archaeoprepona amphimachus amphimachus	F	2	2	2
Archaeoprepona demophon thalpius	F	4	12	8
Archaeoprepona demophoon antimache	E	0	0	6
Biblis hyperia	E	0	0	1
Caligo brasiliensis brasiliensis	E	0	3	3
Caligo idomeneus	F	0	1	0
Caligo illioneus illioneus	E	0	0	5
Caligo teucer ssp.	E	0	0	2
Callicore astarte	F	1	0	11
Catonephele acontius	F	1	2	0
Chloreuptychia arnaca	E	1	0	0
Chloreuptychia chlorimene	F	1	3	0
Chloreuptychia herseis	E	2	1	11
Cissia myncea	E	2	0	17
Cissia palladia	E	1	1	21
Cissia terrestris	E	15	4	42
Colobura dirce	E	15	17	39
Ectima thecla	E	1	0	0
Erichthodes antonina	F	4	1	1
Eryphanis automedon	F	1	0	8
Fountainea ryphea phidile	F	1	3	7

Hamadryas amphinome amphinome	F	1	0	0
Hamadryas arinome	F	0	0	1
Hamadryas feronia feronia	F	0	0	2
Hamadryas iphthime iphthime	F	0	1	3
Hermeuptychia atalanta	O	9	0	26
Hermeuptychia fallax	O	0	0	1
Hermeuptychia gisella	O	4	0	11
Hermeuptychia hermes	O	1	0	3
Hermeuptychia spn.	O	1	0	0
Historis odius dious	E	0	0	6
Hypna clytemnestra forbesi	F	1	0	0
Magneuyptychia libye	F	0	0	4
Memphis acidalia	F	3	0	5
Memphis moruus	F	0	0	4
Morpho helenor anakreon	F	2	5	9
Morpho menelaus eberti	F	1	0	0
Myscelia orsis	F	23	17	9
Nica flavilla flavilla	E	0	0	1
Opsiphanes cassiae crameri	F	0	0	1
Opsiphanes invirae remoliatus	F	1	0	6
Opsiphanes quiteria ssp.	F	0	0	1
Pareuptychia sp.	F	13	3	112
Paryphthimoides poltys	E	0	0	6
Paryphthimoides sp.	E	1	0	1
Paryphthimoides sylvina	E	0	0	1
Pharneuptychia sp.	E	0	0	70
Prepona amydon ferdinandi	F	1	1	0

Prepona laertes ssp.	F	0	0	1
Pseudodebis euptychidia	F	0	5	0
Siderone galanthis galanthis	F	0	0	2
Taygetis echo	F	0	1	0
Taygetis laches	E	8	4	58
Taygetis rufomarginata	F	1	0	1
Taygetis sosis	F	2	8	12
Taygetis virgilia	F	2	0	5
Yphthimoides manasses	E	0	0	7
Yphthimoides renata	E	0	1	47
Yphthimoides sp.	E	0	0	2
Zaretis strigosus	F	1	1	3
Zischkaia saundersii	E	0	0	3
Total		128	97	608

Figure S1.Map of Serra Grande landscape of northeastern Brazil (A) showing the 24 sampling sites in Atlantic forest (B). Shaded areas represent remaining Atlantic forest remnants, with sampled fragments represented by darker shaded areas. Blank spaces represent uniform matrix of sugar-cane monoculture. Solid circles represent the sampling unities.

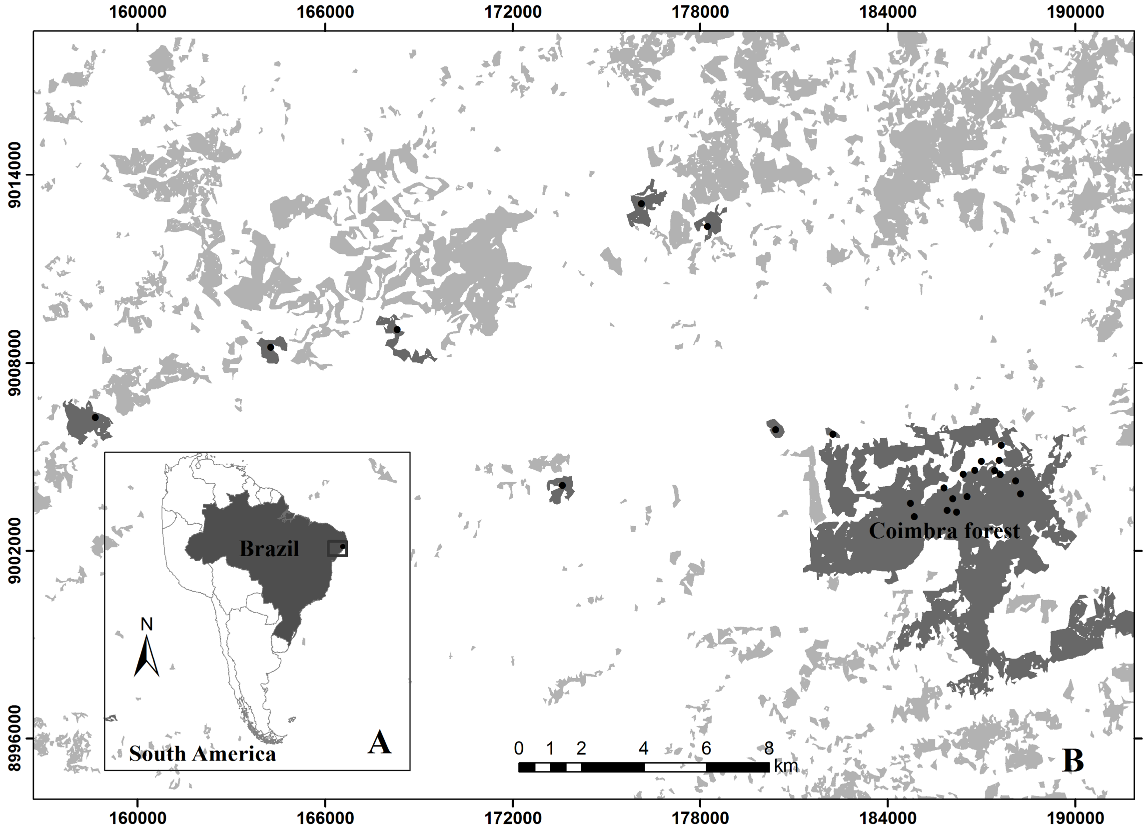
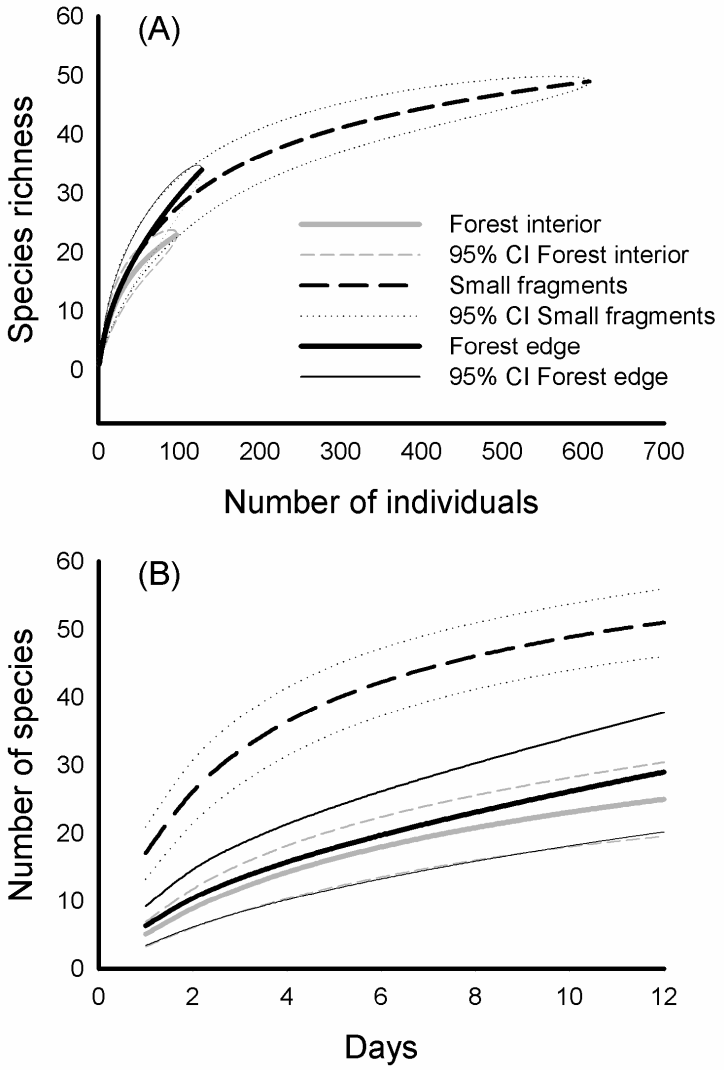


Figure S2. Rarefaction curves for the fruit-feeding butterfly assemblages (A) and species accumulation curves by days (B) in forest edge and interior of Coimbra forest (primary forest) and small forest fragments. Each curve is presented with a 95% confidence interval.



8. CONSIDERAÇÕES FINAIS

Esse estudo realizado na paisagem Serra Grande, representante do Centro de Endemismo Pernambuco, ressalta a importância da elaboração e implementação de planos de conservação para a biodiversidade em paisagens antropizadas localizadas na Floresta Atlântica, onde estudos apontam que apenas 1% desse domínio é protegido de forma integral. Na ausência de grandes áreas florestais intactas a serem conservadas, as paisagens com áreas florestais fragmentadas e uso da terra em seu entorno se tornam opções para estratégias de conservação nos trópicos.

Os resultados do presente estudo sugerem que os besouros escarabeíneos, embora apresentem um maior número de espécies indicadoras nas áreas florestais mais conservadas, podem utilizar habitats afetados por borda e matrizes não florestais como habitats complementares. Mesmo habitats considerados inóspitos para a biodiversidade, como a cana-de-açúcar, local onde há queimada e intensa aplicação de compostos químicos, verifica-se a presença de espécies específicas de besouros escarabeíneos. Salienta-se que para as espécies florestais desses besouros a distância dentro da floresta em relação à matriz circundante apresenta pouca importância com relação à distinção das comunidades. O fator preponderante que garante a distinta composição de espécies entre área florestal e aberta (i.e. matriz) é a cobertura vegetacional.

Adicionalmente em relação a esses besouros, demonstra-se que os efeitos relacionados à fragmentação (i.e. área, efeito de borda e isolamento) mostraram-se determinates para as distinções no *turnover* spacial das assembléias de besouros escarabeíneos, onde diferentes tipos de habitats afetados por borda apresentaram padrões distintos na representatividade da diversidade beta contribuindo para aumentar a diferenciação desses besouros na paisagem. Habitats mais próximos não necessariamente apresentam padrões semelhantes de *turnover e* aninhamento. Embora um conjunto de armadilhas englobando áreas florestais de borda e interior da floresta primaria com diferentes tipos de matrizes adjacentes apresente uma maior diversidade alfa do que um conjunto com pequenos fragmentos isolados por um mesmo tipo de matriz, as variações do *turnover* espacial entre os mesmos faz com que seja necessário um plano de conservação que beneficie as espécies presentes em ambos os habitats, priorizando as áreas com alta diversidade.

Por fim, verifica-se que para as borboletas frugívoras os habitats dominados por borda e com elevada proporção de árvores pioneiras foram os que retiveram a maior parte da riqueza de espécies das mesmas. Espécies de borboletas frugívoras adaptadas as condições encontradas em habitats de borda (i.e. alta luminosidade e elevada temperatura) apresentaram elevada abundância, sugerindo o efeito cascata da fragmentação de habitat. Com a perda e fragmentação de habitat, árvores tolerantes à sombra são drasticamente afetadas, enquanto as árvores pioneiras são beneficiadas aumentando sua abundância em paisagens fragmentadas, principalmente em habitats afetados por borda. Essa mudança nas assembléias de árvores está sendo refletida nas borboletas frugívoras, uma vez que as espécies de borboletas dominantes na paisagem Serra Grande foram afetadas pela elevada presença de árvores pioneiras nesses ambientes.

O presente estudo demonstra como a biodiversidade (representada pelos besouros escarabeíneos e as borboletas frugívoras) está respondendo a mudanças de habitat, sugerindo que os habitats afetados por borda, como os pequenos fragmentos florestais imersos em matrizes não-florestais, não sejam colocados à margem na estruturação teórico-prática de planos de conservação em paisagens antropizadas da Floresta Atlântica. Todavia, ressalta-se que as áreas interiores de florestas primárias presentes na Floresta Atlântica são habitats únicos para as espécies florestais, devendo as mesmas ser prioridade em termos de estratégias de conservação.