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PLANTAS E INSETOS GALHADORES: EFEITOS ASCENDENTES DETERMINANDO PADRÕES NAS ASSEMBLÉIAS DE INSETOS EM DIFERENTES ESCALAS ESPACIAIS

RECIFE, 2013

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal, da Universidade Federal de Pernambuco como parte dos requisitos para a obtenção do grau de Doutor em Biologia Vegetal.
Orientador: Dr. Marcelo Tabarelli (UFPE)
Co-Orientador: Dr. Jean Carlos Santos (UFU)
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Aprovada em 29/05/2013

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RESUMO

As assembléias de insetos herbívoros especializados são componentes fundamentais em florestas tropicais, influenciando diretamente a diversidade de plantas e processos ecossistêmicos. As modificações na paisagem, perda de habitat e os efeitos de borda são considerados primordiais na perda de espécies em níveis global, regional e local. Essa Tese investigou como as modificações antrópicas na paisagem afetaram os padrões das assembléias de plantas jovens, plantas hospedeiras e insetos galhadores em escala local, entre habitats e em uma paisagem hiperfragmentada de floresta Atlântica no Nordeste do Brasil. Detectei que habitats afetados pelos efeitos de borda borda (pequenos fragmentos e bordas florestais) são subgrupos florísticos de interior florestal com notável empobrecimento de plantas hospedeiras que ocasiona em tendência similar para seus insetos galhadores associados. Esses achados reforçam a ideia de que habitats afetados pelas bordas favorecem interações generalista-generalista. Entretanto, nas áreas de floresta madura há maior riqueza de espécies dos grupos bióticos citados anteriormente e por isso sugiro que este habitat é de alta qualidade e fundamental para a manutenção da diversidade deste grupo de herbívoros. Entretanto, a diversidade beta foi maior em pequenos fragmentos devido à susceptibilidade ao hiperdinamismo e eventos estocásticos que direcionam estes fragmentos à distintas trajetórias sucessionais e floras exclusivas. Adicionalmente, examinei os dois principais nichos de regeneração em florestas tropicais: plantas pioneiras e tolerantes a sombra e evidenciei que o principal recurso utilizado pelos insetos foram as plantas tolerantes a sombra. A conectividade estrutural da paisagem influenciou positivamente os grupos bióticos avaliados e finalmente, a análise de ordenação demonstrou composição taxonômica dissimilar entre os habitats avaliados. A tendência emergente do estudo evidencia que os fatores base-topo estruturam as assembléias destes animais e que o desaparecimento das plantas hospedeiras pode conduzir os insetos especializados a co-extinção e perda de história evolutiva.

Palavras-chave: conectividade, diversidade beta, insetos herbívoros.

ABSTRACT

Specialized herbivores assemblages are essential components in tropical forests, directly influencing plant diversity and ecosystem processes. Landscape modifications, loss of habitat and edge effects are considered primordial factors in species loss at the global, regional and local levels. Here I investigated how anthropogenic shifts in the landscape affected patterns of saplings woody plants, sapling host plants and galling insects on a local scale, and among habitats in a fragmented landscape in Atlantic Forest of Northeastern Brazil. I detected that edge-affected habitats (small fragments and forest edges) are floristic subgroups of interior habitats with distinctive impoverishment of host plants on which causes similar trend to their galling insects associated. These findings reinforce the notion in which edge affected habitats support mainly interactions generalist-generalist. However, in areas of old growth forest there are higher species richness of biotic groups previously mentioned and therefore suggests that core area has high quality and critical to maintaining the diversity of this group of herbivores. Nevertheless, beta diversity was higher in small fragments due to susceptibility to hyperdynamism and stochastic events that drives these fragments to different successional pathways and unique flora. Here was confirmed that the main resource consumed for galling insects was shade tolerant host plants. Landscape complexity positively influenced biotic groups evaluated and finally the ordination analysis showed dissimilar taxonomic composition among habitats assessed. Emerging trend from study shows that bottom up effects shapes assemblages of these animals and the disappearance of host plants may lead insects specialized co-extinction and loss of evolutionary history.

Key words: beta diversity, connectivity, herbivore insects.

LISTA DE FIGURAS

SEÇÃO 4- MANUSCRITO 1

Supplementary material

SEÇÃO 5- MANUSCRITO 2

LISTA DE TABELAS

SEÇÃO 4- MANUSCRITO 1

SEÇÃO 5- MANUSCRITO 2

SUMÁRIO

1. INTRODUÇÃO

O aumento da degradação dos ecossistemas tropicais tem incentivado estudos que pretendem entender quais os resultados destas modificações deletérias e como padrões das comunidades bióticas e os processos relacionados estão sendo diretamente implicados (LAURANCE et al. 2002, 2011). As florestas tropicais vêm sofrendo processos contínuos de fragmentação, que degeneram a estrutura florestal e dificultam o avanço da sucessão ecológica. Ruptura de habitats provenientes da fragmentação diminui a área de vida disponível para a sobrevivência e reprodução dos organismos e reorganiza comunidades bióticas (FAHRIG 2003). Nas florestas Amazônica e Atlântica, vem continuamente sido constatado decréscimo na riqueza e nas populações de muitas espécies sensíveis à variações microclimáticas hostis, como plantas tolerantes a sombra, insetos e parasitóides especialistas, direcionando a rupturas nas redes de interações tróficas (TABARELLI et al. 2008; WIRTH et al. 2008). Consequentemente ocorrem modificações nas interações entre plantas e seus dependentes, tais como herbívoros, polinizadores, dispersores de sementes, beneficiando os generalistas e prejudicando os especialistas.

Além da perda de habitat, uma das alterações estruturais mais significativas dos fragmentos são as bordas (HARPER et al. 2005). Borda é uma área ecotonal, situada na interface (fronteira) entre um ambiente florestado e não florestado, possui hiperdinamismo e características bióticas e abióticas peculiares. Como as bordas florestais situam-se no início da entrada dos remanescentes, elas podem apresentar um alto contraste com a matriz influenciando fatores abióticos nos fragmentos, podem favorecer a passagem de algumas espécies animais e vegetais oriundos da matriz para o interior dos fragmentos, alterando, desta forma, o fluxo de entrada e saída de ecossistemas, bem como a composição florística e faunística (MURCIA 1995; HARPER et al. 2005). Então nessas paisagens, o habitat (em *stricto sensu* o habitat é considerado o local onde o organismo vive com recursos e condições peculiares) borda exerce uma importante influência nas interações bióticas.

Alguns estudos demonstraram que os efeitos da fragmentação em florestas tropicais vêm transformando pequenos fragmentos em áreas similares à bordas, quando é levada em consideração a composição florística e funcional do habitat e também, no que concerne ao aumento da razão borda *versus* interior, o que consequentemente aumenta a penetrabilidade destes efeitos de borda abióticos (OLIVEIRA et al. 2008; SANTOS et al. 2008). Em fragmentos de floresta Atlântica do Nordeste do Brasil, os achados apontam que ocorre retenção de plantas pioneiras principalmente nas bordas e pequenos fragmentos florestais e essas plantas podem ser superexploradas por insetos herbívoros generalistas (WIRTH et al. 2007, 2008), podendo causar alterações em processos do ecossistema, tais como fluxos energéticos, produtividade primária, resiliência e ciclagem de nutrientes. Por conseguinte, a qualidade do habitat aumenta para plantas pioneiras e animais generalistas (e.g. formigas cortadeiras) que se beneficiam da perda não aleatória de espécies tolerantes a sombra, padrão contrário ao esperado para herbívoros especialistas que possuem estreita amplitude de nicho e dependem restritamente de suas plantas hospedeiras. Portanto podem ocorrer quedas nas populações e até extinção de insetos herbívoros especializados pelo decréscimo na qualidade do habitat resultantes de diminuição na riqueza, mudanças na composição e empobrecimento da estrutura vertical da comunidade de plantas que resultam em altos níveis de degradação ambiental em diversas escalas espaciais.

A despeito da importância dos insetos herbívoros especializados para a diversidade de plantas e processos do ecossistema em florestas tropicais (BIGGER & MARVIER 1998), mecanismos que regulam as assembléias destes insetos têm sido negligenciados nas regiões da floresta Atlântica brasileira. Aqui, foram utilizados insetos galhadores como modelo de estudo porque estes animais são importantes endófagos em ecossistemas florestais causando impacto nas populações de plantas hospedeiras com a diminuição do sucesso reprodutivo, alterações no metabolismo secundário e biomassa de plantas galhadas. Adicionalmente, estes animais possuem uma relação extremamente especializada com suas plantas hospedeiras, e a simplificação e empobrecimento das assembléias de plantas conduz a previsões de possíveis co-extinções entre os táxons envolvidos nestas interações em paisagens depauperadas. Os estudos realizados até agora com esta guilda de herbívoros mostraram relações contraditórias dos atributos de fragmentos (área, efeito de borda) e da paisagem (conectividade) que certamente influenciam o comportamento dos insetos e os padrões em suas assembléias em diferentes escalas espaciais. Adicionalmente, os padrões de organização das assembléias destes insetos tem sido negligenciados na floresta Atlântica, a despeito deste ecossistema ser um "*hotspot*" de biodiversidade. Nesta Tese, a motivação foi entender como disponibilidade de recursos, modificações do habitat e da paisagem influenciam a diversidade alfa, beta e gama, riqueza de espécies e composição taxonômica de insetos galhadores em uma grande paisagem severamente fragmentada de floresta Atlântica.

Este estudo pretende preencher a lacuna no conhecimento sobre os padrões planta-herbívoro especializado e possíveis implicações eco-evolutivas em um hotspot de biodiversidade e está estruturado em dois manuscritos. No apêndice 1: *"Depauperation and* *divergence of plant-galling insect assemblages in a fragmented tropical landscape"* teve o objetivo central de avaliar se modificações na paisagem influenciam várias dimensões na diversidade: alfa, beta e gama, um estudo inédito e que possui grande importância para a compreensão da estruturação das assembleias de plantas e insetos galhadores e de possíveis mecanismos subjacentes. As perguntas foram: (i) a composição de espécies nos habitats afetados pelos efeitos de borda seriam um sub conjunto das espécies de um fragmento grande?; (ii) Qual padrão das assembleias de espécies seria encontrado na paisagem fragmentada avaliada: homogeneização (i.e. menor diversidade beta) ou diferenciação (i.e. maior diversidade beta) taxonômica?; (iii) a perda de espécies das assembleias de insetos galhadores seguem o mesmo padrão das suas plantas hospedeiras?; e finalmente, (iv) a distância da borda mais próxima e conectividade desempenham papel na estruturação e distribuição espacial das assembleias de plantas e insetos galhadores?. O manuscrito deste apêndice com autoria de Danielle G. Souza e co-autoria de Julia C. Sfair, Víctor Arroyo-Rodríguez, Jean C. Santos e Marcelo Tabarelli será submetido ao periódico Oecologia. No anexo 1: *"Shifts in plant assemblages reduce the richness of galling insects across edge-affected habitats in the Atlantic Forest",* teve como objetivo central a compreensão da influência dos efeitos de borda e da proliferação de plantas pioneiras nos padrões das assembléias de insetos galhadores e testou as seguintes hipóteses: (i) a riqueza de plantas jovens hospedeiras e insetos galhadores será menor nos habitats afetados pelos efeitos de borda (i.e. bordas, pequenos fragmentos) quando comparado ao interior florestal; (ii) composição taxonômica das assembléias de plantas hospedeiras e de insetos galhadores será dissimilar entre os habitats interior, pequenos fragmentos e bordas. O manuscrito foi publicado no periódico Environmental Entomology com a autoria de Danielle G. Souza e co-autoria de Jean Carlos Santos, Marcondes A. Oliveira e Marcelo Tabarelli.

2. FUNDAMENTAÇÃO TEÓRICA

2.1- FLORESTA ATLÂNTICA E CENTRO DE ENDEMISMO PERNAMBUCO

A floresta Atlântica brasileira é uma das maiores florestas das Américas, cobrindo originalmente 150 milhões de hectares, em condições ambientais heterogêneas. A extensão longitudinal da floresta é ampla e fundamental na produção de diferentes composições da floresta, por causa do aumento do regime de chuva da área costeira. Áreas na costa recebem em torno de 4.000mm anuais de precipitação, enquanto áreas distantes da costa recebem em torno de 1.000mm/ano (CÂMARA 2003). Estas características geográficas, combinadas com ampla extensão altitudinal favorecem altas taxas de diversidade com mais de 20.000 espécies de plantas, 261 espécies de mamíferos, 688 espécies de aves, 200 espécies de répteis, 280 espécies de anfíbios (MITTERMEIER et al., 1999; SILVA & CASTELETI, 2003), bem como alto endemismo. Esta grande diversidade de fauna e flora estão distribuídos ao longo cinco centros de endemismo (Bahia, Brejos nordestinos, Pernambuco, Diamantina e Serra do Mar) que foram categorizados baseados nas distribuições de aves, borboletas e primatas (SILVA & CASTELETI 2003).

Este ecossistema vem há séculos sofrendo os impactos antrópicos e, por isso, tornou-se um dos mais ameaçados do mundo (MYERS et al 2000). Desde o século XVI a floresta Atlântica vem sofrendo impactos iniciados pela agricultura colonial onde a floresta cedeu lugar a contínuos ciclos agrícolas como os da cana-de-açúcar, as lavouras de cacau, café, banana, a agricultura de subsistência, retirada de madeira para carvão e a criação de áreas para pastagem (GALINDO-LEAL & CÂMARA 2003). Tais fatos fizeram com que a floresta Atlântica se transformasse em uma das áreas mais ameaçadas do Brasil (LIMA & CAPOBIANCO 1997) com área florestal atual remanescente estendendo-se de 11,4 a 16% em todo o ecossistema (RIBEIRO et al 2009). Os fragmentos florestais remanescentes, em todas as regiões biogeográficas da floresta Atlântica são, em média, menores do que 50 ha (RIBEIRO et al 2009) e por isso, mais de 70% das 199 espécies de aves endêmicas estão fortemente ameaçadas de extinção (PARKER et al., 1996; STOTZ et al., 1996; GOERCK, 1997). Por esses motivos, a Floresta Atlântica é atualmente classificada como um dos “hotspots” de biodiversidade, ou seja, é uma das áreas prioritárias para conservação em decorrência dos altos índices de diversidade, endemismos e pelo avançado estado de fragmentação (MYERS et al. 2000).

Na região Nordeste do Brasil restam apenas fragmentos pequenos e isolados, não havendo grandes extensões florestais, como se observam ainda nas regiões Sul e Sudeste do

Brasil (BROWN JR. & BROWN 1992; LIMA & CAPOBIANCO 1997; RIBEIRO et al 2009). Um dos trechos mais ameaçado e extremamente explorado é o trecho ao Norte do rio São Francisco, onde está situado o Centro de Endemismo Pernambuco. O Centro de Endemismo Pernambuco está localizado ao Norte do rio São Francisco e se estende até o sul do estado do Rio Grande do Norte, estando inserido dentro dos limites da floresta Atlântica Nordestina com uma área de 36,6.10Km^2 (SILVA & TABARELLI 2000). O Centro de Endemismo Pernambuco se encontra entre as latitudes 5º08'S e 10º31'S, e é delimitado a leste pelo mar e a oeste pelo planalto da Borborema, com altitudes entre 300 e 1.100 m, aproximadamente. Ao sul, é delimitado pelo rio São Francisco, de acordo com os estudos de endemismo de Silva &Casteleti (2005). Este centro é importante na contribuição dos níveis de endemismos animais e vegetais na América do Sul. Sua biota recebe influência da biota Amazônica (PRANCE 1982) e dos trechos de floresta Atlântica do Sul e Sudeste do Brasil (ANDRADE-LIMA 1966), o que a torna bastante peculiar do restante da floresta Atlântica brasileira.

De acordo com Silva & Tabarelli (2000), aproximadamente 49% da flora de plantas lenhosas desta área podem extinguir-se regionalmente por consequência da interrupção da dispersão de diásporos. Os autores observaram uma tendência de que mecanismos de dispersão abióticos tornem-se dominantes, bem como árvores com pequenas sementes. Em consequência deste fato, uma flora prevista e dominada por espécies de Melastomataceae, Myrsinaceae, Rubiaceae, entre outras, já tem sido observada em pequenos fragmentos florestais e em áreas de regeneração (TABARELLI & MANTOVANI 1999; TABARELLI et al 1999; SILVA &TABARELLI 2000; TABARELLI & PERES 2002). A interrupção da dispersão de sementes está associada ao desaparecimento de vertebrados frugívoros de médio e grande porte que é conseqüência direta da perda de habitat e caça (SILVA &TABARELLI 2000; ALVES-COSTA 2004). Desta forma, entender como será o funcionamento da floresta com estas comunidades vegetais que estão se estabelecendo no CEP e qual sua influência na dinâmica dos processos do ecossistema são fundamentais para futuras ações de conservação da flora e fauna desta região.

2.2 - FRAGMENTAÇÃO DE HABITATS

A fragmentação de habitats é uma das mais prejudiciais modificações na paisagem (LAURANCE & PERES 2006) produzidas por ação antrópica, como resultado do uso da terra para a agricultura (GIBBS et al 2010), corte seletivo de madeira (ASNER et al 2005) e outras atividades (TABARELLI & GASCON 2005). A fragmentação consiste em mudanças na configuração do habitat que resultam em “ruptura em fragmentos” (WILCOVE *et al* 1986), reduzindo a área do habitat, aumentando o número de manchas e isolando-as (FAHRIG 2003). Estes fragmentos ficam imersos em uma matriz, que na maioria das vezes é inóspita e age como um filtro hostil do fluxo de animais e propágulos entre remanescentes (veja LAURANCE 2008). Desta forma, a fragmentação de habitats é uma causa importante no comprometimento de espécies e ecossistemas (WILCOX & MURPHY 1985), e por isso é um dos maiores responsáveis pela queda da biodiversidade e modificações nos processos ecológicos (dispersão, predação, polinização, herbivoria) em florestas tropicais (MELO et al 2006; AIZEN & FEINSINGER 1996; WIRTH et al 2008).

Algumas características da paisagem, como a matriz, têm influência nos efeitos de borda, influenciam movimentos de polinizadores e dispersores de sementes e, afetam fortemente a chuva de sementes que chegam nos fragmentos (veja LAURANCE et al 2011). Em paisagens modificadas, a diminuição da área do fragmento torna a perda de espécies de pequenos fragmentos muito rápida (STOUFFER et al 2008): estudos empíricos já inferiram que a riqueza de espécies de briófitas (ZARTMAN 2003), plântulas (BENÍTEZ-MALVIDO & MARTINEZ -RAMOS 2003), palmeiras (SCARIOT 1999), pássaros insetívoros do subdossel (FERRAZ et al 2007) e primatas (GILBERT &SETZ 2001) tendem a declinar com a diminuição do tamanho do fragmento. Além disso, o isolamento entre fragmentos, a proporção e a orientação de bordas e a qualidade do habitat influenciam de maneira efetiva a abundância das populações e diversidade de comunidades (KAREIVA & WENNERGREN 1995; ZABEL & TSCHARNTKE 1998; THIES *et al* 2003; LAURANCE *et al* 2002; RIES *et al* 2004; EWERS & DIDHAM 2006). Fahrig (2003), em sua revisão destacou que a fragmentação provoca perda de habitat influenciando negativamente as taxas de crescimento das populações, influencia a diminuição do tamanho das cadeias alimentares, reduz número de espécies especialistas e com o corpo grande, afeta gestação de fêmeas, padrões de dispersão, predação e comportamento animal.

Com a fragmentação, algumas espécies tendem a desaparecer, outras permanecem com estabilidade precária e outras aumentam drasticamente (LAURANCE 2008). Este processo é importante na contribuição da perda de biodiversidade e taxa de extinção de espécies (DIDHAM *et al* 1996). Geralmente espécies de níveis tróficos superiores (HOLT *et al*., 1999), com menor mobilidade (WRIGHT 1981) e com grande especialização ecológica (KRAUSS *et al*., 2003) têm quedas nas densidades populacionais, assim respondendo negativamente ao isolamento (LAURANCE 2008) e podendo se extinguir localmente.

Modificações da paisagem, decorrentes das alterações do habitat resultam em perda e simplificação da vegetação e mudanças na distribuição espacial de comunidades vegetais, perturbam sistemas de polinização (GIRÃO *et al* 2007) e degeneram a estrutura da vegetação com a retenção de espécies pioneiras nas manchas ocasionando em redução de biomassa (SANTOS *et al* 2008). Assim, muitas extinções podem ocorrer e algumas espécies de vegetais e animais generalistas podem se beneficiar de menor riqueza de espécies e de sucessão tardia (veja Fischer & Lindenmayer 2007). Na Amazônia, Michalski et al (2007) constataram que vem ocorrendo a substituição de táxons de plantas tolerantes à sombra por pioneiras, mudando padrões e processos dos dependentes das comunidades vegetais (ex., animais herbívoros, polinizadores, dispersores de sementes) e consequentemente modificando a trajetória do ecossistema. Em fragmentos de floresta Atlântica ao norte do rio São Francisco já foi percebido que está ocorrendo substituição de árvores tolerantes à sombra por pioneiras em áreas de borda e de pequenos fragmentos (OLIVEIRA *et al* 2008; SANTOS *et al* 2008). Oliveira *et al* 2008 notaram uma clara similaridade entre a vegetação de pequenos fragmentos e áreas de borda e que estes habitats perderam plantas emergentes, já em áreas nucleares, foi percebido haver maior abundância de plantas tolerantes à sombra e maior riqueza de espécies (OLIVEIRA *et al* 2008; SANTOS *et al* 2008). Tabarelli *et al* (2010), adicionalmente concluíram que há maior predominância de espécies decíduas e empobrecimento nos caracteres da história de vida das comunidades arbóreas nos pequenos fragmentos e bordas. Assim, está ocorrendo uma convergência funcional de fragmentos às características de borda, consequentemente modificando todos os processos físicos e bióticos destas áreas. De acordo com os achados do ecossistema de floresta amazônico e da floresta Atlântica é razoável pensar que está ocorrendo uma mudança de paradigma nestes ecossistemas: as espécies vencedoras (pioneiras) são resilientes e estão gradualmente substituindo as espécies perdedoras que são as que não toleram distúrbios antropogênicos (tolerantes à sombra). As plantas tolerantes a sombra são substituídas por plantas nativas filogeneticamente não relacionadas – *r* estrategistas- direcionando a uma assembléia de plantas embobrecida em qualquer escala da paisagem, interrompendo interações tróficas e beneficiando interações generalista-generalista (TABARELLI et al 2012).

O impacto de tal mudança ainda é desconhecido, mas precisa ser urgentemente investigado. Diante de tal cenário, há necessidade de ações efetivas para a proteção da biota, como por exemplo, mais estudos com interações bióticas em paisagens fragmentadas e quais as implicações que esta convergência funcional está trazendo para as florestas tropicais fragmentadas, e que estas ofereçam ferramentas teóricas para se delinear planos de manejo e restauração do ecossistema.

2.3 - EFEITOS DE BORDA

A modificação da paisagem aumentou a proeminência das bordas de floresta (CADENASSO & PICKET 2000; LAURANCE *et al* 2006). Entende-se por borda florestal, a interface abrupta entre ambientes florestados e não florestados (ex., matriz) ou entre duas florestas de estruturas ou composição contrastantes (HARPER *et al.* 2005). Efeitos de borda alteram a estrutura, dinâmica, microclima e composição de espécies em ecossistemas fragmentados (LAURANCE *et al* 2002, 2006, 2011; OLIVEIRA *et al* 2004; MICHALSKI et al 2007; LAURANCE 2008). Dependendo da configuração espacial do fragmento e área de penetração, a influência da borda pode ser um componente dominante da matriz na paisagem (SAUNDERS *et al* 1991; HARPER *et al* 2005), tendo seus efeitos estendidos a centenas de metros para dentro dos fragmentos (LAURANCE *et al* 1991). Por exemplo, a forma irregular e área pequena do fragmento têm suma importância na magnitude e intensidade dos efeitos de borda, principalmente para populações de animais (EWERS & DIDHAM 2007).

Murcia (2005) classificou os efeitos de borda em três tipos: abiótico, biótico direto e biótico indireto. Entre os abióticos, podem-se citar mudanças microclimáticas como maior variabilidade térmica, maior penetração de luz, que promove o crescimento de uma vegetação característica de áreas perturbadas, maior exposição aos ventos de grande velocidade e turbulência ocasionando maior número de clareiras, (LOVEJOY *et al.* 1986; LAURANCE 1991; MURCIA 1995; LAURANCE, 1997), redução na umidade (KAPOS 1989), acumulação abundante de serrapilheira e facilitação da entrada de incêndios que ocorram na matriz circundante. Outro fator preocupante é a possível queda no sequestro de carbono atmosférico por árvores, contribuindo com o aquecimento global (FEARNSIDE 2000).

Do ponto de vista biótico direto, posterior à criação das bordas ocorrem respostas estruturais nas comunidades arbóreas, tais como diminuição da cobertura do dossel, queda na densidade de árvores, mudanças na composição florística e decréscimo na riqueza de espécies (HARPER *et al.* 2005; LAURANCE *et al.* 2006). A partir disto, as principais conseqüências são quedas nos padrões de dispersão e migração em conseqüência do empobrecimento ou desaparecimento de espécies-chave de animais, redução do recrutamento de plântulas de espécies tolerantes à sombra devido à dessecação e a conseqüente regeneração de populações vegetais (BENÍTEZ-MALVIDO 1998; BRUNA 1999; BENÍTEZ MALVIDO & MARTÍNEZ-RAMOS 2003), decréscimo de populações vegetais características de estágios sucessionais tardios (SILVA & TABARELLI 2000; OLIVEIRA *et al* 2004), proliferação de espécies animais e vegetais ruderais, generalistas e invasoras (TABARELLI *et al* 1999) e perda de biomassa vegetal (LAURANCE *et al*. 1997).

Os efeitos biológicos indiretos envolvem aumentos nas taxas de herbivoria na borda por herbívoros generalistas (CADENASSO & PICKET, 2000; BENÍTEZ-MALVIDO & LEMUS ALBOR 2005; URBAS *et al.* 2007; WIRTH *et al.* 2007a; WIRTH *et al.* 2008; DOHM et al 2011), aumento na disseminação de doenças causadas por patógenos (BENÍTEZ-MALVIDO & LEMUS ALBOR 2005) alterações em processos ecológicos e genéticos, aumento da mortalidade de árvores jovens por competição com lianas (LAURANCE *et al* 2002), alterações nas taxas de parasitismo (KRUESS & TSCHARNTKE 1994; KRUESS 2003; ALMEIDA *et al.* 2008), predação (WRIGHT *et al.* 2000; WRIGHT & DUBBER 2001), decomposição (DIDHAM *et al.* 1996) e polinização (AIZEN & FEINSINGER 1994; MURCIA 1995; LAURANCE *et al.* 1997).

Assim, haverá uma grande influência dos efeitos de borda em padrões e processos nas paisagens modificadas por ação antrópica e entender como esses efeitos agem sobre as comunidades biológicas pode ser de fundamental importância para a permanência de organismos nos fragmentos.

2.4 - ALTERAÇÕES NAS INTERAÇÕES PLANTA-HERBÍVORO

Insetos herbívoros são responsáveis pela maior parte da remoção da biomassa vegetal em florestas tropicais (COLEY & BARONE 1996). Bigger & Marvier (1998) inferiram que herbívoros têm um impacto negativo na biomassa das plantas que eles consomem e seu impacto pode ser semelhante ou mais alto do que competição dentro da comunidade vegetal. Estes animais são altamente suscetíveis aos efeitos adversos da fragmentação de habitats (TSCHARNTKE *et al.* 2002) e têm seus padrões de abundância e diversidade e, os processos dentro de suas assembléias modificados pela fragmentação (DIDHAM *et al* 1996; WIRTH *et al* 2007; WIRTH *et al* 2008).

Qualidade do habitat afeta a sobrevivência das populações e diversidade de espécies. A posição de um nível trófico influencia a suscetibilidade do táxon a distúrbios, então, a paisagem adjacente aos fragmentos é muito importante para especialistas já que estes dependem de habitats e recursos bem específicos (TSCHARNTKE & BRANDL 2004). Alguns estudos afirmaram que parasitóides de insetos fitófagos podem ser prejudicados pela fragmentação, perda e isolamento de habitats, alterações microclimáticas e efeitos de borda, assim sendo mais suscetíveis à extinção local e alterações em sua distribuição espacial (ZABEL &

TSCHARNTKE 1998; ALMEIDA *et al* 2008). Portanto, a modificação de paisagens atinge principalmente animais dos níveis tróficos mais elevados devido ao grande requerimento de área, de energia e ao fato de suas populações apresentarem tamanho pequeno (Holt 1996). Quando os parasitóides apresentam abundância e desempenho diminuídos, aumentam a probabilidade de liberação de herbívoros fitófagos de nível trófico inferior do controle topo-base devido ao aumento de suas taxas de forrageamento e sucesso reprodutivo (THIES & TSCHARNTKE 1994; KRUESS & TSCHARNTKE 1994; DIDHAM *et al.* 1996; TSCHARNTKE *et al.* 2002; KRUESS 2003; TSCHARNTKE & BRANDL 2004; ZEIPEL *et al.* 2006; ELZINGA *et al.* 2007; THIES *et a.l* 2008; ALMEIDA *et al.* 2008).

As interações tróficas em fragmentos florestais são influenciadas pela quantidade e qualidade da cobertura vegetacional. Diversos estudos vêm reportando a ruptura de cadeias tróficas em áreas fragmentadas, estas sendo fortemente influenciadas por alterações no padrão de distribuição, produtividade de espécies vegetais e configuração da paisagem dentro e adjacente aos remanescentes (CADENASSO & PICKET 2000; TERBORGH *et al.* 2001; FISCHER & LINDENMAYER 2007; WIRTH *et al.* 2007; URBAS *et al* 2007; WIRTH *et al.* 2008).

Em uma revisão, Wirth *et al.* (2008) destacaram que nas áreas de borda há eventos que proporcionam o aumento das atividades de herbívoros generalistas (ex.,para florestas tropicais: formigas cortadeiras e para florestas temperadas: veados), tais como as mudanças estruturais e físicas da borda da floresta que modificam a oferta de recursos por facilitar a hiper abundância de espécies de plantas pioneiras, alteram a qualidade da composição química das folhas e modificam as condições microclimáticas influenciando diretamente as interações tri-tróficas entre organismos (URBAS *et al* 2007; WIRTH *et al* 2007).

Na Floresta Atlântica Nordestina, estudos realizados na paisagem fragmentada da Usina Serra Grande (AL) demonstraram que a fragmentação de paisagens beneficia formigas cortadeiras (herbívoro generalista) e estes insetos atuam como engenheiros do ecossistema causando modificações nas condições do solo, luz e consequentemente alterando o recrutamento de plântulas de espécies lenhosas (LEAL *et al* 2012). Neste ecossistema, Urbas *et al.* (2007) constataram o relaxamento do controle base-topo sobre formigas cortadeiras do gênero *Atta* com a diminuição das áreas de forrageamento das formigas, bem como a sobre-exploração de recursos vegetais nas bordas dos fragmentos florestais. Os autores atribuíram maior forrageamento no habitat borda à presença abundante de espécies pioneiras, que segundo Oliveira *et al.* (2004) indivíduos deste nicho de regeneração perfazem em torno de 80% da borda . Espécies pioneiras são r estrategistas, ou seja investem principalmente em crescimento, e muito pouco de suas reservas energéticas em defesas químicas contra herbivoria (COLEY *et al* 1985). Ademais, estas plantas possuem grandes quantidades de nitrogênio nas folhas que somados aos fertilizantes inseridos nas matrizes não florestadas dos fragmentos, aumenta a probabilidade de palatabilidade da vegetação por herbívoros (PICKET *et al* 2000).

O controle topo base das formigas cortadeiras também foi estudado nesta mesma paisagem. Almeida *et al.* (2008) hipotetizaram que em áreas de borda de um grande fragmento (Coimbra) haveria menores taxas de ataque e em áreas nucleares dos fragmentos haveria maiores taxas de ataque à formigas *Atta cephalotes* por seus inimigos naturais especialistas, as moscas forídeas do gênero *Myrmosicarius* e *Neodohrniphora*. Os autores tiveram sua hipótese corroborada e atribuíram a diminuição dos ataques das moscas forídeas parasitas às hostis condições microclimáticas da borda que atuam negativamente em várias fases do ciclo de vida destes parasitóides (ALMEIDA *et al.* 2008). No entanto, ainda são obscuros os efeitos da fragmentação/modificação de paisagens em herbívoros especializados. Diante de tais evidências empíricas, torna-se óbvio que os efeitos degenerantes da fragmentação de habitat exercem influência significativa nas interações planta-herbívoro e presa-predador dos grupos de insetos generalistas e tornam-se necessários o entendimento do papel da fragmentação e modificação de paisagens em herbívoros especialistas.

2.5 - INSETOS GALHADORES

Insetos galhadores estão entre as guildas de insetos herbívoros mais importantes. Estes são em sua maioria das Ordens Homoptera, Hymenoptera, Coleoptera, Lepidoptera e Diptera; que ovipositam principalmente em tecidos meristemáticos não diferenciados das plantas (SANTOS et al 2012). Estes insetos são altamente especializados, endófagos e induzem modificações morfo-fisiológicas nas plantas, formando tumores que são utilizados para abrigar, prover alimento e favorecer estes insetos contra adversidades do habitat e de seus inimigos naturais (FERNANDES & MARTINS 1985; MANI 1992; PRICE & ROININEN 1993; SANTOS et al 2012). A galha é induzida pelo crescimento no volume celular (hipertrofia celular) ou número de células (hiperplasia celular) provocada por insetos e constitui-se na expressão da planta que é resultante do esforço das plantas hospedeiras em isolar o indutor no espaço e tempo e consequentemente influenciar os indutores até a especialização extrema, o que proporciona as galhas de insetos, por exemplo, o status de espécies indicadoras de táxons de plantas (RAMAN 1996; RAMAN et al 2005). Em diversos ecossistemas, os galhadores ajustam a duração do seu desenvolvimento especialmente à sincronização das estações de floração, frutificação e produção de folhas e ramos de suas plantas hospedeiras (RAMAN et al 2005).

A formação de tumores estimulada pelos galhadores influencia negativamente o sucesso reprodutivo das plantas hospedeiras, reduzindo sua produção de flores, frutos e sementes (MCCREA *et al.* 1985; FERNANDES & RIBEIRO 1990; FERNANDES *et al.*, 1993; FAY *et al* 1996). Esta guilda especializada tem a capacidade de agir como um agregador (poço) de nutrientes e de alguns metabólitos secundários das plantas, assim podendo utilizar fenóis e taninos hidrolizáveis, por exemplo (HARTLEY 1998; PASCUAL ALVARADO 2008), que teoricamente seriam repelente para folívoros, para sua própria proteção contra seus inimigos naturais (WARING & PRICE 1990, FERNANDES &PRICE 1992, PASCUAL-ALVARADO et al 2008). Sendo assim, estas espécies possuem a capacidade de manipular o crescimento e o desenvolvimento de tecidos da planta (CUEVAS- REYES *et al.* 2003, 2004a; WEIS *et al.* 1988) e ainda possuem maior habilidade competitiva contra folívoros dentro do ecossistema (PASCUAL- ALVARADO *et al* 2008). Todavia, a "corrida armamentista" das plantas com relação aos seus herbívoros moldou relações bem estabelecidas entre insetos galhadores e seus inimigos naturais, bem como reações químicas de resistência induzida pós-ataque destes herbívoros.

Em escala global, a riqueza de insetos galhadores é estimada em torno de 21.000 a 211.000 espécies com uma média aproximada de 132.930 espécies (ESPÍRITO SANTO & FERNANDES 2007). Na região Neotropical, insetos galhadores são muito ricos em espécies, entretanto são poucos conhecidos do ponto de vista taxonômico (GONÇALVES ALVIM &FERNANDES 2000). Ainda nesta região, os cecidomiídeos (Diptera: Cecidomyiidae) representam o principal táxon que mais induz galhas em plantas (FERNANDES et al 1996; CARNEIRO et al 2009). Estudos apontam para duas linhas de raciocínio explicando os padrões de riqueza de comunidades e distribuição de insetos indutores de galhas: 1- menor mortalidade causada por inimigos naturais e resistência de plantas em habitats xéricos reforçam o hábito galhador, aumentam a radiação adaptativa e a especiação; 2- o número de espécies de galhadores é maior quando a riqueza de espécies de plantas é maior (Raman et al 2005). Mendonça (2001) inferiu que o aumento do número e da previsibilidade de plantas hospedeiras no tempo evolutivo poderia explicar os padrões globais de riqueza de insetos galhadores. Então, o autor formulou a "hipótese da sincronização de recursos" que prevê que a produção sincronizada de novos brotos entre espécies de plantas diferentes aumentaria as chances dos erros de oviposição das fêmeas e a ocorrência de substituição de hospedeiros, principal mecanismo de especiação simpátrica para insetos herbívoros. Atualmente, é correto afirmar que fatores bióticos (idade, isolamento geográfico e qualidade dos tecidos da planta hospedeira, fenologia e riqueza de espécies de plantas) e abióticos (disponibilidade de luz, estresse hídrico, fertilidade do solo, sazonalidade) explicam os padrões de riqueza de insetos indutores de galhas em regiões tropicais (FERNANDES & PRICE 1991; LARA & FERNANDES 1996; RIBEIRO *et al.* 1998; OYAMA *et al* 2003; CUEVAS-REYES *et al.*2004; 2011). Da mesma forma, compostos químicos e palatabilidade da folha influenciam a seleção de sítios de oviposição por fêmeas de insetos, visto que muitas espécies de plantas têm nutrientes, fenologia foliar e compostos secundários variando bastante ao longo de seu ciclo de vida (AIDE & ZIMMERMAN 1990; COLEY & BARONE 1996).

2.6- GALHAS, FRAGMENTAÇÃO DE HABITATS E EFEITOS DE BORDA

Um tópico que tem sido estudado na ecologia diz respeito às interações entre plantas e seus dependentes e, tem sido evidenciado que a modificação das paisagens interrompe ou altera muitas interações tri-tóficas (ex., entre plantas-herbívoros- inimigos naturais) (citações sobre o assunto no tópico 2.3). Alguns estudos foram realizados em ecossistesmas florestais no intuito de compreender a relação entre insetos galhadores e a fragmentação de habitat e/ou efeitos de borda. Nas florestas de carvalho da Espanha, Chust e colaboradores (2007) investigaram relações entre a fragmentação de plantas hospedeiras e declínio potencial de vespas galhadoras Cinipídeas e de seus parasitóides. Os autores inferiram que a abundância de Cinipídeos permaneceu constante até a cobertura de floresta estar reduzida a 40%, e abaixo deste valor limiar crítico, as vespas galhadoras foram mais abundantes. No que concerne a ecossistemas tropicais, o primeiro estudo com relação espécie-área e efeitos de borda agindo sobre insetos galhadores foi realizado no pantanal (JULIÃO et al 2004). Neste caso, foram verificadas relações neutras na riqueza de insetos galhadores com o número de espécies similar entre fragmentos grandes e pequenos e, também foram refutadas as previsões sobre diferenças na riqueza entre os habitats borda e núcleo. Entretanto, Araújo & Santo-Filho (2012) encontraram respostas positivas aos efeitos de borda na Amazônia, com maior riqueza de galhadores nas áreas fragmentadase próximas à borda, semelhante aos achados de Araújo e colaboradores (2011) no cerrado, e ambos atribuíram tais resultados a relação positiva entre esta guilda de herbívoro a habitats estressados e menor pressão de parasitismo.

Distúrbios de habitat relacionados a atividades humanas são consideráveis em áreas de florestas tropicais e estes e outros estudos prévios atestaram (ALMEIDA et al 2008) e sugeriram (ARAÚJO et al 2011; ARAÚJO & SANTO-FILHO et al 2012) que modificações abióticas, como incremento da luminosidade, temperatura, fluxo de ventos, queda na complexidade do habitat alteram o microclima das bordas e de pequenos fragmentos florestais e, assim, atuam negativamente em diferentes fases do ciclo de vida que por conseguinte, diminuem o desempenho dos insetos parasitóides (inimigos naturais) dos herbívoros (ALMEIDA *et al* 2008; OLIVEIRA 1999). Considerando que o tecido das galhas é consumido principalmente por parasitóides (ex., vespas) (ESPÍRITO-SANTO et al 2004) que os animais de terceiro nível quanto os de segundo nível trófico podem ser afetados pela fragmentação e perda de habitat (EWERS & DIDHAM 2006), pode-se sugerir que alterações nas populações de inimigos naturais são espacialmente previsíveis em habitats florestais.

Adicionalmente, insetos galhadores podem ser controlados pelo controle base-topo, determinados principalmente pela disponibilidade de recursos (ex., plantas hospedeiras) e por defesas de plantas [ex., reação de hipersensitividade (RH)]. (FERNANDES & NEGREIROS 2001). Nesta reação, ocorre uma resposta de defesa do hospedeiro em que a planta desenvolve mecanismos estimulados por genes, resultando em eventos em cascata que envolve alterações bioquímicas, fisiológicas, morfológicas, acúmulos de fotoalexina e outros metabólitos tóxicos que culmina na localização, envolvimento e morte de células da galha (FERNANDES 1990; FERNANDES *et al.* 2000; FERNANDES & NEGREIROS 2001; FERNANDES *et al* 2003). Segundo Fernandes & Negreiros (2001), RH é a principal defesa induzida de plantas contra insetos herbívoros com alta especificidade e patógenos e esta reação pode ser diminuída pelos regimes de mudança de luminosidade nos ecossistemas. Levando-se em consideração que as assembléias de plantas dos fragmentos de floresta Atlântica Nordestina vêm passando por processos de empobrecimento (ex. diminuição na riqueza de espécies e na composição taxonômica), convergência funcional e perda de complexidade estrutural (ex., diminuição na abundância de plantas do estrato emergente nas bordas e pequenos fragmentos), a hiperproliferação de plantas pioneiras, representadas em cerca de 80% de indivíduos nas bordas e nos pequenos fragmentos, é evidente que pequenos fragmentos são taxonomicamente e funcionalmente similares a bordas (OLIVEIRA *et al* 2008). Nas bordas e fragmentos pequenos há um aumento da abundância de espécies de plantas decíduas (TABARELLI *et al* 2010), o que pode influenciar os regimes abióticos, principalmente a entrada de luz e diminuição da umidade. Desta forma, a perda de habitat e a reorganização das comunidades vegetais podem afetar positivamente alguns herbívoros generalistas (ex., formigas cortadeiras) e/ou negativamente algumas guildas de insetos herbívoros especializados. Em contraste aos generalistas, herbívoros especializados possuem uma amplitude de nicho estreita e tendem a decrescer a diversidade como resultado às mudanças na distribuição de plantas e no balanço entre os diferentes grupos funcionais destas (ex. pioneiras e tolerantes à sombra) quando é considerado que estes animais dependem exclusivamente de suas plantas hospedeiras (TERBORGH & FEELEY 2008).

Apesar da importância dos insetos herbívoros especializados para a diversidade de plantas e processos ecossistêmicos nas florestas tropicais, os mecanismos que moldam as comunidades destes organismos são poucos conhecidos em paisagens modificadas. Diante de tais exposições, a motivação deste trabalho foi investigar e entender os padrões que influenciam as interações entre planta-insetos herbívoros especializados em paisagens fragmentadas e as prováveis implicações deste processo para a manutenção das interações co-evolutivas interespecíficas. Com a evidente perda não aleatória de espécies e grupos funcionais vegetais, a previsão é que a simplificação da comunidade vegetal direciona a perda de espécies de plantas hospedeiras culminando na erosão da diversidade e riqueza de insetos galhadores em habitats afetados pela borda e com menor complexidade estrutural.

3- OBJETIVOS

3.1. OBJETIVO GERAL

O objetivo geral deste estudo é investigar a influência da modificação da paisagem e do habitat sobre a riqueza, composição e diversidade em diferentes escalas espaciais de plantas hospedeiras e insetos galhadores na floresta Atlântica Nordestina.

3.1.1 Objetivos Específicos

♦ Avaliar se riqueza de espécies, densidade de indivíduos e composição taxonômica das assembleias de plantas e insetos galhadores são afetados negativamente pelos efeitos de borda e da modificação de paisagem em várias escalas espaciais.

♦ Quantificar se a diversidade alfa, beta e gama de plantas hospedeiras e insetos gahadores são afetados negativamente pelos habitats afetados pelos efeitos de borda.

♦ Avaliar se atributos dos fragmentos e da paisagem influenciam as assembléias de plantas hospedeiras e insetos galhadores.

4. **DEPAUPERATION AND DIVERGENCE OF PLANT-GALLING INSECT ASSEMBLAGES IN A FRAGMENTED TROPICAL LANDSCAPE**[1]

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[1] Artigo a ser submetido ao periódico Oecologia.

Abstract

Community structure and spatial organization of plant-specialist herbivore assemblages have been rarely assessed in human-modified tropical landscapes despite the importance of these organisms across multiple levels of biological organization. Here, we examine whether galling insects and their host plants experience a taxonomic differentiation (increase β diversity) or homogenization (decrease of β diversity) between forest fragments and along edges and whether edge-affected habitats influence structure of assemblages in local and landscape scale (alpha and gamma diversity). Additionally, we assess how plot-edge distance and connectivity affect these species assemblage in a severely fragmented landscape from the Brazilian Atlantic forest. We recorded saplings and galling insects in 30 0.1-ha plots located in forest interior stands, forest edges and core areas of small forest fragments. Local diversity (alpha diversity) of both assemblages was significantly higher in reference (interior) plots, than in edge and fragment plots. Regarding the between-plot patterns of species diversity, host plants and galling insects showed similar trends: β-diversity was significantly lower in reference than in fragment and edge plots and was neither correlated to geographical distance among plots nor to fragment size and connectivity. Finally, forest interior supported higher species diversity at the landscape level (gamma diversity), whereas plant-galling insect assemblages inhabiting edge-affected areas was a subsample of those in interior forest. Our results suggest that small forest fragments and forest edges show impoverished (with lower number of individuals and species) assemblages of plant-galling insects at local (α-diversity) and landscape (γ-diversity) scales, although these edge-affected areas support higher β-diversity (i.e., taxonomic divergence), thus supporting the landscape-divergence hypothesis.

Introduction

Tropical forests are undergoing a pervasive process of anthropogenic modifications (Barlow et al. 2016; Butchart et al. 2010; Lewis et al. 2015). It is estimated that ca. 2100 km^2 of tropical forest are lost per year (Hansen et al. 2013) due to the advance of agriculture, livestock and urban areas (Laurance et al. 2007; Hansen et al. 2013). This extensive land-use changes has deep effect on biodiversity, resulting on species loss and decrease on ecosystem function (Laurance et al. 2002, 2014; Mitchel et al. 2015). The habit loss and the subsequent forest fragmentation are some of the main forces negatively affecting tropical biodiversity (Laurance et al. 2002, 2011; Fahrig 2003, 2013; Haddad et al. 2017).

One of the effects of fragmentation is the loss of species in small and isolated fragments (Haddad et al. 2017; Leroux et al. 2016). This loss is not random, since rarer habitat specialists species are more prone to be extinct than abundant generalist species in small fragments (Ulrich et al. 2009). Therefore, this sequential extinction of species results on a pattern in which small fragments have a subset of species assemblage of larger fragments, in a nested pattern of species composition (Patterson and Atmar 2000; Ulrich et al. 2009; Baselga 2012). Many factors can influence the intensity of nestedness in fragmented landscape, such as forest fragment size and species dispersal limitation: smaller fragments are more prone to be have a subset of species than larger fragments, whereas harsher matrices can intensify the nested pattern (Wang et al. 2010; Hill et al. 2011).

Regarding dispersal limitation, many species are not able to cross surrounding matrix of forest fragments and are doomed to go locally extinct, resulting on biotic differentiation, i.e., increase in beta diversity (Arroyo-Rodríguez et al. 2013; Solar et al. 2015; Sfair et al. 2016). Differentiation can also emerge in forest fragments due to post-fragmentation pressures, such as hunting, logging, edge effects, and other human-induced disturbances (Laurance et al. 2007; Norden et al. 2015). These disturbances promote hyperdynamism in forest remnants in which increases probability of stochastic forces in modified landscapes (Laurance 2002).

Consequently, each forest fragment is likely to experience a particular trajectory of vegetation dynamic, resulting on unique biota in each forest fragment and multiple successional pathways (Laurance et al. 2007; Norden et al. 2015; Arroyo-Rodríguez et al. 2017).

On the other hand, some species are favored in fragmented landscapes, resulting on species similarity among forest fragments (Tabarelli et al. 2012) in a process called biotic homogenization (Mckinney and Lockwood 1999). Biotic homogenization could be driven by edge effects, in which microclimate changes and light regimes affects spatial distribution, rearranging spatially plant assemblages in modified landscapes (Laurance et al. 2002; 2011). This is particularly the case of tree assemblages remaining in some of neotropical forests, since some shade-tolerant species become rare, while a small set of pioneer species proliferate, reducing species richness and incrementing cross-community species similarity among forest fragments (Lobo et al. 2011; Laurance et al. 2002, 2011; Michalski et al. 2007; Tabarelli et al. 2012). Therefore, biotic homogenization and differentiation are two opposite ecological processes on species assemblages in fragmented landscapes (Solar et al. 2015).

Since plant species communities are altered in human-modified landscapes, plant-attendant communities can be altered in a cascade effects or can be directly influenced by fragmentation and edge effects (Lopes et al. 2009; Morante-Filho et al. 2016). Herbivores are a key ecological group within forest ecosystems, and play key evolutionary pressures on plant life-history traits (Karban and Baldwin 1997; Novotny et al. 2006; Dyer et al. 2007; Lewinsohn et al. 2011), population demography and forest regeneration (Bigger and Marvier 1998; Coley and Barone 1996; Schmitz 2008). Among herbivores, galling insects are a specialist group and, for this reason, their diversity is deeply affected by species richness and taxonomic composition of host plant communities (Araújo et al. 2013; Malinga et al. 2014; Maldonado-Lopes et al. 2015, 2016; Souza et al. 2016). Previously studies showed that galling insects are strongly affected by edge effects and landscape modifications (Malinga et al. 2014; Maldonado Lopes et al. 2015, 2016; Souza et al. 2016), but no study as performed to understand the role of and homogenization/differentiation of specialist herbivores in fragmented landscapes.

Here we studied a severely fragmented landscape of Atlantic forest, which is one of the most diverse tropical forests in the world, with a high level of plant and animal endemism (Tabarelli et al. 2010; Silva and Tabarelli 2000), but also located in areas with high human density and is experiencing huge forest loss since the 16th century (Silva and Casteleti 2003). Most forest remnants (80%) are very small (<50 ha), and nearly 88% of the natural vegetation in this biome has been modified or replaced by anthropogenic environments (Ribeiro et al. 2009). We used galling insects as a model to exam how specialist herbivores and their host plants assemblages are spatially distributed and structured in a severely fragmented landscape. Particularly, we answered the following questions: 1. is species composition in edge- affected habitats a subset of species in large fragment?, 2. which pattern of species assemblage is found in this fragmented landscape: homogenization (i.e., lower beta diversity) or differentiation (i.e., higher beta diversity)?, 3. do species loss and species assemblage of galling herbivores follow the same pattern of their host plants? And finally, 4. plot-edge distance and connectivity plays role in structuration and spatial distribution of host plant and galling insects assemblages?

Methods

Study area

The study was carried out during the dry season (from September 2010 to March 2011) at Usina Serra Grande, Alagoas, Brazil (8º30’S and 35º50’W), a private sugarcane landholding in northeastern Brazil. The Serra Grande landscape is composed of over 100 different-sized forest fragments (1.67-3500 ha), which are completely immersed into a stable and uniform matrix of sugarcane fields (Santos et al. 2008). Sugarcane cultivation in the area started in the early 18th century by clearing large tracts of old-growth forests, and the remaining forest fragments have been reported to be at least 60-yr old. These forest fragments are protected from fire and logging (Santos et al. 2008). The landscape is located on a low-altitude plateau (300-400 m a.s.l.) that contains two similar classes of dystrophic soil with high clay fractions: yellow-red latosols and yellow-red podzols, according to the Brazilian soil classification system (IBGE 1985). Annual rainfall ~2000 mm, with a 3-month dry season (<60 mm/month) from November to January. The predominant lowland forest includes two physiognomic subtypes of the Atlantic Forest Region: evergreen and semi-deciduous forests (Veloso et al. 1991). The largest and best preserved forest remnant in the region is the Coimbra forest (3500 ha), which has undisturbed core areas that can be used as reference sites because they maintain many plant and vertebrate groups typical of vast undisturbed tracts of Atlantic forest (Santos et al. 2008).

Study sites and host plants and gall-inducing insect surveys

We sampled all tree saplings (woody stems with diameter at breast height, dbh ≤ 10 cm, and height from 1.2 to 2.5 m) in 30 permanent plots (a total of 100 m^2 per plot and 0.1 ha for each forest condition), previously located in three land cover types (Santos et al. 2008; Sfair et al. 2016): (1) 10 plots in old-growth forest interior (> 200 m apart from the edge) of the Coimbra forest (reference plots, hereafter); (2) 10 plots along forest edges (<50 m apart from the edge) of the Coimbra forest (edge plots, hereafter); and (3) 10 plots in the geometric center of small (8.2 to 79.6 ha) forest fragments surrounded by sugarcane fields (fragment plots, hereafter). Our definition for forest edge and core area/interior forests are based on the fact that most edge effects penetrate less than 200 m into forest fragments (Laurance et al. 2002), and has been adopted elsewhere (e.g., Santos et al. 2008; Oliveira et al. 2008; Sfair et al. 2016). The inter-plot isolation distances were higher in fragments plots (8.35 ± 3.55 km) than in edge (1.57 ± 1.03 km) and reference plots (1.42 ± 0.96 km). These isolation distances are large enough to avoid spatial dependence among samples (see detailed analysis in Santos et al. 2008; Sfair et al. 2016).

We identified the identity (up to the species level) and estimated the abundance of each sapling (i.e., host plants) and galling insect in a subsample consisting of four 25-m^2 subplots (5 x 5 m) randomly located in the center of each permanent plot (see above). Sapling taxonomic identification followed the Angiosperm Phylogeny Group III (APG III 2009) and subsequently, we done our analysis considering only sapling host plants of galling insects.

Galling insects were recorded through a direct and meticulous inspection of all saplings recorded within each subplot. Samples of galls in leaves and shoots were photographed and galling insects were assigned to morphospecies based on their external morphology and taxonomic identity of host plants (Cuevas-Reyes et al. 2004; Santos et al. 2011). In general, 92 percent of Cecidomyiidae species induce galls on a specific tissue, plant organ and plant species (Carneiro et al. 2009), resulting in different gall morphologies. Therefore, we assumed that every gall morphotype belongs to an exclusive herbivore species and is plant specific (Carneiro et al. 2009). This procedure is considered taxonomically and ecologically acceptable (Carneiro et al. 2009), and has been used in previous studies (e.g., Cuevas-Reyes et al. 2004; Santos et al. 2012).

Response variables

To avoid pseudoreplication problems in our analyses, we summed up the data of the four 25-m^2 subplots from each 0.01-ha plot and considered each the reference, fragment and edge plots as independent samples for the following analyses. We first recorded the total abundance of individuals for both host plants and insects within each plot. We measured species diversity with Hill numbers, or effective number of species (Jost 2006). We considered Hill numbers of order 0 (^0D, species richness), 1 (^1D, exponential Shannon entropy) and 2 (^2D, inverse Simpson concentration). ^0D is the total number of species, independently of abundance, so it gives a disproportionate weight to rare species. ^1D weights each species according to its abundance in the community, without favouring rare or dominant species, and are interpreted as the diversity of 'typical' or 'common' species in the community (Jost 2006). Finally, ${}^{2}D$ favors dominant species, and is therefore interpreted as the number of 'very abundant' or 'dominant' species in the community (Jost 2006). The formulas for the Hill numbers are detailed elsewhere (e.g., Jost 2006). Because ${}^{0}D$ is strongly dependent on variations in sampling completeness among plots, we assessed the inventory completeness for each plot using the coverage estimator recommended by Chao and Jost (2012). The sample completeness was highly variable among plots in both host plants (mean ± SD, 0.78 ± 0.21) and insects (0.56 ± 0.35). Thus, to avoid any bias related to differences among plots in sample completeness (see Chao and Jost 2012), we focused our diversity analyses on ${}^{1}D$ and ${}^{2}D$, which are known to be weakly affected by variations in the number of rare species and sample completeness (Chao and Jost 2012; Chao et al. 2014). In other words, ${}^{1}D$ and ${}^{2}D$ mainly depend on variations among communities in the number of common and dominant species, which are easily recorded with relatively small sampling efforts (Chao et al. 2014).

We also assessed variations in the compositional differentiation of both host plants and insect communities among plots within each land cover type (i.e., forest edges, reference areas and forest fragments), using a multiplicative diversity decomposition of Hill numbers. The formulas for gamma (${}^{q}D_{\gamma}$) and mean alpha (${}^{q}D_{\alpha}$) diversities are detailed elsewhere (Jost 2007; Tuomisto 2010), and β-diversity is simply calculated as: ${}^{q}D_{\beta} = {}^{q}D_{\gamma}/{}^{q}D_{\alpha}$, which represents the 'effective number of completely distinct communities' (Jost 2007). It ranges between 1, when all communities are identical, and the number of communities (N), when all communities are completely different from each other. Thus, when making pairwise comparisons between plots within each land cover type (i.e., reference, fragment and edge plots), ${}^{q}D_{\beta}$ can vary between 1 and 2. Again, we only considered β-diversity measures for $q = 1$ (${}^{1}D_{\beta}$) and $q = 2$ (${}^{2}D_{\beta}$), which are known to be weakly affected by sample completeness (Chao and Jost 2012; Chao et al.

2014). We calculated all diversity metrics with the ‘entropart’ package (Marcon and Hérault 2013) in R (R Development Core Team 2013).

Predictor variables

We considered fragment size, fragment connectivity and plot-edge distance as predictor variables. Connectivity was defined as the percentage of natural vegetation within a 1-km external buffer from the perimeter of each fragment as adopted by Santos et al 2008. All metrics were quantified using two GIS softwares (ArcView 3.2 and Erdas Imagine 8.4) and we build a digitized map after image classification in ERDAS on the basis of: (1) three Landsat and Spot images (years 1989, 1998, 2003); and (2) complemented by a mosaic of 160 aerial photos (1:8000) taken from helicopter overflights commissioned in April 2003 as described in Santos et al. (2008). Fragment size was significantly correlated with plot-edge distance (r = 0.82; *P* = 0.004), so we did not include fragment size in our analyses.

Data analyses

To test for differences among land cover types in the abundance and within-plot (alpha) diversity of host plants and insect communities we used generalized linear models. As recommended for count response variables we fixed a Poisson distribution error for the abundance of individuals, and a Gaussian error for ${}^1D_\alpha$ and ${}^2D_\alpha$ (continuous response variables) (Crawley 2007). When we found differences among land cover types, we used contrast tests to identify which condition differed from each other (Crawley 2007). We also used generalized linear models and the same distribution errors (i.e., Poisson for abundance, and Gaussian for ${}^1D_\alpha$ and ${}^2D_\alpha$) to test whether the abundance of individuals, ${}^1D_\alpha$ and ${}^2D_\alpha$ were related to fragment size and connectivity, which were not statistically correlated (r = 0,28; P = 0.43). Finally, we used Mantel tests to evaluate whether variations in ${}^1D_\beta$ and ${}^2D_\beta$ between plots (i.e., a matrix of ${}^qD_\beta$) were related to plot location (i.e., geographical distances between plots). We performed one analysis per land cover type. Also, considering only fragment plots, we used Mantel tests to evaluate whether values in $^{1}D_{\beta}$ and $^{2}D_{\beta}$ between plots were related to differences between plots in plot-edge distance and connectivity. We calculated the *P*-values with the distribution of the *R* coefficients obtained from 10,000 permutations, and then adjusted with a Bonferroni correction for multiple comparisons.

Additionally, we performed a nestedness analysis to verify if species found in small fragments and edge plots are a subset of species found in reference plots. In nested landscapes, species assemblage of a site with smaller richness is a subset of species from a richer area (Baselga 2010, 2012; Almeida-Neto et al. 2012; Ulrich and Almeida-Neto 2012; Ulrich et al. 2009). For this analysis, we performed wNODF (Nested based on Overlap and Decreasing Fill weighted by species abundance), in which plants or galling insects were columns and plots were rows. The advantage of wNODF over others nestedness metrics is its independence of matrix shape and size (Almeida-Neto et al. 2008), the use of abundance over only presence-absence data and can be computed for species and sites separately (Almeida-Neto and Ulrich 2011). The wNODF value was compared against 1000 null models in which the row and column sums were the same as the original matrix. We also tested nestedness (wNODF) only for sites, as indicated by Almeida-Neto and Ulrich (2011). The nestedness analysis was performed in vegan package in R (Oksanen et al. 2016).

Results

At landscape level (γ-diversity), we recorded 59 host plants, in which 42 were in reference plots, 33 species in fragment plots and 22 species in edge plots. Seventeen plant species were exclusive from reference plots, seven species from fragment plots, and three species from edge plots (Fig. 1A). The number of common species ($^{1}D_{\gamma}$) varied from 13.5 species (edge plots), to 17.6 (reference plots) and 20.7 species (fragment plots). Fragment plots also exhibited the highest number of dominant species (${}^2D_\gamma$ = 13.9 species), followed by edge plots (10.3 species), and reference plots (10.2 species).

Similarly, forest interior supported almost twice as many galling insect species (42 species) than fragments (28 species) and forest edge (19 species). We found a total of 62 galling insects species. Among these species, 26 were exclusive of forest interior, 11 of fragments and four of forest edge (Fig. 1B). Gamma diversity of galling insects varied from ${}^1D_\gamma$ = 19.17 in forest interior, ${}^1D_\gamma$ = 14.39 in forest edges to ${}^1D_\gamma$ = 16.35 in fragments. By giving higher weight for abundant species, forest interior achieve ${}^2D_\gamma$ = 12.71, while edge and fragments achieved ${}^2D_\gamma$ = 11.12 and ${}^2D_\gamma$ = 10.75, respectively.

Regarding the differences in α-diversity, reference plots supported higher ${}^1D_\alpha$ than edge and fragments plots in both host plants and galling insects (Table 1). The abundance and ${}^2D_\alpha$ of host plants and galling insects did not differ among land cover types. Abundance and species diversity of host plants and galls were not related to fragment connectivity and plot-edge distance (Table 2).

In both host plants and galling insects, β-diversity of common (${}^1D_\beta$) and dominant (${}^2D_\beta$) species were significantly lower between reference plots than between fragment plots and between edge plots (Fig. 2). The higher the ${}^1D_\beta$ and ${}^2D_\beta$ of host plants, the higher the ${}^1D_\beta$ and ${}^2D_\beta$ of galling insects were in fragment plots, but not in reference and edge plots (Table 3). Finally, ${}^1D_\beta$ and ${}^2D_\beta$ of host plants and galling insects were not correlated to inter-plot geographical distance (Table 3), nor to any spatial variable (Table 4). Despite higher scores of ${}^1D_\gamma$, ${}^1D_\beta$ and ${}^1D\beta$ in edge and in fragments, host plant species (wNODF = 8.85, $P < 0.01$; wNODF for sites = 7.71, $P < 0.01$; Fig, 1A; Fig. S1A) and galling insects (wNODF = 5.63, $P < 0.05$; wNODF = 4.95, $P < 0.01$; Fig. 1B; Fig. S1B) of fragments and forest edges were a subset of the species recorded in forest interior.

Discussion

Our results suggest that forest fragments and forest edges support less abundant and diverse plant-galling insect assemblages at local (α diversity) and landscape level (γ diversity), although these edge-affected habitats can support higher scores of beta diversity. It is particularly the case of galling community at forest edges and small fragments, since these taxa exhibited the highest deviation as compared to forest interior assemblages. Accordingly, there is a slight signal assigning plant-galling insect assemblages inhabiting edge-affected habitats as a taxonomic subset of those inhabiting forest interior at community/landscape level, although these habitats may retain some particular species (i.e., fewer species as compared to forest interior). Finally, plot spatial location and metrics related to modified landscapes have no influence on community attributes. These uncovered patterns indicate a sort of taxonomic differentiation experienced by edge-affected habitats (i.e., a higher cross-plot species turnover), but such plot level differentiation is not strong enough to support taxonomically distinct and more diverse plant-galling insect assemblages inhabiting these habitats at local and landscape level, at least in the case of common and dominant species.

Our findings support the notion that several taxa experience community-level impoverishment at local and landscape level while inhabiting edge-affected habitats. We refer to wide array of taxa, including plants and animals (Santos et al. 2008; Filgueiras et al. 2011). Furthermore, some of these taxa, such as trees (Arroyo-Rodriguez et al. 2013, Sfair et al. 2016), dung beetles (Filgueiras et al. 2016), gall insets (this study), also exhibit increased beta diversity in edge-affected habitats, supporting the landscape-divergence hypothesis. However, increased species turnover not necessarily result in taxonomic or ecologically distinct assemblages at spatial scales higher than plot level, as suggested by our findings. Reinforcing this results, a nested pattern show that galling insects and host plants assemblages of edge-affected habitats are a nested subset of reference area (Coimbra interior), and we suggest that deterministic factors could be underlying of this nesting because of absence of pattern related to spatial variables (i.e., connectivity which indirectly indicates colonization and extinction). Accordingly, two responses have been documented relative to species richness and taxonomic composition of assemblages inhabiting edge-affected habitats in human-modified landscapes: (1) reduced alpha and gamma diversity, with increased β-diversity (divergence) but with little or no taxonomic differentiation at landscape level (i.e., the sum of plots); (2) increased diversity (from alpha to gamma) with distinct taxonomic and ecological composition as compared to forest interior assemblages (Santos et al. 2008; Arroyo-Rodriguez et al 2013; Filgueiras et al. 2016; Sfair et al. 2016).

Particularly in the case of tropical tree species assemblages, reduced alpha and gamma diversity is likely to result from increased environmental filtering via edge-effects (particularly physical effects such as increased wind turbulence and dissecation) and seed dispersal limitation (Laurance et al. 2002, Oliveira et al. 2008). On the other hand, community-level taxonomic divergence in edge-affected habitats has been argued to emerge from a combination of biological hyperdynamism and contrasting environmental conditions experienced by forest fragments due to differences in terms of matrix type, historical land uses and fragment spatial configuration (Laurance 2002, Laurance et al. 2007, Arroyo-Rodriguez et al. 2013). As consequence, sum of these processes or their individual effect provides support to taxonomic differentiation in edge- affected habitats to galling insects and host plants in Serra Grande. In fact, Amazonian and Atlantic forests fragments, edge-affected habitats tend to be dominated by few disturbance-adapted taxa (particularly light-demanding species), while several components of the old-growth flora become rare (e.g., shade-tolerant, large, resulting in from local to regional level (Laurance et al. 2006a, 2006b; Santos et al. 2008; Lobo et al. 2011). In the Serra Grande landscape, however, fragments are embedded in the same matrix (i.e., sugar cane fields) and exposed to the lack of several vertebrate seed dispersers such as primates and large-gaped birds (Melo et al. 2006). Seed dispersal limitation or the failure of tree species in reaching all forest fragments is likely to favor increased cross-fragment beta diversity, particularly in the case of large-seeded tree species (see Melo et al. 2006).

As galling insect species are species-specific herbivores (Carneiro et al. 2009; Santos et al. 2012), they have been demonstrated to be strongly affected by the resource availability and identity (Wright and Samways 1998; Souza et al. 2016). Accordingly, it is not surprisingly that their assemblages experience the same response exhibited by tree species assemblages in human-modified landscapes. Although we have not explicitly addressed the causal mechanisms leading to community-level changes in both tree and galling species in the Serra Grande landscape, we argue for an edge-driven bottom-up cascade, on which edge effects impoverish plant assemblages at local and landscape level, reducing the richness and the abundance of plant hosts for galling insects as already proposed (Souza et al. 2016). We particularly refer to those galling species specific of shade-tolerant, large-tree or large-seeded tree species that have been demonstrated to become rare across edge-affected habitats in the Serra Grande landscapes from seedling to adult stage (Santos et al. 2008; Tabarelli et al. 2010; Santo-Silva et al. 2013).

The highest abundance of galling insects in reference plots agree with resource concentration hypothesis, which predicts that specialized insects abundance and herbivory levels are positively related to proportion of individuals of the same host plant species (Root 1973; Nichols et al. 1999; Malinga et al. 2014). Shade-tolerant species produce chemical compounds that are attractive for galling insects and the local extinction of this functional group of plants can result on a cascading effect on the extinction of specialized galling insect (Hunter and Price 2002; Malinga et al. 2014; Maldonado-Lopez et al. 2015). This is not the first time that an edge-related bottom-up cascade has been proposed to explain changes on herbivores assemblages, but in contrast to galling insects, the generalist leaf-cutting ants largely benefit from the proliferation of palatable pioneer plants (Wirth et al. 2008; Leal et. 2014) that usually replace the old-growth flora (Tabarelli et al. 2008). Changes on plant assemblages obviously do not exclude other forces negatively affecting the life cycle of gall insects across edge-affected habitats, such as habitat desiccation and light exposure. Finally, we shall mention the fact that assemblages did not respond to some fragmentation metrics such as edge-plot distance and connectivity. In fact, previous studies in Serra Grande landscape have failed in demonstrate strict correlations among fragmentation metrics and tree assemblages attributes, probably because a high spatial complexity exhibited by forest fragments in terms of both physical environmental conditions and biological organization (see Santos et al. 2008; Mendes et al. 2016).

Conclusions

In synthesis, the creation of forest edges is apparently able to trigger a trophic cascade up which result in impoverished assemblages at local and landscape scale, while species turnover tend to increase in edge-affected habitats (i.e., increased cross-plot species turnover as compared to forest interior plots). We refer to incomplete local assemblages inhabiting edge-affected habitats, which at landscape level may represent subsamples of those more diverse assemblages. These uncovered patterns reinforce the notion that habitat loss and fragmentation reorganize native communities at multiple spatial scales. Regardless of the causes, plot-level taxonomic divergence experienced by edge-affected habitats emerges as a cross-taxa response and its implications for biodiversity persistence in human-modified landscapes demands further exam.

References

Almeida-Neto M, Ulrich W (2011) A straightforward computational approach for measuring nestedness using quantitative matrices. Environ Model Softw 26: 173–178

Almeida-Neto M, Frensel DMB, Ulrich W (2012) Rethinking the relationship between nestedness and beta diversity: A comment on Baselga (2010) Glob Ecol Biogeogr 21: 772–777

Almeida-Neto M, Guimarães P, Guimarães Jr PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117: 1227–1239

Araújo WS (2013) Different relationships between galling and non-galling herbivore richness and plant species richness: a meta-analysis. Arthr Plant Interac 7: 373-377

Araújo WS, Scareli-Santos C, Guilherme FAG, Cuevas-Reyes P (2013) Comparing galling insect richness among Neotropical savannas: effects of plant richness, vegetation structure and super-host presence. Biod Conserv 22: 1083-1094

Arroyo-Rodríguez V, Pineda E, Escobar F, Benítez-Malvido J (2009) Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. Conser Biol 23:729–739.

Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, Tabarelli M, Chazdon R (2013) Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J Ecology 101:1449–1458

Arroyo-Rodríguez V, Saldaña-Vázquez RA, Fahrig L. et al. Ecol Res (2017) 32: 81. doi:10.1007/s11284-016-1411-6

Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Mac Nally R, Thomson JR, Ferraz SF, Louzada J, Oliveira VH, Parry L, Solar RR, Vieira IC, Aragão LE, Begotti RA, Braga RF, Cardoso TM, de Oliveira RC Jr, Souza CM Jr, Moura NG, Nunes SS, Siqueira JV, Pardini R, Silveira JM, Vaz-de-Mello FZ, Veiga RC, Venturieri A, Gardner TA. (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535:144-147

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19: 134–143.

Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Glob Ecol Biogeogr 21:1223–1232

Butchart SH, Walpole M, Collen B, van Strien A, Scharlemann JP, Almond RE, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328: 1164-1168.

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93: 2533–2547.

Cuevas-Reyes P, Quesada M, Hanson P, Dirzo R, Oyama K (2004) Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life forms, host plant age and plant density. J Ecology 92: 707-716.

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Syst 34: 487–515.

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis J. Biogeogr: http://doi.wiley.com/10.1111/jbi.12130

Fernandes GW, Santos JC (2014) Neotropical Insect Galls, 1nd. Springer, Dordrecht.

Filgueiras BK, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biol Conserv 144: 362-369.

Filgueiras BKC, Tabarelli M, Leal IR, Vaz-de-Mello FZ, Peres CA, Iannuzzi L (2016) Spatial replacement of dung beetles in edge-affected habitats: Biotic homogenization or divergence in fragmented tropical forest landscapes? Divers Distrib 22 (4): 400-409

Haddad NM, Holt RD, Jr Fletcher RJ, Loreau M, Clobert J (2017) Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects. Ecography 40: 1–8. doi:10.1111/ecog.02974

Fonseca CR (2009) The silent mass extinction of insect herbivores in biodiversity hotspots. Conserv Biol 23: 1507-1515

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342:850-853

Hernández-Ruedas MA, Arroyo-Rodríguez V, Maeve JA, Martínez-Ramos M, Ibarra-Manríquez G, Martínez, Jamangapé G, Melo FPL, Santos BA (2014) Conserving tropical tree diversity and forest structure: the value of small rainforest patches in moderately managed landscapes. PLoS ONE 9:e98931

Hill JK, Gray MA, Vun Khen C, Benedick S, Tawatao N, Hamer KC (2011) Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? Phil Trans R Soc B 2011 366 3265- 3276; DOI: 10.1098/rstb.2011.0050

Hubbell SP (2001) The unified theory of biodiversity and biogeography. Monographs in Population Biology, vol. 32. Princeton University Press, Princeton, USA

IBGE (1985). Atlas Nacional do Brasil: Região Nordeste. IBGE, Rio de Janeiro.

Jost L. (2006) Entropy and diversity. Oikos 113:363–375.

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. Tren Ecol Evol 29:107–116

Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamsom GB, Benítez-Malvido J, Vasconcelos HL, Van Houtan KS, Zartman CE, Boyle SA, Didham RK, Andrade A, Lovejoy T (2011). The fate of Amazonian forest fragments: a 32-year investigation. Biol Conserv 144: 56–67

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv Biol 16: 605–618

Leal IR, Wirth R, Tabarelli M (2014) The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified Neotropical forests. Biotropica 46: 516–528

Leroux SJ, Albert CH, Lafuite AS, Rayfield B, Wang S, Gravel D (2017) Structural uncertainty in models projecting the consequences of habitat loss and fragmentation on biodiversity. Ecography 40: 36–47

Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. Science 349:827-832

Lobo D, Leão T, Melo FPL, Santos AMM, Tabarelli M (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Diver Distrib 17:287–296

Laurance WF (2002) Hyperdynamism in fragmented habitats. J. Veg. Scie 13:595–602.

Laurance WF, Nascimento HE, Laurance SG, Andrade A, Ewers RM, Harms KE, Luizão RC, Ribeiro JE (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PloS one 2:e1017

Lopes AV, Girão LC, Santos BA, Peres CA, Tabarelli M (2009) Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic Forest fragments. Biol Conserv 142: 1154–1165

Maldonado-López Y, Cuevas-Reyes P, Oyama K (2016) Diversity of gall wasps (Hymenoptera: Cynipidae) associated with oak trees (Fagaceae: Quercus) in a fragmented landscape in Mexico. Arthr Plan Inter 10: 29-39

Maldonado-López Y, Cuevas-Reyes P, Stone GN, Nieves-Aldrey JL, Oyama K (2015) Gall wasp community response to fragmentation of oak tree species: importance of fragment size and isolated trees. Ecosphere 6: 1–15

Malinga GM, Valtonen A, Vesterinen P, Nyeko P, Roininen H (2014) Communities of galling insects on *Neoboutonia macrocalyx* trees in continuous forests and remnants of forest fragments in Kibale, Uganda. Afr. Entom. 22: 742–754

Mckinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Tr Ecol Evol 14:450–453

Melo FPL, Dirzo R, Tabarelli M (2006) Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. Bioll Conserv 132: 50-60

Michalski F, Nishi I, Peres CA (2007) Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. Biotropica 39:691–701

Mitchell MGE, Suarez-Castro AF, Martinez-Harms M, Maron M, McAlpine C, Gaston, K.J. et al. (2015). Reframing landscape fragmentation’s effects on ecosystem services. Trends Ecol Evol 30:190–198

Morante-Filho JC, Arroyo-Rodríguez V, Lohbeck M, Tscharntke T, Faria D (2016), Tropical forest loss and its multitrophic effects on insect herbivory. Ecology 97: 3315–3325. doi:10.1002/ecy.1592

Norden N, Angarita HA, Bongers F, Martínez-Ramos M, Granzow-de la Cerda I, van Breugel M, Lebrija-Trejos E, Meave JA, Vandermeer J, Williamson GB, Finegan B, Mesquita R, Chazdon RL (2015) Successional dynamics in Neotropical forests are as uncertain as they are predictable. Proc Nat Acad Sci USA 112:8013–8018

Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD (2006) Why are there so many species of herbivorous insects in tropical rainforests? Science DOI:10.1126/science.1129237

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016). vegan: Community Ecology Package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

Oliveira MA, Santos AMM, Tabarelli M (2008) Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. For Ecol Manage 256: 1910–1917

R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org

Santos BA, Peres CA, Oliveira MA, Grillo A, Alves-Costa CP, Tabarelli M (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biol Conserv 141: 249-260

Santos JC, Almeida-Cortez JS, Fernandes GW (2011) Diversity of gall-inducing insects in the high altitude wetland forests in Pernambuco, Northeastern Brazil. Brazil. Braz J Biol 71: 47-56

Solar RRC, Barlow J, Ferreira J, Berenguer E, Lees AC, Thomson JR, Louzada J, Maués M, Moura NG, Oliveira VHF, Chaul JCM, Schoereder JH, Vieira ICC,

Mac Nally R, Gardner TA (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecol Lett 18:1108-1118

Souza DG, Santos JC, Oliveira MA, Tabarelli T (2016) Shifts in Plant Assemblages Reduce the Richness of Galling Insects Across Edge-Affected Habitats in the Atlantic Forest. Env Entom doi: 10.1093/ee/nvw115

Tabarelli M, Peres CA, Melo FPL (2012) The “few winners and many losers” paradigm revisited: emerging prospects for tropical forest biodiversity. Biol Conserv 155: 136-140

Tuomisto H (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1.Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2–22

Ulrich W, Almeida-Neto M, Gotelli NJ (2009) A consumer’s guide to nestedness analysis. Oikos 118: 3–17

Ulrich W, Almeida-Neto M (2012) On the meanings of nestedness: back to the basics. Ecography 35: 1–7.

Veloso HP, Rangel-Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira adaptada a um sistema universal. IBGE, Rio de Janeiro, Brazil.

Wang Y, Bao Y, Yu M, Xu G, Ding P (2010) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. Diver Distrib 16: 862–873.

Table 1. Differences among land cover types (reference, edge and fragment plots) in the abundance of individuals, and number of common (${}^{1}D_{\alpha}$) and dominant (${}^{2}D_{\alpha}$) species of host plants and galling insects in a fragmented landscape in the Brazilian Atlantic forest. Mean ± standard deviation are indicated in each case, and differences between cover types were tested with generalized linear models (df = 2, in all cases). Different letters indicate significant differences between land cover types (contrast tests; $^{*}P < 0.05$, $^{**}P < 0.001$).

	Reference	Edge	Fragment	χ^2
Plant abundance	40.5 ± 12.3^{b}	11.9 ± 4.5^{a}	15.8 ± 9.8^{a}	198.7**
Galling abundance	22.8 ± 16.5^{b}	4.9 ± 3.6^{a}	6.9 ± 5.3^{a}	155.9**
Plant ${}^{1}D_{\alpha}$	7.6 ± 2.0^{b}	3.7 ± 1.2^{a}	5.1 ± 2.9^{a}	16.08 *
Plant ${}^{2}D_{\alpha}$	5.2 ± 1.7^{a}	3.2 ± 1.1^{a}	4.5 ± 2.6^{a}	5.70
Gall ${}^{1}D_{\alpha}$	6.2 ± 2.7^{b}	3.1 ± 0.6^{a}	3.7 ± 2.5^{a}	11.35*
Gall ${}^{2}D_{\alpha}$	5.1 ± 2.0^{a}	3.0 ± 0.6^{b}	$3.4 \pm 2.3^{a,b}$	6.79*

Table 2. Effect of plot-edge distance and fragment connectivity on the abundance of individuals and the number of common (${}^1D_\alpha$) and dominant (${}^2D_\alpha$) species of host plants and galling insects in a fragmented landscape of Brazilian Atlantic forest. For plant and species abundance, we performed generalized linear models (GLM) with Poisson distribution, whereas for ${}^1D_\alpha$ and ${}^2D_\alpha$ we performed GLM with Gaussian distribution. All analyses were non-significant after Bonferroni correction ($P < 0.004$)

	Distance to the edge			Connectivity		
	χ^2	Parameter estimates	Explained deviance (%)	χ^2	Parameter estimates	Explained deviance (%)
Host plants						
Abundance	4.32	0	39.24	0.24	0.01	3.11
${}^1D_\alpha$	0.72	-0.01	8.32	8.07	0.22	50.22
${}^2D_\alpha$	0.58	-0.01	6.78	7.61	0.19	48.74
Galling insects						
Abundance	6.02	-0.01	46.83	1.08	0.03	12.15
${}^1D_\alpha$	1.01	-0.01	11.24	6.65	0.18	45.41
${}^2D_\alpha$	0.86	-0.01	9.74	7.29	0.17	47.7

Table 3. Association between β-diversity (${}^{q}D_{\beta}$) of host plants and galling insects, and between ${}^{q}D_{\beta}$ and inter-plot isolation distance (ID) within three land cover types (reference, fragment, and edge plots) in a severely deforested landscape from the Brazilian Atlantic forest. Associations were tested with Mantel tests, and we considered two different q orders (q = 1 and q = 2), which determine the sensitivity of β-diversity to species abundances. ${}^{1}D_{\beta}$ represents the number of completely distinct communities considering common species, and ${}^{2}D_{\beta}$ is the same, but considering dominant species.

Land cover type	β-diversity component	Plant vs. gall	${}^{q}D_{\beta}$ plant vs. ID	${}^{q}D_{\beta}$ gall vs. ID
Reference plots				
	${}^{1}D_{\beta}$	0.42	-0.28	-0.12
	${}^{2}D_{\beta}$	0.42	-0.3	-0.31
Edge plots				
	${}^{1}D_{\beta}$	0.22	0.45	-0.18
	${}^{2}D_{\beta}$	0.21	0.4	-0.22
Fragment plots				
	${}^{1}D_{\beta}$	0.73*	-0.23	-0.06
	${}^{2}D_{\beta}$	0.80*	0.01	-0.05

* $P < 0.05$. The *P*-values were adjusted by Bonferroni correction.

Table 4. Mantel correlations (*r*) between ${}^{q}D_{\beta}$ against difference of distance to the edge and connectivity of small fragments in a severely deforested landscape from the Brazilian Atlantic forest. All results were non-significant after Bonferroni correction ($P < 0.006$). We considered two different q orders ($q = 1$ and $q = 2$), which determine the sensitivity of β-diversity to species abundances: ${}^{1}D_{\beta}$ represents the number of completely distinct communities considering common species, and ${}^{2}D_{\beta}$ is the same, but considering dominant species. All values of *r* were non-significant after Bonferroni correction

	Distance to the edge	Connectivity
Host plants		
${}^{1}D_{\beta}$	0.09	-0.01
${}^{2}D_{\beta}$	0.16	-0.01
Galling insects		
${}^{1}D_{\beta}$	-0.01	0.03
${}^{2}D_{\beta}$	0.02	0.02

Figure 1. Venn diagram indicating the percentage of exclusive species in Reference, Edge and Fragment plots and the shared plant (A) and galling insects (B) species among these forest conditions.

Figure 2: Taxonomic β-diversity of woody host saplings (A) and galling insects (B) among forest fragments, among forest edge plots and among forest interior (i.e., reference) plots in the severely deforested Brazilian Atlantic forest. Differences among forest conditions were tested considering medians and 95% confidence intervals. When assessing taxonomic β-diversity, we evaluated two orders of q (1 and 2), which determine the sensitivity of each diversity component to the relative abundances. When q = 1, β-diversity weights each species according to its abundance in the community, and hence, it is interpreted as the diversity of ‘typical’ or ‘common’ species in the community. Finally, if q = 2, abundant species are favored and rare species are discounted, and hence, it refers to the β-diversity of very abundant’ or ‘dominant’ species in the community.

Figure 1

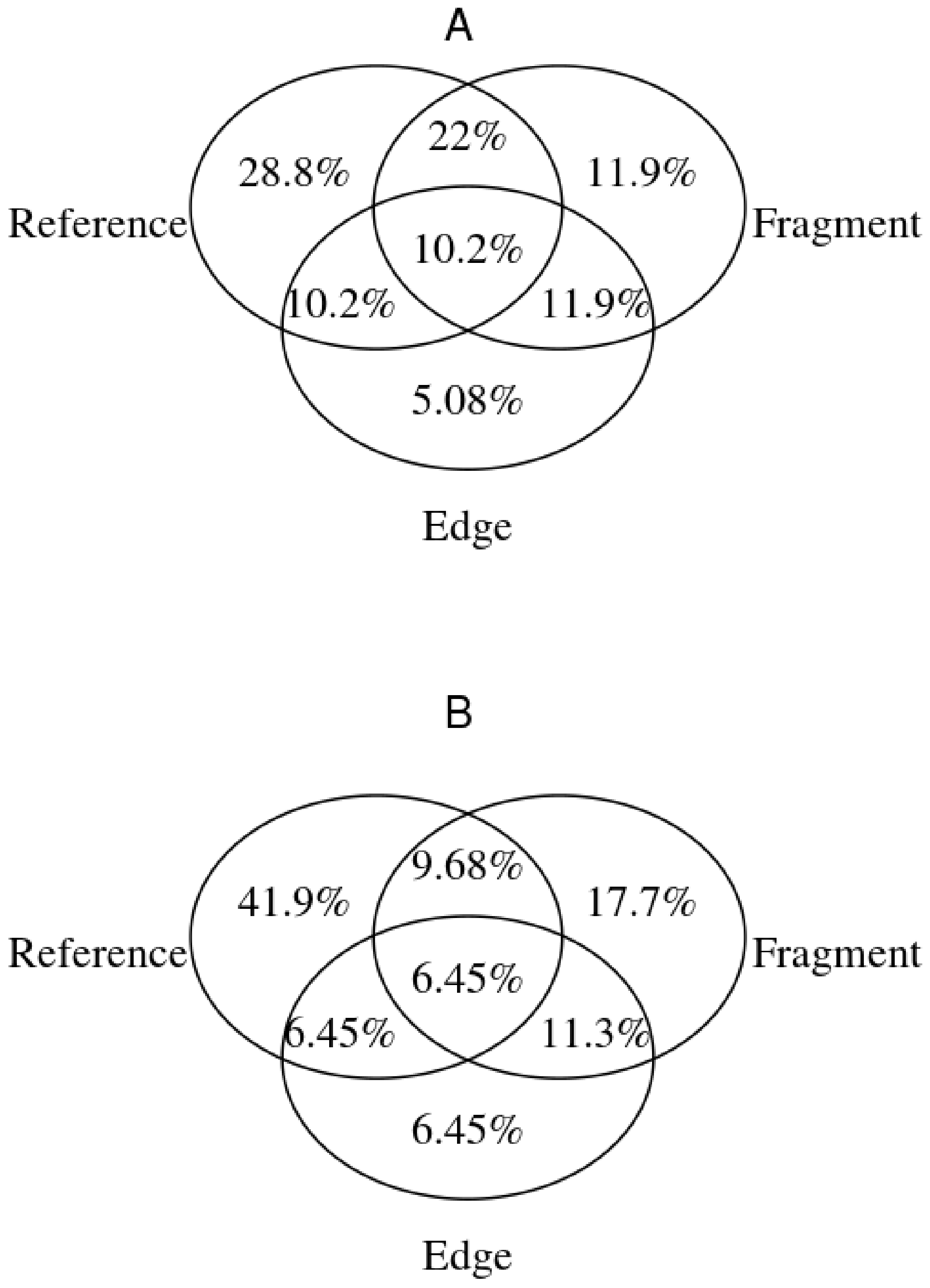
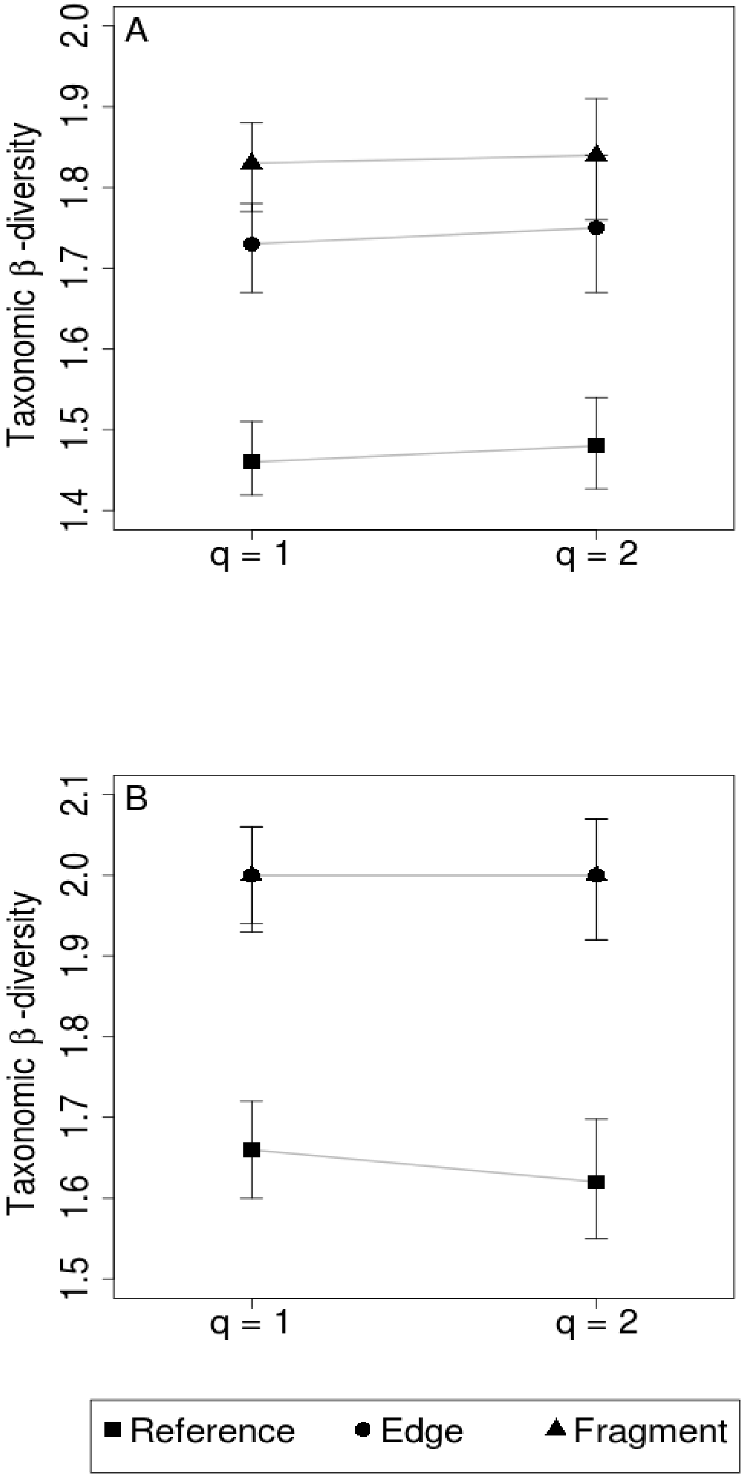
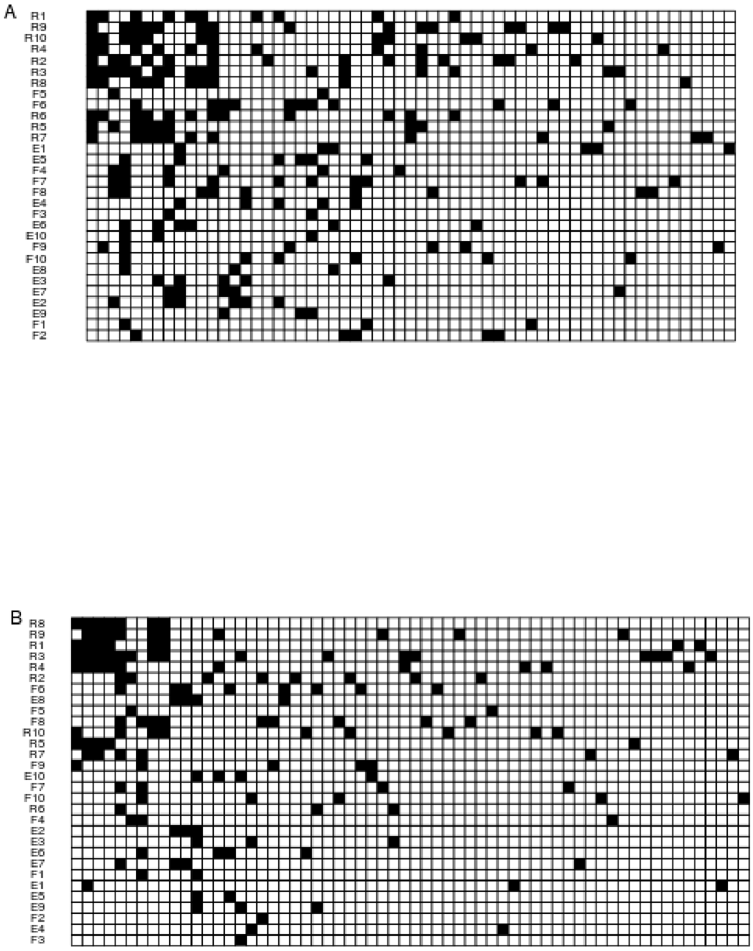

A
22%
28.8%
11.9%
Reference
Fragment
10.2%
10.2%
11.9%
5.08%
Edge
B
9.68%
41.9%
17.7%
Reference
Fragment
6.45%
6.45%
11.3%
6.45%
Edge

Figure 2


A
Taxonomic β -diversity
1.4
1.5
1.6
1.7
1.8
1.9
2.0
q = 1
q = 2
B
Taxonomic β -diversity
1.5
1.6
1.7
1.8
1.9
2.0
2.1
q = 1
q = 2
■ Reference
● Edge
▲ Fragment

Supplementary material

Fig. S1: Ordered matrix between R = reference, F = fragment, E = edge plots superposed plant (A) and galling insects (B). Rows are plots and columns are species. The matrix is ordered to maximize nestedness of both matrices, i.e., last rows have a subset of species assemblage in relation to first rows. White cells indicate absence, whereas black cells indicate presence of species in the plot. We did not show species names to maximize the visualization of nestedness in plots



5. SHIFTS IN PLANT ASSEMBLAGES REDUCE THE RICHNESS OF GALLING INSECTS ACROSS EDGE-AFFECTED HABITATS IN THE ATLANTIC FOREST [2]

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Abstract

Impacts of habitat loss and fragmentation on specialist herbivores have been rarely addressed. Here we examine the structure of plant and galling insect assemblages in a fragmented landscape of the Atlantic forest to verify a potential impoverishment of these assemblages mediated by edge effects. Saplings and galling insects were recorded once within a 0.1 ha area at habitat level covering forest interior stands, forest edges and small fragments. A total of 1,769 saplings from 219 tree species were recorded across all three habitats, with differences in terms of sapling abundance and species richness. Additionally, edge-affected habitats exhibited reduced richness of both host-plant and galling insects at plot and habitat spatial scale. Attack levels also differed among forest types at habitat spatial scale (21.1% of attacked stems in forest interior, 12.4% in small fragments but only 8.5% in forest edges). Plot ordination resulted in three clearly segregated clusters: one formed by forest interior, one by small fragments and another formed by edge plots. Finally, the indicator species analysis identified seven and one indicator plant species in forest interior and edge-affected habitats, respectively. Consequently, edge effects lead to formation of distinct taxonomic groups and also an impoverished assemblage of plants and galling insects at multiple spatial scales. The results of the present study indicate that fragmentation related changes in plant assemblages can have a cascade effects on specialist herbivores. Accordingly, hyper-fragmented landscapes may not be able to retain an expressive portion of tropical biodiversity.

Key words: Edge effects, herbivory, galls, plant-insect interactions, specialist herbivores.

Introduction

Tropical old-growth forests have been rapidly converted into human-modified landscapes, largely altering the nature and the abundance of forest habitats (Ferraz et al. 2014). Instead of pristine patches, human-modified landscapes tend to be dominated by a collection of components, including remaining forest fragments, secondary forest stands, stands of exotic tree species and patches of agroforestry, among others (Tabarelli et al. 2010a). Immersed into open-habitat matrices forest components (1) remain structurally isolated, (2) may experience dynamic cycles of clearance and regrowth, and (3) are exposed to edge effects and a myriad of other matrix-mediated disturbances such as fire, biological invasion, and collection of forest products, such as bushmeat and fuel wood (Melo et al. 2013). It is not surprisingly that remaining forests usually experience drastic shifts (from population to ecosystem level) while immersed into human-modified landscapes (Laurance et al. 2011).

In the tropical forests, one of the most pervasive and deleterious effects imposed by habitat fragmentation refers to the creation and maintenance of forest edges, particularly in the case of tree assemblages (Laurance et al. 2006a, 2006b; Santos et al. 2010). Although the generality of some patterns remains to be examined, tree assemblages inhabiting edge-affected habitats may exhibit (1) reduced species richness, (2) lower frequency of species within several groups of old growth tree species, such as large trees and those bearing supra-annual reproduction, and (3) increased abundance of fast-growing and successional species (Laurance et al. 2006b, Tabarelli et al. 2010b). Such impoverished and largely deviated tree assemblages have supported the notion that biotic interactions are likely to be disrupted (Tabarelli et al. 2012). Basic possibilities refers to the extirpation of faunal attendants of the declining old-growth flora, including frugivorous, specialized pollinators, and specialist herbivores (Wirth et al. 2008, Lopes et al. 2009) in parallel to the proliferation of those attendants interacting with the proliferating flora, such as generalist herbivores (Tabarelli et al. 2012). We are particularly referring to disruptions on plant-animal interactions that represent bottom-up cascades with shifts (1) on the taxonomic composition in both assemblages (plants and their consumers) and (2) on the nature of interactions; i.e., an increment of generalist interactions.

In fact, empirical evidence suggests considerable alterations in herbivore insect assemblages and herbivory rates in response to shifts on the spatial configuration of landscapes (Didham et al. 1996, Tscharntke et al. 2002, Tscharntke and Brandl 2004) and related edge effects (Barbosa et al. 2005, Wirth et al. 2008, Meyer et al. 2010). For instance, patch size and connectivity are expected to correlate with resource availability (i.e., proliferation of pioneer plant species), population dispersal and patch occupancy by herbivore species (Hanski and Gilpin 1997, Arnold and Asquit, 2002, Elzinga et al. 2005, Valladares et al. 2006, Ruiz-Guerra et al. 2010). However, the majority of empirical evidence related to assemblages or single species patterns are mainly for generalist herbivore (Wirth et al. 2008), which have been reported to benefit due to (1) increments in the availability of palatable plants (i.e., pioneer plants) (Wirth et al. 2008, Silva et al. 2012); (2) microclimatic changes, which decrease parasitoid populations relaxing top down control (Almeida et al. 2008); and (3) higher amounts of edge-affected habitats (Wirth et al. 2008). In contrast, little information is still available about specialist herbivores, although large amount of herbivorous insects can be considered highly specialized (Novotny and Basset 2005) such as the gall-inducing insects (Shorthouse et al. 2005, Carneiro et al. 2009).

Galling insects represent a special guild of specialist, endophytic herbivores that induce morphological and physiological modifications in plants through abnormal tissue growth, which provides shelter, feed on high quality tissues and thus protects offspring against habitat harshness and natural enemies (Price et al. 1987, Stone and Schönrogge 2003, Shorthouse et al. 2005). In addition to being specialist insects, local patterns of abundance and species richness of gall-inducing insects in terrestrial ecosystems respond to both abiotic characteristics (light availability, hydrothermal stress, soil fertility, seasonality) and the abundance and richness of host plants (Oyama et al. 2003, Cuevas Reyes et al. 2004, Fernandes et al. 2010, Araújo et al. 2013). Such characteristics have been recognized as conferring to galling insects some sensitivity to habitat loss and fragmentation, offering an interesting model to investigate potential disruptions on plant-animal interactions in human-modified landscapes (Toma et al. 2014, Malinga et al. 2014a, Maldonado –López et al. 2015). In synthesis galling insects represent an excellent model to examine key hypotheses addressing fragmentation-related effects, the biological dynamic and the conservation value of human-modified landscapes such as: (1) fragmentation-related changes in plant assemblages cascade over plant attendants, (2) specialist herbivores tend to be negatively affected, (3) bottom-up forces play a major role in ecosystem functioning in human-disturbed habitats, and (4) hyper-fragmented landscapes are not able to retain an expressive portion of tropical biodiversity (Wirth et al. 2008, Lopes et al. 2009, Tabarelli et al. 2012, Melo et al. 2013).

Here we examine the structure of plant and galling insect assemblages across three habitat types of a fragmented Atlantic forest landscape: forest interior, forest edges and small fragments. We were particularly interested on the occurrence of altered plant assemblages and the impoverishment of galling insect assemblages across edge-affected habitats (small fragments and forest edges); i.e., a bottom-up trophic cascade or a disruption on plant-animal interactions mediated by edge-effects as proposed in the literature. We first offer scores of species richness at plot and habitat spatial scale (i.e., the sum of all plots within each habitat), and correlate them with habitat type and patch metrics considered to affect herbivory. Further, we examine sapling attack across habitats and functional groups of plants, ordinate host-plant and insect assemblages, and offer plant species-rank curves and indicator species. Finally, we discuss the uncovered patterns in the light of theories that address herbivore responses to landscape modification (i.e., the generalist–generalist paradigm), speculate about the persistence of particular plant-insect assemblages and examine the implications of our findings in the context of the forces driving the biological dynamics and the conservation value of human-modified landscapes.

Methods

Study area. The present study was carried out during the 2010-dry season (September 2010 to march 2011) at Usina Serra Grande (8º30'S and 35º50'W), a private sugarcane landholding in the state of Alagoas, northeastern of Brazil. The Serra Grande landscape still contains over 100 forest fragments (1.67- 3,500 ha), which are completely immersed into a stable and uniform matrix of sugarcane fields (Santos et al. 2008). Sugarcane cultivation in the area started in the early 19th century by clearing large tracts of old-growth forests and remaining forest fragments have been reported to be at least 60-yr old, protected from fire and logging (Santos et al. 2008). Therefore, this landscape provides a unique opportunity to study the effects of fragmentation in Atlantic forest (e.g., Santos et al. 2008, Tabarelli et al. 2008, Lopes et al. 2009, Tabarelli et al. 2012). The Serra Grande landscape is located on a low-altitude plateau (300 – 400 m above sea level) that contains two similar classes of dystrophic soil with high clay fractions: yellow-red latosols and yellow-red podzols, according to the Brazilian soil classification system (IBGE 1985). Annual rainfall is ~2000 mm, with a 3-month dry season (<60 mm/month) from November to January. The predominantly lowland forest includes two physiognomic subtypes of the Atlantic Forest Region: evergreen and semi-deciduous forests (Veloso et al. 1991).

Sapling and galling insect surveys. A set of permanent plots (40 m *x* 40 m) were established across 10 forest fragments, and 20 permanent plots in the 3500-ha Coimbra forest. The Coimbra forest represents the best preserved and largest Atlantic forest fragment in northeastern Brazil as its old-growth forest interior areas still retain a full offset of plant species typical of vast undisturbed tracts of Northeast Atlantic forest (Santos et al. 2008). For this reason, undisturbed areas in its interior can be used as reference sites (see Oliveira et al. 2008, Santos et al. 2008, 2010; Sfair et al. 2016). We are aware that the Coimbra forest consists of a single and unreplicated tract of forest at the landscape and regional level as already argued (Santos et al. 2008). However, by addressing a single remnant we assessed the same pool of plant species and galling insects that inhabit forest edges and interior areas, and thus we control for other variables (i.e., patch isolation and metapopulation dynamics) that would mask between-habitat differences. To detect potential shifts in plant-herbivore assemblages due to forest fragmentation, we used only the permanent plots located in the two main habitats of the Coimbra forest: (1) forest edge - peripheral areas within 50 m of the border, and (2) forest interior - old-growth forest interior areas, beyond 200 m of the border, that show no detectable edge influence; and (3) small forest fragments: plots embedded in the geometric center of forest fragments ranging from 6.4 to 71.28 ha in size, and entirely surrounded by sugarcane fields. In Coimbra forest, permanent plots were at least 300 m apart to reduce the possibility of spatial dependence (see Santos et al. 2008). These definitions for forest edge and core area/interior forests considered that most edge-effects penetrate less than 200 m into forest fragments (Laurance et al. 2002), and have been adopted elsewhere (Santos et al. 2008, Oliveira et al. 2008). Ontogenetic stage chosen was saplings of tree species, including woody stems with diameters ≤ 10 cm at breast height and from 1.2 to 2.5 m in height and were recorded across habitats based on a subsample consisting of four 25 m^2 subplots (5 *x* 5 m) located randomly in the central part of 30 permanent plots: 10 in the forest interior, 10 in the forest edge, and 10 in the geometric center of small fragments (a total of 100 m^2 per plot and 0.1 ha for each habitat). Saplings were quantified through assessment within each subplot (25 m^2) and this permitted us to evaluate sapling species richness and density per subplot (25 m^2), host plant assemblages and its functional groups. Plant species were identified to species level at the Herbarium of the

Universidade Federal de Pernambuco (HUFPE) according to the Angiosperm Phylogeny Group III (APG III 2009).

Sapling species were assigned into two mutually exclusive functional groups relative to regeneration strategy as follows: (a) shade-tolerant – species that are capable of regenerating in the shaded understory of old-growth forests; and (b) pioneer species –those species that require high-light environments provided by tree fall gaps and forest edges as viable regeneration sites (Hartshorn 1978). The pioneer group also included large or long-lived pioneer species (*sensu* Whitmore 1989), which usually exhibit adult individuals that inhabit the canopy or emergent stratum of old-growth forests (Swaine and Hall 1983) and can be referred as successional species (Laurance et al. 2006b).

Galling insects were recorded within the 25-m^2 plots through direct inspection of all saplings. Attacked saplings were collected for further taxonomic identification of both plant and insect species. Samples of galls in leaves and shoots were photographed and galling insects were assigned into morphospecies based on their external morphology and the taxonomic identity of host plants (Fernandes and Price 1988, Price et al. 1998, Cuevas-Reyes et al. 2004, Fernandes et al. 2010, Santos et al. 2011). In general, 92 percent of Cecidomyiidae species induce galls on a specific tissue, plant part and plant species (Carneiro et al. 2009). Therefore, we assumed that every gall morphotype belongs to an exclusive galling species and accordingly gall morphotypes are both insect and plant specific (see Carneiro et al. 2009). This procedure is considered taxonomically and ecologically acceptable (see Carneiro et al. 2009), and has been widely adopted in ecological studies of insect gall diversity (Fernandes and Price 1988, Price et al. 1998, Cuevas-Reyes et al. 2004, Fernandes et al. 2010, Santos et al. 2011, Fernandes and Santos 2014).

Explanatory variables and data analysis. In addition to habitat type, fragment size and connectivity were considered as explanatory variables for both plant and galling insect assemblages inhabiting forest fragments. Connectivity was defined as the percentage of forest within a 1-km external buffer from the perimeter of each fragment. Patch and landscape metrics 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 over flights commissioned in April 2003 (Santos et al. 2008). To perform data analysis, first, forest habitats were compared in terms of sapling density and species richness via ANOVAs. Differences in host plant and galling insect richness between forest edge, forest interior (control) and small fragment plots were examined using complementary approaches. Initially, we performed a Generalized Linear Model (GLM) adopting sapling host species richness and forest habitat type as explanatory variables, and the richness of galling insects as a response variable. As suggested for count-dependent variables (i.e., species richness), we selected a Poisson distribution with a log-link function and corrected for overdispersion (Crawley 2002) as well as their interaction term. Other GLM with Poisson distribution and log-link function were also used to evaluate whether explanatory variables fragment size and connectivity affected galling insect species richness. At habitat spatial scale, we adopted individual-based accumulation curves, with host-plant and insect species richness estimated via Sobs and the non-parametric estimator Chao 2 as widely adopted (Gotelli and Colwell 2001). In this scale, we assessed the inventory completeness for each plot using the coverage estimator recommended by Chao and Shen (2010). Sample coverage estimators did not differ significantly between forest habitat type for host plants [Kruskal-Wallis test, H = 3.30, P = 0.19, 78.20 % ± 20.67 % ($\bar{x}$ ± SD), range = 0 - 100% per plot] and insect galls [Kruskal-Wallis test, H = 2.87, P = 0.24, 55.69 % ± 35.37 % ($\bar{x}$ ± SD), range = 0 – 100 %], indicating that both groups inventory were accurate with our sampling effort (Chao and Jost 2012).

Relationships between plant functional groups considering the whole assemblages (pioneers and shade tolerant) and the proportion of attacked saplings by galling insects across forest habitats were tested (log linear) with the function *loglm* available in the package MASS in R (R Core Team 2013). The initial model consisted of a saturated or complete model with all main effects and interactions (habitat + regeneration + galling insects +habitat*regeneration + habitat*galling insects +regeneration* galling insects). We considered "galling insects" as the abundance of attacked plants by galling insects and "regeneration" as pioneer and shade tolerant plants. Model selection was based on the Akaike Information Criterion (AIC) and lowest AIC which indicates the best fitted model.

A non-metric multi-dimensional scaling (NMDS) ordination was used to visualize the patterns in the assemblages of plant and galling insect species across the 30 sampling plots. NMDS ordination analyses were based on the Bray-Curtis similarity index of host plant and galling species. Species abundance data were square-root transformed (Clarke and Gorley 2001) in order to avoid any bias resulting from highly abundant species and differences in sample sizes (i.e. stem density per plot). To test if plant and galling insect assemblage composition differed among the three forest habitat type, we conducted an ANOSIM test in PRIMER-E (Clarke and Gorley 2001).

To address potential effects of plot location on levels of taxonomic similarity of host plant assemblages, we performed a Mantel test with a weighted Spearman rank correlation through permutations in two distance matrices: geographic distance and taxonomic composition. Mantel test, that accounted for spatial dependence of plots within the forest condition, was performed with straight-line distances between plots *ln*-transformed as suggested by Condit et al. (2002) and postulated by Hubbell's (2001) neutral theory. Finally, we performed an indicator species analysis (*sensu* Dufrêne and Legendre 1997), which indicates species that can be used as ecological indicators of community types or habitat conditions, in order to highlight taxonomic and functional differences (i.e., pioneers and shade tolerant) among the host-plant assemblages, with top indicator species being identified into species-rank abundance curves. Shapiro-Wilk tests were used to verify normality of all explanatory variables and analyses were carried out in EstimateS 8 (Colwell 2006), JMP 8, Primer 6 (Clark and Gorley 2001), and R software (R Core Team 2013).

Results

A total of 1,769 saplings from 219 native tree species were recorded across all three habitats –interior and edge of Coimbra forest and small forest fragments in the Serra Grande Landscape. Habitat types exhibited similar scores in terms of sapling density but with a relatively great variation within each habitat: 57.9 ± 11.3 ($\bar{x}$ ± SD) in forest interior *vs.* 48.9 ± 20.9 in small fragments and 41.6 ± 12.6 stems/100m^2 in forest edges (F = 2.74, d.f. = 2, P = 0.08). In terms of total numbers, however, forest interior supported much more saplings: 698 saplings in forest interior, 539 in forest edges, and 532 in forest fragments. A similar within-habitat variation was recorded relative to sapling species richness: 23.2 ± 5.37 saplings/100 m^2 in forest interior *vs.* 21.1 ± 9.18 in small fragments and 15.9 ± 3.7 in forest edges, but in this case differences were marginally significant (F = 3.33, d.f. = 2, P = 0.051). At plot scale, habitats differed in terms of host plant species richness (F = 75.50, P = 0.0001) (Fig. 1b), and GLM revealed a significant relationship between host plant species richness and richness of galling insects (Fig. 1A; χ^2 = 5.49, d.f. = 1, P = 0.02) with no effect of habitat type (χ^2 = 3.78, d.f. = 2, P = 0.15). There was an interaction between habitat type and host plant richness (χ^2 = 6.86, P = 0.03), indicating that the influence of host plants varied across habitats. In addition to the richness of host plants, among fragments galling-insect species was positively associated with the amount of forest cover retained in the surrounding landscape (χ^2 =5.69, d.f. =1, P =

0.02), while fragment size (χ^2 = 1.55, d.f. = 1, *P* = 0.21) did not show any influence on galling insect assemblages.

At habitat spatial scale, richness estimators revealed the occurrence of 104 observed sapling species in forest interior *vs.* 121 in fragments and 91 species in forest edges. However, habitats differed in terms of attacked sapling species, with a total of 38 observed host plant species (23 plant families) in forest interior *vs.* 34 host species in fragments (21 plant families) and 22 host species from 17 families in edge plots. Accordingly, forest interior supported twice as many galling insect species than edge-affected habitats: 42 *vs.*28 and 20 observed species in small fragments and forest edges, respectively. Other species richness estimators confirmed the patterns revealed by number of observed species (Sobs); sapling host plant species richness ranged from 38 ± 4.78 species (sobs mean ± SD) to 76.4 ± 25.4 (Chao 2) in forest interior, whereas it was half that number in forest edges: from 22 ± 2.5 (Sobs) up to 28.7 ± 5.7 (Chao 2). Galling insects reached 42 ± 5.26 species (Sobs) up to 107.2 ±35.2 (Chao 2) in forest interior, but it ranged between 28 ± 4.05 (Sobs) to 59.5 ± 19.1 species (Chao 2) in small fragments, and between 20 ± 3.12 (Sobs) to 34.04 ± 10.5 species (Chao 2) in the edge habitat. However, edge-affected habitats and forest interior did not exhibited differences in richness of both host plants and galling insects as sapling abundance was controlled (Figs. 2A and B).

Levels of attack were also marginally significant among forest types at habitat spatial scale with entire sapling assemblages supporting 21.1% of attacked stems (forest interior), 12.4% in small fragments and 8.% in forest edges (χ^2= 5.94, d.f. = 2, *P* = 0.051). Attack varied across plant groups with a significant interaction between ‘‘habitat’’ and ‘‘functional groups” (χ^2= 8.33, d.f. = 2, *P* = 0.02, a log-linear model). Shade-tolerant stems were more frequent in forest interior (χ^2 = 6.80, d.f. = 2, *P* = 0.03) summing up 386 saplings (55%) from 44 species (52% of all species), while this group accounted for less than 40 percent of all stems and species across edge-affected habitat (Fig. 3). Furthermore, both pioneer and shade-tolerant stems experienced lower levels of attack across edge-affected habitats: pioneer attack was reduced by a half in forest fragments and forest edges (nearly 10%), and attack was reduced by two thirds among shade-tolerant stems inhabiting forest edges.

Ordination of plots through NMDS, based on species similarity of host species saplings (*stress*: 0.2; Fig. 4A) and galling insects (*stress*: 0.1; Fig. 4B) assemblages, resulted in three clearly segregated clusters: one formed by forest interior plots, one by small fragments and another formed by edge plots. This segregation was confirmed by an ANOSIM, which identified habitat as a variable correlated to species taxonomic similarity for host sapling species ($r = 0.51$, $P = 0.0001$) and galling insects ($r = 0.37$, $P = 0.0001$). A Mantel test did not detect a significant correlation between plot location and patterns of plant species similarity (*Rho* 0.12; $P = 0.07$). In relation to host plant species which support more than one galling insect species, we found *Miconia prasina* D.C. (Melastomataceae) and *Anaxagorea dolichacarpa* Sprague & Sandwith (Annonaceae) with two species per host plant species and *Tovomita mangle* G. Mariz (Clusiaceae) with three species. Although habitats shared some host plant species, dominant species (Fig. 5) varied as follow: *Tovomita mangle* (forest interior), *Guapira* sp. (small fragments), and *Erythroxylum mucronatum* (forest edges). Finally, the Indicator Species Analysis revealed that the floristically cohesive group of plots formed by forest interior (Group 1, Table 1) was characterized by seven indicator tree species (majority of which shade tolerant). In contrast, one indicator species emerged in forest edge: the pioneer tree species *Erythroxylum mucronatum* (Group 2, Table 1). Collectively, NMDS, species-rank abundance curves and indicator species analysis clearly indicated a taxonomic segregation between forest habitats, which resulted from differences in relative importance of functional groups describing distinct regeneration strategies.

Discussion

Relatively few studies have examined the impact of habitat loss and/or fragmentation on the antagonistic plant-animal interaction such as the herbivory by specialist insects (Julião et al. 2004, Araújo et al. 2011, Araújo and Santo-Filho 2012, Malinga et al. 2014a, Maldonado-López et al. 2015, 2016). Our results suggest that forest habitats support distinct relationship between host-plant and galling insect assemblages. With a reduced number of host-plant species per unit of area, edge-affected habitats support taxonomically distinct but impoverished assemblages at plot and landscape spatial scales, with reduced levels of stem attack as compared to patches of old-growth forests. Precisely, edge-affected habitats lack a large team of shade-tolerant species and their insect attendants (such as the indicator species), a group of plants that apparently support a substantial part of galling insect diversity across stands of old-growth forests. However, even this group of plants appears to be much less attacked across edge-affected habitats, as in pioneer species. In fact, higher attack rate in sapling assemblage indicate that dominant sapling species were more attacked in forest interior. Finally, we should point out that in the Serra Grande landscape, tangible differences in both plant and insect assemblages were recorded by comparing forest edges and forest interior patches in the same large forest remnant (i.e., the Coimbra forest), which eliminated the possibility of explaining cross-habitat differences by baseline variables.

Previous studies have found both neutral (Julião et al. 2004) and positive associations between galling insects and edge-affected habitats (Araújo et al. 2011, Araújo and Santo-Filho 2012, Maldonado-Lopez et al. 2015) with authors arguing for lower parasitism pressure across a sort of physically stressed habitat. Most galling insects are species-specific and they exhibit a close relationship with their host plants (i.e., Blanche and Westoby 1995, Veldtman and McGeoch 2003, Shorthouse et al. 2005, Carneiro et al. 2009, Santos et al. 2011) with galling insect richness correlated to taxonomic turnover in plant communities (Wright and Samways 1998). In addition to the dependence on monophagous interactions with host plants, a substantial portion of gall-inducing insects evidently rely on shade-tolerant species as host plants, as we have documented in the Coimbra forest. Such a close relationship makes evolutionary sense, since shade-tolerant species or old-growth flora represent the majority of plant diversity in tropical forests (Whitmore 1991, Richards 1996). A recent meta-analysis (Araújo 2013) confirmed that the "plant richness hypothesis" is the strongest predictor of gall-forming insect distribution (i.e., Wright and Samways, 1996, 1998; Blanche and Ludwig 2001, Araújo et al. 2013).

A potential lower number of saplings in the plant assemblages across edge-affected habitats obviously represent a causal mechanism, but it is not enough to explain the whole set of shifts experienced by the host plant-insect assemblages we documented in the Serra Grande landscape. Edge-affected habitats, such as those of the Serra Grande landscape (Oliveira et al. 2004), are expected to support impoverished tree assemblages (Michalski et al. 2007), particularly in terms of shade-tolerant taxa, including emergent, large-seeded, and vertebrate-pollinated tree species (Laurance et al. 2006a, Michalski et al. 2007, Lopes et al. 2009, Tabarelli et al. 2010b). Additionally, some shade-tolerant taxa, although present in edge-affected habitats, occurs with reduced abundance or just as immature individuals (Oliveira et al. 2008). Increased wind turbulence, habitat desiccation, herbivory and disease pressure, and competition with successional species have been referred as edge-effects leading to population decline or collapse among these functional groups (see Tabarelli et al. 2010a, 2010b). Coimbra forest edges in fact support only half the number of tree species found in the forest interior (Oliveira et al. 2004). Moreover, tree assemblages along forest edges can consist of over 80% pioneer stems and species (Santos et al. 2008). In this context of extirpation and rarity of host plants it is not surprising that insect assemblages are also impoverished locally and at the habitat scale. Edge-effects leading to the extirpation of host plants and consequent cascades is also consistent to the relationship we found between gall-insects and habitat connectivity since this landscape metric tend be negatively correlated to intensity of edge effects and the abundance of edge-affect habitats (Harper et al. 2005).

In addition to the extirpation of host plants, other process may be involved in the emergence of impoverished galling insect assemblages across edge-affected habitats, as pioneer (usually abundant in edge-affected habitats) and shade-tolerant stems and taxa also experienced lower levels of attack as compared to forest interior. In fact several taxa, such as *Eugenia umbrosa* O. Berg (Myrtaceae), *Guapira* sp. (Nyctaginaceae), *Quiina* sp. (Ochnaceae), *Sorocea hilarii* Gaudich (Moraceae) and *Styrax* sp. (Styracaceae) were attacked in forest interior but were recorded non-attacked across forest edges; i.e., host plants lacking their attendants. Overall, several insect species and herbivory levels are likely to respond negatively to the establishment of human-modified landscapes (Valladares et al. 2006, Fáveri et al. 2008, Ruiz-Guerra et al. 2010, Santos and Benítez-Malvido 2012, Rossetti et al. 2014). This human intervention may reduce population size due to habitat loss (Zabel and Tscharntke 1998, Krauss et al. 2003a, 2003b), reduce meta-population colonization and migration rates due to habitat fragmentation (Hanski 1994, Cronin 2004, Haynes and Cronin 2006), and impose adverse microclimatic conditions for insects (Almeida et al. 2008). In this perspective, increased structural connectivity may result in higher insect dispersal and movement between patches (Holzchuh et al. 2010, Rösch et al. 2013), while it reduces edge-effects and thus amelioration of abiotic conditions for galling insects.

Our findings and conclusions reveal causal relationships between sapling abundance, the impoverishment of certain groups of plants and their specialist herbivores due the conversion of old-growth forest into edge-affected habitats with interesting implications for our understanding of which ways human-modified landscapes alter plant-animal interactions, particularly herbivory by insects. Precisely, several previous papers have argued for the occurrence of bottom-up disruptions on plant-animal interactions triggered by habitat loss and fragmentation (Lopes et al. 2009, Tabarelli et al. 2012). Perhaps, the most dictated example of this phenomenon refers to proliferation of leaf-cutting ants, a generalist herbivore, across edge-affected habitats in response to the proliferation of palatable plants, particularly pioneer species (Urbas et al. 2007, Wirth et al. 2007, Leal et al. 2014).

Here, we offer empirical evidence for a bottom-up disruption of plant-animal interactions marked by tangible impoverishment in the assemblages of a specialist herbivore (galling insects) at multiple spatial scales. These findings support key general hypotheses such as (1) fragmentation-related changes in plant assemblages cascade over plant attendants (Lopes et al. 2009, Tabarelli et al. 2012), (2) generalist plant attendants tend to benefit from creation of forest edges, particularly from the proliferation of palatable plants, while specialist herbivores may decline; i.e., the generalist-generalist paradigm (Wirth et al. 2008, Leal et al. 2014), and (3) bottom-up effects are conspicuous in trophic webs (Hunter and Price 1992, Haddad et al. 2001, Scherber et al. 2010, Petermann et al. 2010, Malinga et al. 2014b), and in many situations they result in co-extinctions across multiple trophic levels (Koh et al. 2004, Fonseca 2009, Tabarelli et al. 2012). Finally, the winner-loser plant replacements experienced by edge-affected habitats represent one of the major forces in human modified landscapes (Tabarelli et al. 2012).

In the context of conservation, human-modified landscapes dominated by edge-affected habitats and their altered plant assemblages may not be able to retain the full complement of galling insects. In other words, hyper-fragmented landscapes may exhibit limited conservation value (Tabarelli et al. 2008, Melo et al. 2013). Further studies should investigate the generality of the patterns (i.e., other ontogenetic plant stages) and mechanisms discussed here as they question the potential of human-landscapes as effective repositories for tropical biodiversity.

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References Cited

Almeida, W. R., R. Wirth, and I. R. Leal. 2008. Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic forest. Entom. Experim. Et Appl. 128: 551–557.

Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161: 105-121.

Araújo, W. S. 2013. Different relationships between galling and non-galling herbivore richness and plant species richness: a meta-analysis. Arthr. Plant Interac. 7: 373-377.

Araújo, W. S., C. Scareli-Santos, F. A. G. Guilherme, and P. Cuevas-Reyes. 2013. Comparing galling insect richness among Neotropical savannas: effects of plant richness, vegetation structure and super-host presence. Biod. Conserv. 22: 1083-1094.

Araújo, W. S., and K. E. Santo-Filho. 2012. Edge effect benefits galling insects in the Brazilian Amazon. Biod. Conserv. 22: 1083-1094.

Araújo, W. S., G. R. Julião, B. A. Ribeiro, I. P. Silva, and B. B. Santos. 2011. Diversity of galling insects in *Styrax pohlii* (Styracaceae): edge effect and use as bioindicators. Rev. Biol. Trop. 29: 1589-1597.

Arnold, A. E., and N. M. Asquith. 2002. Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatún, Panama. Biod. Conserv. 11:1663-1680.

Barbosa, V. S., I. R. Leal, L. Iannuzzi, and J. Almeida-Cortez. 2005. Distribution pattern of herbivorous insects in a remnant of Brazilian Atlantic forest. Neot. Entom. 34: 701–711.

Blanche, K. R., and J. A. Ludwig. 2001. Species richness of gall-inducing insects and host plants along an altitudinal gradient in Big Bend National Park, Texas. The Amer. Midl. Natur. 145**:** 219-232.

Blanche, K. R., and M. Westoby. 1995. Gall-forming insect diversity is linked to soil fertility via host plant taxon. Ecology 76: 2334 - 2337.

Carneiro, M. A. A., C. S. A. Branco, C. E. D. Braga, E. Almada, M. B. M. Costa, G. W. Fernandes, and V. C. Maia. 2009. Are gall midges species (Diptera: Cecidomyiidae) host plant specialists? Rev. Bras. Entom. 53: 365-378.

Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93: 2533–2547.

Chao, A., and T. J. Shen. 2010. Program SPADE: Species prediction and diversity estimation. Program and user's guide. CARE, Hsin-Chu, Taiwan.

Clarke, K. R., and R. N Gorley. 2001. PRIMER v5: User manual/tutorial. Primer-E Ltd.

Colwell, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples, version 8.00.

Condit, R., N. Pitman, E. G. Leigh, J. Chave, J. Terborgh, R. Foster, P. V. Nuñez, S. Aguilar, R. Valencia, V. Gorky, H. C. Muller-Landau, E. Losos, and S. Hubbell. 2002. Beta-diversity in tropical forest trees. Science 295: 666–669.

Crawley, M. J. 2002. Statistical computing. An introduction to data analysis using S-Plus. John Wiley & Sons, London.

Cronin, J. T. 2004. Host-parasitoid extinction and colonization in a fragmented prairie landscape. Oecologia 139: 503–514.

Cuevas-Reyes, P., M. Quesada, P. Hanson, R. Dirzo, and K. Oyama. 2004. Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life forms, host plant age and plant density. J. Ecology 92: 707-716.

Didham, R. K., J. Ghazoul, N. E. Stork, and A. J. Davis. 1996. Insects in fragmented forests: a functional approach. Trends Ecol. Evol. 11: 255–260.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monog. 67: 645–666.

Fáveri, S. B., H. L. Vasconcelos, and R. Dirzo. 2008. Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. J. Trop. Ecol. 24: 57-64.

Fernandes, G. W., and P. W. Price. 1988. Biogeographical gradients in galling species richness: tests of hypotheses. Oecologia 76: 161–167.

Fernandes, G. W., and J. C. Santos. 2014. Neotropical Insect Galls. Springer, Dordrecht.

Fernandes, G. W., E. D. Almada, and M. A. A. Carneiro. 2010. Gall-inducing insect species richness as indicators of forest age and health. Environ. Entom. 39: 1134-1140.

Ferraz, S. F. B., K. M. P. M. B. Ferraz, C. C. Cassiano, P. H. S Brancalion, D. T. A. da Luz, T. N. Azevedo, L. R., Tambosi, and J. P. Metzger. 2014. How good are tropical forest patches for ecosystem services provisioning? Lands. Ecol. 29: 187–200.

Fonseca, C. R. 2009. The silent mass extinction of insect herbivores in biodiversity hotspots. Conserv. Biol. 23: 1507-1515.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379-391.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. Amer. Natur. 158: 17-35.

Hanski, I., and M. E. Gilpin. 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA, USA.

Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. Trend. Ecol. Evol. 9: 131–135.

Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brosofske, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh, and P. A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. 19: 768–782.

Hartshorn, G. S. 1978. Treefalls and tropical forest dynamics. pp. 617–638. *In* P. B. Tomlinson and M. H. Zimmermann (eds.). Tropical trees as living systems, Cambridge University Press, New York.

Haynes, K. J., and J. T. Cronin. **2006**. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos 113: 43–54.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2010. How do landscape composition and configuration, organic farming and fallow strips affects the diversity of bees, wasps and their parasitoids? J. Anim. Ecol. 79: 491-500.

Hubbell, S. P. 2001. The unified theory of biodiversity and biogeography. Monographs in Population Biology, vol. 32. Princeton University Press, Princeton, USA.

Hunter, M. D. and P. Price. 1992 Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top- down forces in natural communities. Ecology 73: 724–732.

IBGE. 1985. Atlas Nacional do Brasil: Região Nordeste. IBGE, Rio de Janeiro.

Julião, G. R., M. E. C. Amaral, G. W. Fernandes, and E. G. Oliveira. 2004. Edge effects and species area relationships in the gall forming insect fauna of natural forest patches in the Brazilian pantanal. Biod. Conserv. 13: 2055-2066.

Koh, L. P., N. S. Sodhi, and B. W. Brook. 2004. Co-extinctions of tropical butterflies and their host plants. Biotropica 36: 272–274.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003a. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J. Biog. 30: 889–900.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003b. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia 137: 591–602.

Laurance, W. F., J. L. C. Camargo, R. C. C., Luizão, S. G., Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. B. Williamsom, J. Benítez-Malvido, H. L. Vasconcelos, K. S. Van Houtan, C. E., Zartman, S. A., Boyle, R. K. Didham, A. Andrade, and T. Lovejoy. 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biol. Conserv. 144: 56–67.

Laurance, W. F., H. E. M., Nascimento, S. G. Laurance, A. Andrade, J. E. L. S. Ribeiro, J. P. Giraldo, T. E. Lovejoy, R. Condit, J. Chave, K. E. Harms, and S. D'Angelo. 2006a. Rapid decay of tree-community composition in Amazonian forest fragments. Proc. Natl Acad. Sci. 103: 19010-19014.

Laurance, W. F., H. E. M., Nascimento, S. G., Laurance, A. C. Andrade, P. M. Fearnside, J. E. L Ribeiro, and R. L. Capretz. 2006b. Rain forest fragmentation and the proliferation of successional trees. Ecology 87: 469–482.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16: 605–618.

Leal, I. R., R. Wirth, and M. Tabarelli. 2014. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified Neotropical forests. Biotropica 46: 516–528.

Lopes, A. V., L. C. Girão, B.A. Santos, C. A. Peres, and M. Tabarelli. 2009. Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic Forest fragments. Biol. Conserv. 142: 1154–1165.

Maldonado-López, Y., P. Cuevas-Reyes, and K. Oyama. 2016. Diversity of gall wasps (Hymenoptera: Cynipidae) associated with oak trees (Fagaceae: Quercus) in a fragmented landscape in Mexico. Arthr. Plan. Inter. 10: 29-39.

Maldonado-López, Y., P. Cuevas-Reyes, G. N. Stone, J. L. Nieves-Aldrey, and K. Oyama. 2015. Gall wasp community response to fragmentation of oak tree species: importance of fragment size and isolated trees. Ecosphere 6: 1–15.

Malinga, G. M., A. Valtonen, E. J. Vesterinen, P. Nyeko, P. and H. Roininen. 2014a. Communities of galling insects on *Neoboutonia macrocalyx* trees in continuous forests and remnants of forest fragments in Kibale, Uganda. Afr. Entom. 22: 742–754.

Malinga, G. M., A. Valtonen, P. Nyeko, E. J. Vesterinen, and H. Roininen. 2014b. Bottom-up impact on the cecidomyiid leaf galler and its parasitism in a tropical rainforest. Oecologia 176: 511–520.

Melo, F. P. L., V. Arroyo-Rodriguez, L. Fahrig, M. Martinez-Ramos, and M. Tabarelli. 2013. On hope for biodiversity-friendly tropical landscapes. Trends Ecol. Evol. 28: 462-468.

Meyer, S. T., I. R. Leal, M. Tabarelli, and R. Wirth. 2010. Ecosystem engineering by leaf-cutting ants: nests of *Atta cephalotes* drastically alter forest structure and microclimate. Ecol. Entom. 36: 142–24.

Michalski, F., I. Nishi, and C. A. Peres. 2007. Disturbance-mediated drift in tree functional groups in Amazonian forest fragments. Biotropica 39: 691–701.

Novotny, V., and Y. Basset. 2005. Host specificity of insects herbivores in tropical forests. Proc. Royal Soc. B. 272: 1083-1090.

Oliveira, M.A., A. S. Grillo, and M. Tabarelli. 2004. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. Oryx 38: 389–394.

Oliveira, M. A., A. M. M. Santos, and M. Tabarelli. 2008. Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. For. Ecol. Manage. 256: 1910–1917.

Oyama, K., M. A. Pérez-Pérez, P. Cuevas-Reyes, and R. Luna-Reyes. 2003. Regional and local species richness of gall-inducing insects in two tropical rain forest in Mexico. J. Trop. Ecol. 19: 595-598.

Petermann, J. S., C. B. Müller, C. Roscher, A. Weigelt, W. W. Weisser, and B. Schmid. 2010. Plant species loss affects life-history traits of aphids and their parasitoids. PLOSOne DOI: 10.1371/journal.pone.0012053

Price, P. W., G. W. Fernandes, and G. L. Waring. 1987. Adaptive nature of insect galls. Environ. Entomol. 16:15–24.

Price, P. W., G. W. Fernandes, A. C. F, Lara, J. Brawn, H. Barrios, M. G. Wright, S. P. Ribeiro, and N. Rothcliff. 1998. Global patterns in local number of insect galling species. J. Biogeogr. 25: 581–591.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org

Richards, P. W. 1996. The tropical rain forest. Cambridge University Press, Cambridge, UK.

Rösch, V., T. Tscharntke, C. Scherber, and P. Batáry. 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. J. Appl. Ecol. 50: 387–394.

Rossetti, M. R., E. González, A. Salvo, and G. Valladares. 2014. Not all in the same boat: trends and mechanisms in herbivory responses to forest fragmentation differ among insect guilds. Arthr. Plan. Inter. 8: 593–603.

Ruiz-Guerra, B., R. Guevara, N. A. Mariano, and R. Dirzo. 2010. Insect herbivory declines with forest fragmentation and covaries with plant regeneration mode: evidence from a Mexican tropical rain forest. Oikos 119: 317–325.

Santos, B. A., and J. Benítez-Malvido. 2012. Insect herbivory and leaf disease in natural and human disturbed habitats: lessons from early-successional *Heliconia* herbs. Biotropica 44: 53–62.

Santos, B. A., V. Arroyo-Rodríguez, C. Moreno, and M. Tabarelli, M. 2010. Edge related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. PLOSOne, DOI: 10.1371/journal.pone.0012625

Santos, B. A., C. A. Peres, M. A. Oliveira, A. Grillo, C. P. Alves-Costa, and M. Tabarelli. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biol. Conserv. 141: 249-260.

Santos, J. C., J. S. Almeida-Cortez, and G. W. Fernandes. 2011. Diversity of gall-inducing insects in the high altitude wetland forests in Pernambuco, Northeastern Brazil. Brazil. Braz. J. Biol. 71: 47-56.

Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E. D. Schulze, C. Roscher, A. Weigelt, E. Allan, H. Beßler, M. Bonkowski, N. Buchmann, F. Buscot, L.W. Clement, A. Ebeling, C. Engels, S. Halle, I. Kertscher, A. M. Klein, R. Koller, S. König, E. Kowalski, V. Kummer, A. Kuu, M. Lange, D. Lauterbach, C. Middelhoff, V. D. Migunova, A. Milcu, R. Müller, S. Partsch, J. S. Petermann, C. Renker, T. Rottstock, A. Sabais, S. Scheu, J. Schumacher, V. M. Temperton, and T. Tscharntke. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468: 553–556.

Sfair, J. C., V. Arroyo-Rodriguez, B. A. Santos, and M. Tabarelli. 2016. Taxonomic and functional divergence of tree assemblages in a fragmented tropical forest. Ecol. Applic. DOI: 10.1890/15-1673.1.

Shorthouse, J. D., D. Wool, and A. Raman. 2005. Galling-inducing insects – nature of most sophisticated herbivores. Basic App. Ecol. 6: 407- 411.

Silva, P. S. D., I. R. Leal, R. Wirth, F. P .L. Melo, and M. Tabarelli. 2012. Leaf-cutting ants alter seedling assemblages across second-growth stands of Brazilian Atlantic forest. J. Trop. Ecol. 28: 361-368.

Stone, G. N., and K. Schönrogge. 2003. The adaptive significance of insect gall morphology. Trend. Ecol. Evol. 18: 512-522.

Swaine, M. D., and J. B. Hall. 1983. Early succession on cleared forest land in Ghana. J. Ecol. 71: 601-627.

Tabarelli, M., A. V. Lopes, and C. A. Peres. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica 40: 657-661.

Tabarelli, M., A. V. Aguiar, M. C. Ribeiro, J. P. Metzger, and C. A. Peres. 2010a. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. Biol. Conserv. 143: 2328-2340.

Tabarelli, M., A. V. Aguiar, L. C. Girão, C. Peres, and A. V. Lopes. 2010b. Effects of pioneer tree species hyperabundance on forest fragments in northeastern Brazil. Conserv. Biol. 24: 1654-1663.

Tabarelli, M., C. A. Peres, and F. P. L Melo. 2012. The "few winners and many losers" paradigm revisited: emerging prospects for tropical forest biodiversity. Biol. Conserv. 155: 136-140.

Toma, T. S., G. W. Fernandes, D. G. Souza, M. Tabarelli, and J. C. Santos. 2014. Galling insects as indicators of habitat quality, pp. 143-150. *In* G.W. Fernandes and J.C. Santos (eds), Neotropical Insect Galls. Springer, Dordrecht.

Tscharntke, T., and R. Brandl. 2004. Plant-insect interactions in fragmented landscapes. Ann. Rev. Entom. 49**:** 405-430.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Characteristics of insect populations on habitat fragments: A mini review. Ecol. Res.17: 229-239

Urbas, P., M. V. Araújo-Júnior, I. R. Leal, and R. Wirth. 2007. Cutting more from cut forests - edge effects on foraging and herbivory of leaf-cutting ants. Biotropica 39: 489-495.

Valladares, G., A. Salvo, and L. Cagnolo. 2006. Habitat fragmentation effects on trophic processes of insect–plant food webs. Conserv. Biol. 20: 212-217.

Veldtman, R., and M. A. McGeoch. 2003. Gall forming insect species richness along a non scleromorphic vegetation rainfall gradient in South Africa: the importance of plant community composition. Aust. Ecol. 28: 1-13.

Veloso, H. P., A. L. R. Rangel-Filho, and J. C. A. Lima. 1991. Classificação da vegetação brasileira adaptada a um sistema universal. IBGE, Rio de Janeiro, Brazil.

Whitmore, T. C. 1989. Canopy gaps and the two major groups of tropical trees. Ecology 70: 536-538.

Whitmore, T. C. **1991**. An introduction to tropical rain forests. Clarendon Press, Oxford, UK.

Wirth, R., S. T. Meyer, W. R., Almeida, M. V. Araújo-Junior, V. S. Barbosa, and I. R. Leal. 2007. Living on the edge: Drastic increase of leaf-cutting ant (*Atta* spp.) densities at the edge of a Brazilian Atlantic Forest remnant. J. Trop. Ecol. 23: 501-505.

Wirth, R., S. T. Meyer, I. R. Leal, and M. Tabarelli, M. 2008. Plant–Herbivore Interactions at the Forest Edge. Progr. Botany 68: 423-448

Wright, M. G., and M. J. Sanways. 1996. Gall insects species richness in African fynbos and karoo vegetation: the importance of plant species richness. Biodiv. Lett. 3: 151-155.

Wright, M. G., and M. J. Sanways. 1998. Insect species richness in a diverse flora: galls insects in Cape floristic region, South Africa. Oecologia 115: 427-433.

Zabel, J., and T. Tscharntke. 1998. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? Oecologia 116: 419-425.

Table 1: Indicator species (sensu Dufrêne and Legendre 1997) of host plant sapling assemblages recorded in forest interior (Group 1) and forest edge (Group 2) with their respective botanical family and regeneration strategy at Serra Grande landscape, northeast Brazil. I.V. refers to Indicator value.

Indicator species	Family	Regeneration Strategy	Group	I.V.[a]	*P* values[a]
Tovomita mangle	Clusiaceae	S- Tolerant	1	100	0.001
Paypayrola blanchetiana	Violaceae	S- Tolerant	1	84.8	0.001
Micropholis mensalis	Sapotaceae	S- Tolerant	1	70	0.002
Tovomita brevistaminea	Clusiaceae	S- Tolerant	1	58.9	0.001
Quiina sp	Ochnaceae	S- Tolerant	1	57.3	0.006
Pouteria grandiflora	Sapotaceae	S- Tolerant	1	50	0.001
Anaxagorea dolichocarpa	Annonaceae	Pioneer	1	44.7	0.004
Erythroxylum mucronatum	Erythroxylaceae	Pioneer	2	70	0.001

[a] Significant values of the Indicator Species Analysis according to Dufrêne and Legendre (1997).

Figure legends

Figure. 1. Relationships between galling insect richness and host plant richness (A). Relationships between and host plant richness and habitat type (B) in forest interior, small fragments and edge forest stands at Serra Grande, northeastern Brazil. In B are indicated: the mean (dashed line), median (solid line), 25th and 75th percentiles (boundaries of boxes), and the black points (outlying plots) within (SF) small forest fragments, (FI) forest interior and (FE) forest edges.

Figure. 2. Individual- based accumulation curves of (A) sapling host plants, and (B) galling insect species sampled in forest interior, small fragments and edge forest stands in the Serra Grande landscape, northeastern Brazil. The vertical bars indicate the limits of the 95% confidence interval.

Figure. 3. Relative abundance of saplings/stems within categories of regeneration and attack by galling insects across forest interior (n = 10), small fragments (n=10) and forest edge (n = 10) in the Serra Grande landscape, northeastern Brazil. Numbers above bars represent the absolute number of saplings.

Figure. 4. Ordination of host plant plots (A), and galling insect plots (B) via NMDS as recorded in the Serra Grande landscape; forest interior plots as dark circles, small fragments as open circles, and edge plots as triangles. Stress 0.2 and 0.1, respectively.

Figure. 5. Species-rank curves for sapling host plants in (A) forest interior, (B) small forest fragments and (C) forest edges in the Serra Grande landscape. Key to the top indicator species considering indicator species analysis as follows: Tovmang: *Tovomita mangle*; Tovobrev: *Tovomita brevistaminea*; Micromens*: Micropholis mensalis*; Erytmucr: *Erythroxylum* *mucronatum*. PI, pioneer species; ST, shade tolerant species.*indicator species of forest interior;**indicator species of forest edges.

Figure 1

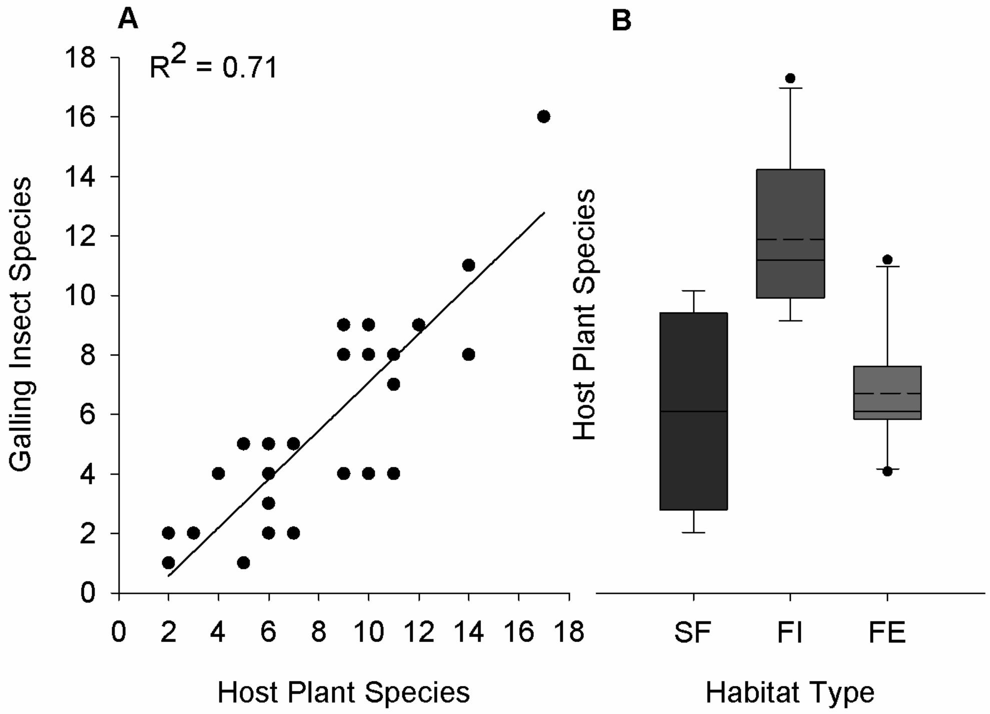

A
B
R^2 = 0.71
Galling Insect Species
0
2
4
6
8
10
12
14
16
18
Host Plant Species
0
2
4
6
8
10
12
14
16
18
Host Plant Species
SF
FI
FE
Habitat Type

Figure 2

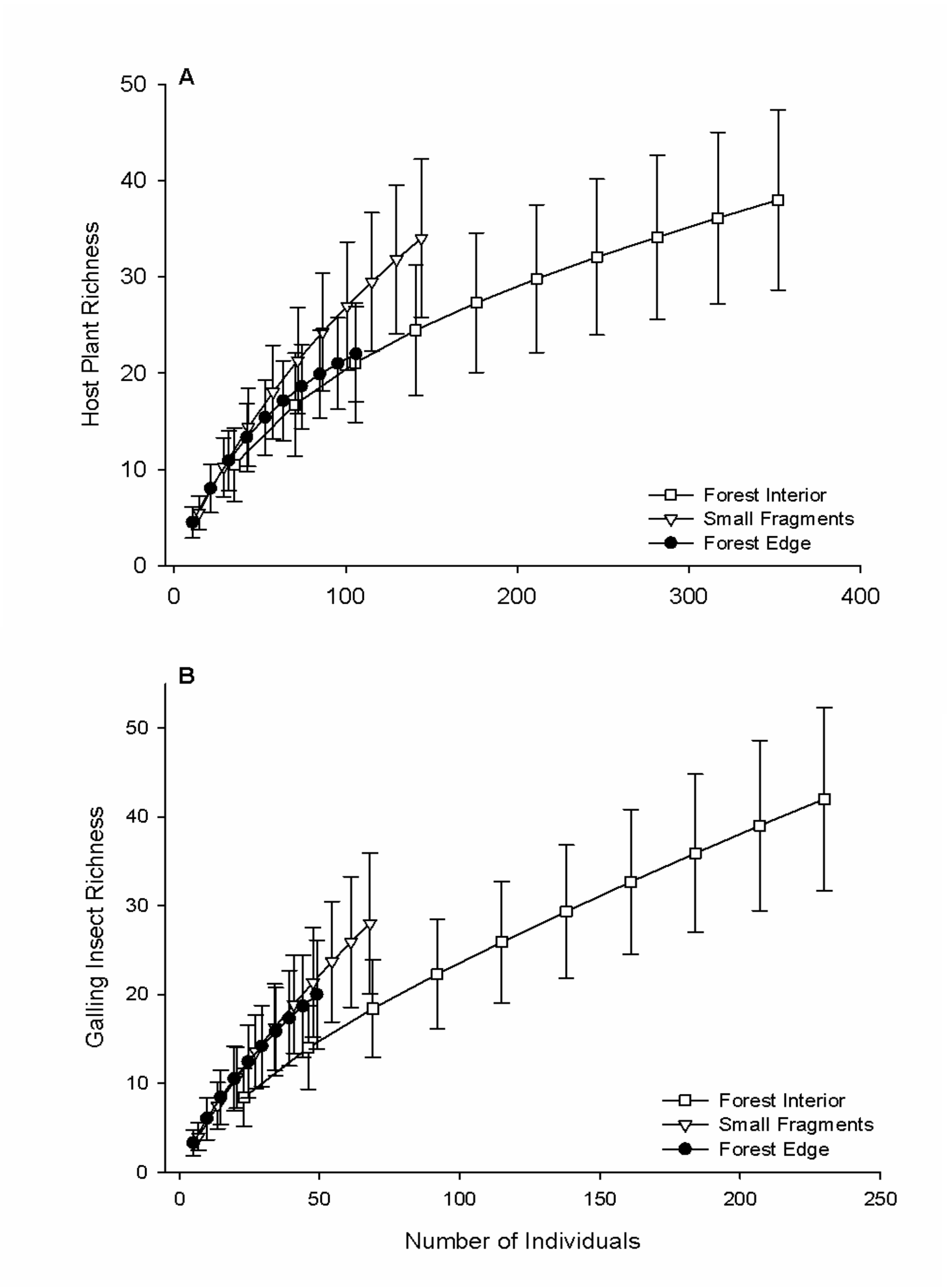

A
Host Plant Richness
0
10
20
30
40
50
0
100
200
300
400
Forest Interior
Small Fragments
Forest Edge
B
Galling Insect Richness
0
10
20
30
40
50
0
50
100
150
200
250
Number of Individuals
Forest Interior
Small Fragments
Forest Edge

Figure 3

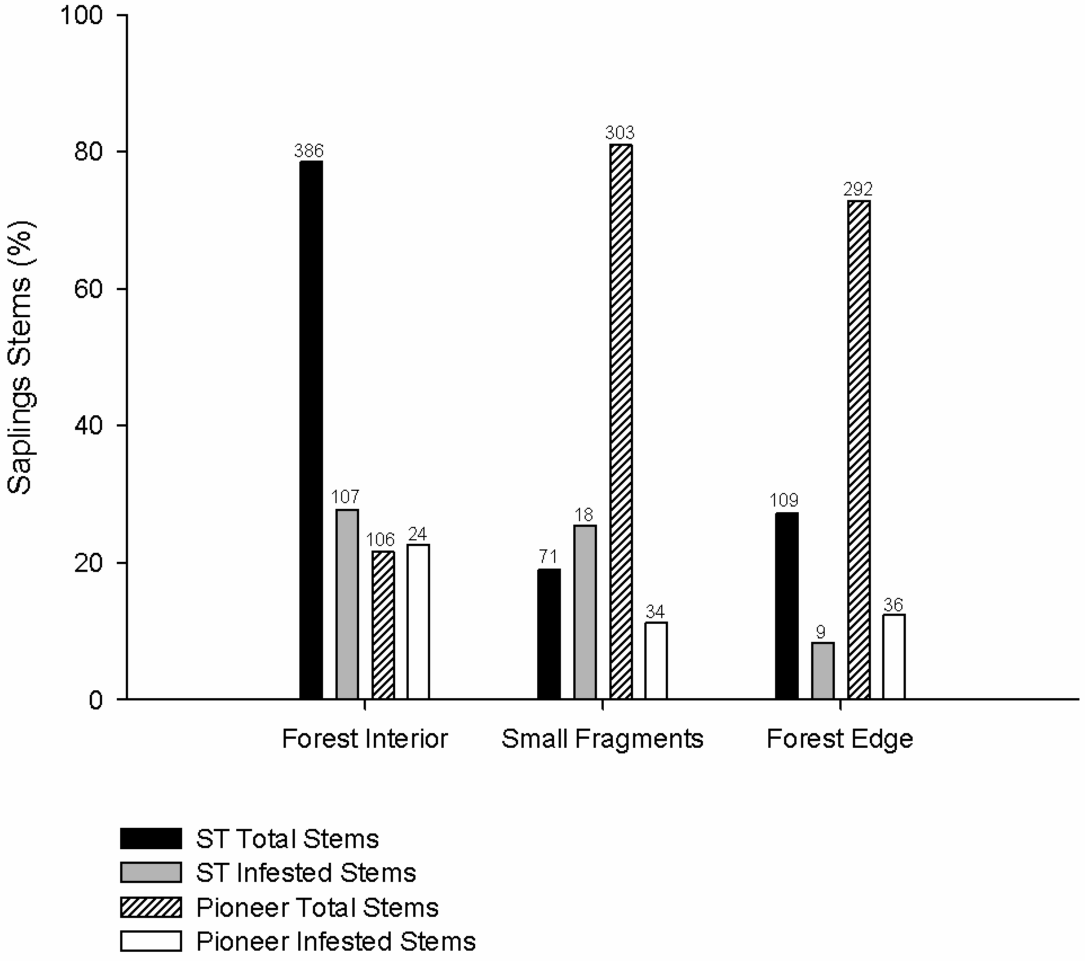

Saplings Stems (%)
100
80
60
40
20
0
386
107
106
24
71
18
303
34
109
9
292
36
Forest Interior
Small Fragments
Forest Edge
ST Total Stems
ST Infested Stems
Pioneer Total Stems
Pioneer Infested Stems

Figure 4

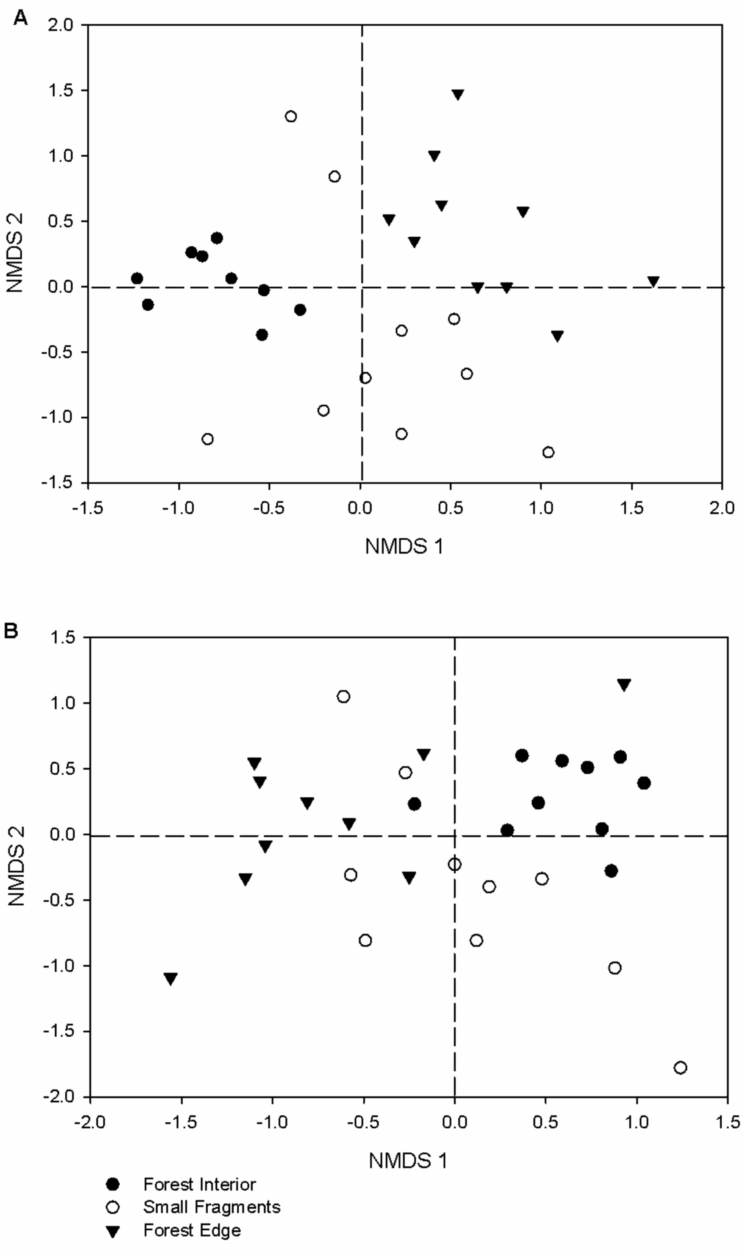
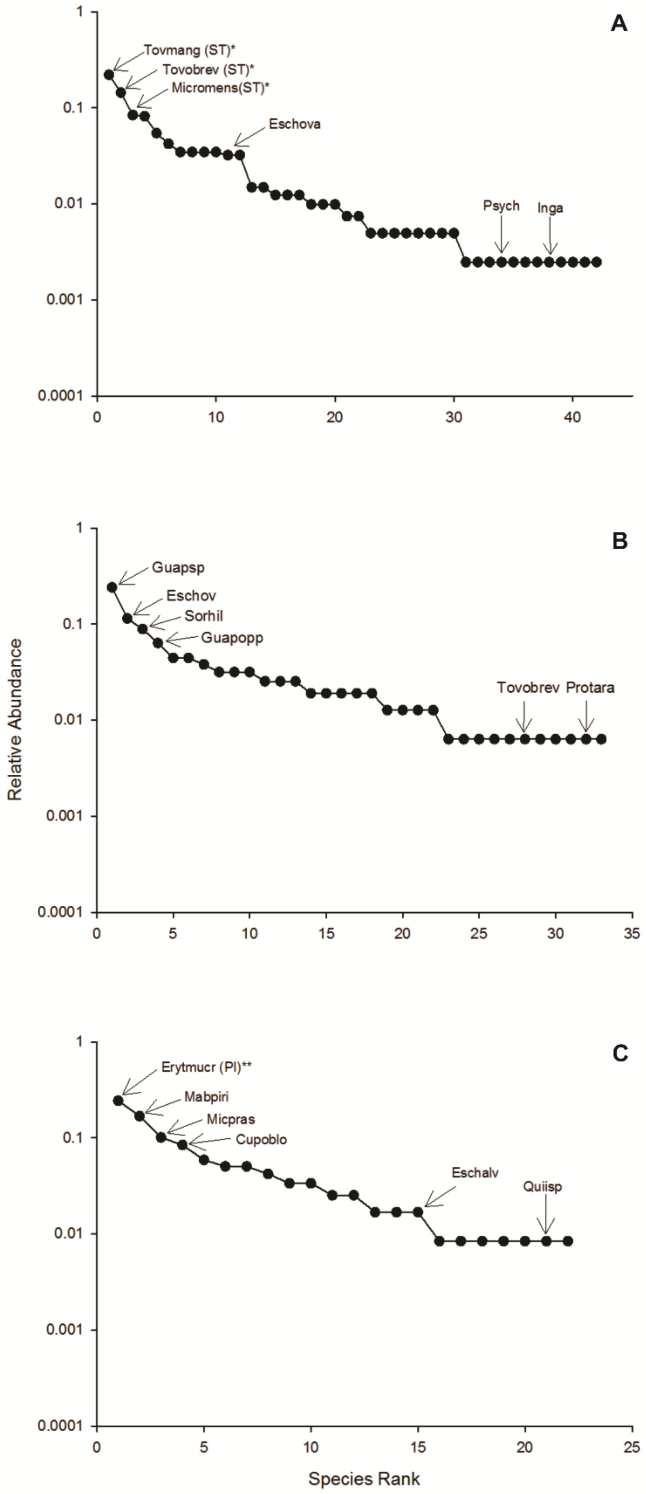

A
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
NMDS 2
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
NMDS 1
B
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
NMDS 2
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
NMDS 1
● Forest Interior
○ Small Fragments
▼ Forest Edge

Figure 5


A
1
0.1
0.01
0.001
0.0001
0
10
20
30
40
Tovmang (ST)*
Tovobrev (ST)*
Micromens(ST)*
Eschova
Psych
Inga
B
1
0.1
0.01
0.001
0.0001
0
5
10
15
20
25
30
35
Guapsp
Eschov
Sorhil
Guapopp
Tovobrev
Protara
Relative Abundance
C
1
0.1
0.01
0.001
0.0001
0
5
10
15
20
25
Erytmucr (PI)**
Mabpiri
Micpras
Cupoblo
Eschalv
Quiisp
Species Rank

6. CONCLUSÕES

Nas escalas espaciais múltiplas que avaliamos neste estudo, evidenciamos que as áreas de interior florestal, por abrigarem maior riqueza de espécies de plantas hospedeiras e densidade de indivíduos vegetais, constituem-se em habitats com maior disponibilidade de recursos e maior capacidade de suporte para as assembléias de insetos herbívoros especializados. Em contraste, as bordas florestais e os pequenos fragmentos em paisagens tropicais hiperfragmentadas abrigam um pequeno subgrupo da flora que não são capazes de manter a alta diversidade alfa e gama e a riqueza de insetos galhadores. Em contraste, há uma alta variabilidade (e.g. turnover, diversidade beta) em habitats afetados pelos efeitos de borda, provavelmente devido às respostas dos processos ecológicos ao hiperdinanismo, diferentes trajetórias sucessionais e maior probabilidade à eventos estocásticos de organização de comunidades.

As plantas tolerantes a sombra, que ocorrem majoritariamente no interior de florestas tropicais, são o recurso preferido para a oviposição das fêmeas dos insetos galhadores. Isso pode ser devido ao maior tempo evolutivo que este grupo funcional teve para estabelecer as interações com seus dependentes. Adicionalmente, a preferência por estas plantas pode estar relacionada à performance larval de insetos endofíticos e a maior qualidade do tecido vegetal que incrementam a sobrevivência da prole. O aumento da conectividade entre fragmentos aparentemente proporciona o melhoramento das condições microclimáticas e fornece mais manchas fontes para as assembléias, com implicações diretas na persistência da biota sensível (i.e. "perdedores") à ação antrópica em paisagens severamente fragmentadas.

Baseando-se nas evidências de que os *hotspots* de biodiversidade são alvos críticos de conservação, a busca de mecanismos subjacentes aos padrões de desaparecimento de espécies e de organização e persistência de biodiversidade são fundamentais. A despeito de incrementar a diversidade beta em escala de paisagem, florestas com grupos de plantas vencedoras (pioneiras) em escala local e homogeneização biótica em escala regional limitarão a distribuição das plantas hospedeiras, influenciarão a diversidade alfa e gama, direcionando estas plantas e insetos herbívoros especializados a co-extinção.

REFERÊNCIAS

AIZEN, M.A.; FEINSINGER, P. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. **Ecology,** v. 75, p. 330–351, 1994.

ALMEIDA, W.R.;WIRTH, R.; LEAL, I. Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic forest. **Entomologia Experimentali et Applicata,** v. 128, p. 551–557, 2008

ARAÚJO, W.S.; SANTO-FILHO, K. Edge effect benefits galling insects in the Brazilian Amazon. **Biodiversity and Conservation,** v. 21, p. 2991-2997, 2012.

ARAÚJO, W.S.; JULIÃO, G.R.; RIBEIRO, B.A.; SILVA, I.P.A.; SANTOS, B.B. Diversity of galling insects in *Styraxpohlii* (Styracaceae): edge effect and use as bioindicators. **Rev Biol Trop,** v. 29, p.1589-1597, 2011.

ASNER, G.P.; KNAPP, D.; BROADBENT, E.; OLIVEIRA, P.; KELLER, M.; SILVA, J. Selective logging in the Brazilian Amazon. **Science**, v. 310, p.480–482, 2005.

BENITEZ-MALVIDO, J. Impact of forest fragmentation on seedling abundance in a tropical rain forest. **Conservation Biology,** 12, 380-389, 1998.

BENÍTEZ-MALVIDO, J.; MARTINEZ-RAMOS, M. Influence of Edge Exposure on Tree Seedling Species Recruitment in Tropical Rain Forest Fragments. **Biotropica, v.** 35, n. 4, p. 530-541, 2003.

BIGGER, D.S.; MARVIER, M.A. How different would a world without herbivory be? A search for generality in ecology. **Integrative Biology**, v. 1, p.60–67, 1998.

BRUNA, E. Seed germination in rainforest fragments. **Nature,** v. 402, p.139, 1999.

CADENASSO, M.L.; PICKETT, S.T.A. Linking forest edge structure to edge function: mediation of herbivore damage. **Journal of Ecology**, v. 88, p. 31-44, 2000.

CÂMARA, I.G. Brief history of conservation in the Atlantic Forest. In: Galindo Leal, C., Câmara, I.G. (Eds.), **The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook.** CABS and Island Press, Washington, p. 31–42, 2003.

CHUST, G., L. GARBIN; PUJADE-VILLAR, J. Gall wasps and their parasitoids in cork oak fragmented forests. **Ecological Entomology**, v. 32, p.82-91, 2007.

COLEY P.D.; BRYANT, J.P.; CHAPIN, F.S. III. Resource availability and plant antiherbivore defense. **Science, v.** 230, p. 895–99, 1985.

COLEY, P.D.; BARONE, J.A. Herbivory and Plant Defenses in Tropical Forests. **Annual Review Ecology and Systematics,** 27, 305–35, 1996.

COLEY P.D.; KURSAR T.A. **Antiherbivore defenses of young tropical leaves: physiological constraints and ecological tradeoffs.** Tropical Forest Plant Ecophysiology.New York: Chapman & Hall. 675p. p. 305–336, 1996.

CUEVAS-REYES; P.; QUESADA, M.; HANSON, P.; DIRZO, R.; OYAMA, K. Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life forms, host plant age and plant density. **Journal of Ecology**, 92, 707-716, 2004.

CUEVAS-REYES, P.; OLIVEIRA-KER, F.T.; FERNANDES, G.W.; BUSTAMANTE, M. Abundance of gall-inducing insect species in sclerophyllous savanna: understanding the importance of soil fertility using an experimental approach. **Journal of Tropical Ecology,** v. 27, n. 6, p. 631-640, 2011.

DIDHAM, R.K.; GHAZOUL, J.; STORK, N.E.; DAVIS, A.J. Insects in fragmented forests: a functional approach. **Trends in Ecology and Evolution,** v. 11, p.255–260, 1996.

DOHM, C.; LEAL, I.R.; MEYER, S.T.; TABARELLI, M.; WIRTH, R. Leaf-cutting ants proliferate in the Amazon: an expected response to forest edge? **Journal of Tropical Ecology,** v. 27, p. 645–649, 2011.

ELZINGA, J.A.; VAN NOUHUYS, S.; LEEUWEN, D.J.; BIERE, A. Distribution and colonization ability of three parasitoids and their herbivorous host in a fragmented landscape. **Basic and Applied Ecology,** v. 8, p.75-88, 2007.

ESPÍRITO SANTO, M.M.; FERNANDES, G.W. How many species of gall inducing insects are there on earth, and where are there? **Annals of Entomological Society of America**, v. 100, n. 2, p.95-99, 2007.

EWERS, R.M.; DIDHAM, R.K. Confounding factors in the detection of species responses to habitat fragmentation. **Biol. Rev,** 81, 117–142, 2006.

FAHRIG, L. Effects of Habitat Fragmentation on Biodiversity. **Annual Review Ecology Evolution and Systematics.** V.34, p. 487–515, 2003.

FAVERI, B. S.; VASCONCELOS, H. L.; DIRZO, R. Effects of Amazonian Forest Fragmentation on the interaction Between plants, Insect Herbivores, and their natural enemies. **Journal of Tropical Ecology,** v. 24, p. 57-64, 2008.

FERNANDES, G.W.; MARTINS, R.P. Tumores de plantas: as galhas. **Ciência Hoje**, v. 19, p. 58-64, 1985.

FERNANDES, G. W.; NETO, E. T.; MARTINS, R. P. Ocorrência e caracterização de galhas entomógenas na vegetação do campus Pampulha da Universidade Federal de Minas Gerais. **Revista Brasileira de Zoologia,** v. 5, p. 11-29, 1988.

FERNANDES, G.W. Hypersensitivity: a neglected plant resistance mechanism against insect herbivores. **Environmental Entomology**, v. 19, p. 1173-1182, 1990.

FERNANDES, G.W.; RIBEIRO, S.P. Plant response to Herbivory: two Examples from the Neotropics Respuesta de las Plantas a la Herbivoria. Dos Ejemplos Del Neotrópico. **Ecotropicos**, v. 3, n. 2, p. 77-86, 1990.

FERNANDES, G.W.; PRICE, P.W. The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. **Oecologia,** v. 90, p.14-20, 1992.

FERNANDES, G.W.; SOUZA, A.F.L.; SACCHI, C.F. Impact of a Neolasloptera (Diptera: Cecydomyiidae) Stem galler on this host plant *Mirabills linearis* (Nyctaginaceae). **Phytophaga,** v. 5, p. 1-6, 1993.

FERNANDES, G.W.; CORNELISSEN, T.G.; LARA, A.C.F.; ISAÍAS, R.M.S. Plant fight gall formation: hypersensitivity. **Ciência & Cultura,** v. 52, p. 49-54, 2000.

FERNANDES, G.W.; NEGREIROS, D. The occurrence and effectiveness of hypersensitive reaction against galling herbivores across host taxa. **Ecological Entomology,** v. 26, p. 46-55, 2001.

FERRAZ, G.; NICHOLS, J.D.; HINES, J.E.; STOUFFER, P.C.; BIERREGAARD JR., R.O.; LOVEJOY, T.E. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. **Science,** v. 315, p. 238–241, 2007.

FISCHER, J.; LINDENMAYER, D.B. Landscape modification and habitat fragmentation: a synthesis. **Global Ecology and Biogeography,** v.16, p. 265–280, 2007.

GAGNÉ, R.J. **The gall midges of the Neotropical Region**. University Press, Ithaca, xiv, 1994. 352p.

GALINDO-LEAL, C.; CÂMARA, I. G. Atlantic forest hotspots status: an overview. P. 3-11. In C. Galindo-Leal & I. G. Câmara (Eds.).**The AtlanticForest of South America: biodiversity status, threats, and outlook**. CABS & Island Press, 2003, Washington.

GIBBS, H.K.; REUSCH, A.S.; ACHARD, F.; CLAYTON, M.K.; HOLMGREN, P.; RAMANKUTTY, N.; FOLEY, J.A. Tropical forests were the primary sources of new agricultural lands in the 1980s and 1990s. **Proceedings of the National Academy of Science,** v. 107, p.16732–16737, 2010.

GIRÃO, L. C.; LOPES, A. V.; TABARELLI, M.; BRUNA, E. M. Changes in Tree Reproductive Traits Reduce Functional Diversity in a Fragmented AtlanticForest Landscape. **PLoS ONE,** v. *2*, n.e908, p. 1-12, 2007.

GOERCK, J.M. Patterns of rarity in the birds of the Atlantic Forest of Brazil. **Conservation Biology,** v. 11, p. 112–118, 1997.

HARPER, K. A.; MACDONALD, S. E.; BURTON, P. J.; CHEN, J.; BROSOFSKE, K. D.; SAUDERS, S. C.; EUSKIRCHEN, E. S.; ROBERTS, D.; JAITEH, M. S.; ESSEEN, P. Edge influence on forest structure and composition in fragmented landscapes. **Conservation Biology**, v. 19, p. 768–782, 2005.

HOLT, R.D.; LAWTON, J.H.; POLIS, G.; MARTINEZ, N.D. Trophic rank and the species–area relationship. **Ecology,** v. 80, p.1495–1504, 1999.

IBGE 1985. **Atlas Nacional do Brasil: Região Nordeste**. IBGE, Rio de Janeiro.

JULIÃO, G.R.; AMARAL, M.E.C.; FERNANDES, G.W.; OLIVEIRA, E.G. Edge effects and species area relationships in the gall forming insect fauna of natural forest patches in the Brazilian pantanal. **Biodiversity and Conservation**, v. 13, p. 2055-2066, 2004.

KAPOS, V. Effects of isolation on the water status of forest patches in the Brazilian Amazon. **Journal of Tropical Ecology**, v. 5, p. 173-185, 1989.

KAREIVA, P.; WENNERGREN, U. Connecting landscape pattern to ecosystem and population processes. **Nature,** v. 373, p. 299- 302, 1995.

KRAUSS, J.; STEFAN-DEWENTER, I.; TSCHARNTKE, T. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. **Oecologia,** v. 137, p. 591-602, 2003.

KRUESS, A. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. **Ecography**, v. 26, p. 283-290, 2003.

KRUESS, A.; TSCHARNTKE, T. Habitat fragmentation, species loss, and biological control. **Science,** v. 264, p. 1581-1584, 1994.

KRUESS, A.; TSCHARNTKE, T. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Viciasepium*. **Oecologia,** v. 122, p. 129–137, 2000.

LARA, A.C.F.; FERNANDES, G.W. The highest diversity of galling insects: Serra doCipó, Brazil. **Biodiversity Letters**, v. 3, p.111-114, 1996.

LAURANCE, W.F.; LAURANCE, S.G.; FERREIRA, L.; RANKIN-DE MERONA, J.; GASCON, C.; LOVEJOY, T.E. Biomass collapse in Amazonian forest fragments. **Science,** v. 278, p. 1117–1118, 1997.

LAURANCE, W.F.; LOVEJOY, T.E.; VASCONCELOS, H.L.; BRUNA, E.M.; DIDHAM, R.K.; STOUFFER, P.C.; GASCON, C.; BIERREGAARD, R.O.; LAURANCE, S.G.; SAMPAIO, E. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. **Conservation Biology**, v.16, p. 605-618, 2002.

LAURANCE, W.F.; NASCIMENTO, H.E.M.; LAURANCE, S.G.; ANDRADE, A.; RIBEIRO, J.E.L.S.; GIRALDO, J.P.; LOVEJOY, T.E.; CONDIT, R.; CHAVE, J.; HARMS, K.E.; D'ANGELO, S. Rapid decay of tree-community composition in Amazonian forest fragments. **Proceedings of the National Academy of Science**, v. 103, p. 19010-19014, 2006.

LAURANCE, W.F. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. **Biological Conservation,** v. 141, p. 1731-1744, 2008.

LAURANCE, W.F.; CAMARGO, J.L.C.; LUIZÃO, R.C.C.; LAURANCE, S.G.; PIMM, S.L.; BRUNA, E.M.; STOUFFER, P.C.; WILLIAMSOM, G.B.; BENÍTEZ-MALVIDO, J.; VASCONCELOS, H.L.; VAN HOUTAN, K.S.; ZARTMAN, C.E.; BOYLE, S.A.; DIDHAM, R.K.; ANDRADE, A.; LOVEJOY, T. The fate of Amazonian forest fragments: a 32-year investigation. **Biological Conservation,** v. 144, p. 56–67, 2011.

LEAL, I.R.; WIRTH, R.; TABARELLI, M. Formigas cortadeiras e a ambigüidade de suas relações com as plantas. pp. 87-94. In K. Del-Claro and H.M. Torezan-Silingardi (Eds), **Ecologia das interações plantas-animais**. 2012, Technical Books Editora, Rio de Janeiro, Brasil.

MELO, F. P.L.; LEMIRE, D.; TABARELLI, M. Extirpation of large-seeded seedling from the edge of a large Brazilian Atlantic Forest fragment. **Ecoscience,** v. 14, p. 124-129, 2007.

MENDONÇA, M.S. Galling insect diversity patterns: the resource synchronization hypothesis. **Oikos**, v. 95, p.171-176, 2001.

MCCREA, K.D; ABRAHAMSON, W.G; WEIS, A.E. Goldenrod ball gall effects of *Solidago altissima*: 14C translocation and growth. **Ecology,** v. 66, p. 1902-1907, 1985.

MITTERMEIER, R.A.; MYERS, N.; ROBLES GIL, P.; MITTERMEIER, C.C. **Hotspots**. 1999. Agrupación Sierra Madre, CEMEX, Mexio City.

MYERS, N.; MITTERMEIER, R.A.; MITTERMEIER, C.G.; FONSECA, G.A.B.; KENT, J. Biodiversity hotspots for conservation priorities. **Nature,** v. 403, p. 853-858, 2000.

MURCIA, C. Edge effect in fragmented forest: implications for conservation. **Trends in Ecology and Evolution,** v. 10, n. 2, p. 58-62, 1995.

OLIVEIRA, M.A.; GRILLO, A. S.; TABARELLI, M. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. **Oryx**, v. 38, n. 4, p. 389- 394, 2004.

OLIVEIRA, M.A.; SANTOS, A.M.M.; TABARELLI, M. Profound impoverishment of the large-tree stand in a hyper-fragmented landscape of the Atlantic forest. **Forest Ecology and Management**, v. 256, p. 1910–1917, 2008.

OLIVEIRA, J.C. **Estudo das interações ecológicas dentro de um sistema trófico envolvendo galhas induzidas por *Lopesia brasiliensis* (Díptera, Cecidomyiidae) em *Ossaeacon fertiflora* (Melastomataceae) e seus parasitóides associados**. Dissertação de Mestrado. 1999, Universidade Federal do Rio de Janeiro, Rio de Janeiro.

OYAMA, K.; PEREZ-PEREZ, M.A.; CUEVAS-REYES, P.; LUNA-REYES, R. Regional and local species richness of gall-inducing insects in two tropical rain forest in Mexico. **Journal of Tropical Ecology,** v. 19, p. 595-598, 2003.

PASCUAL-ALVARADO, E.; CUEVAS-REYES, P.; QUESADA, M.; OYAMA, K. Interactions between galling insects and leaf-feeding insects: the role of plant phenolic compounds and their possible interference with herbivores. **Journal of Tropical Ecology,** v. 24, p. 329-336, 2008.

PRANCE, G.T. **Forest refuges: evidences from woody angiosperms**. In: Biological diversification in the tropics (Prance, G.T. eds). Claredon Press, Oxford. 1982. P. 175-196.

PRICE, P.W.; FERNANDES, G.W.; LARA, A.C.F.; BRAWN, J.; BARRIOS, H.; WRIGHT, M.G.; RIBEIRO, S.P.; ROTHCLIFF, N. Global patterns in local number of insect galling species. **Journal of Biogeography,** v. 25, p. 581–591, 1998.

RAMAN, A.; SCHAEFER, C.W.; WITHERS, T.M. **Biology, Ecology and Evolution of gall inducing arthropods**. Vol 2. Science Publishers. 2005. New Hampshire, 817 pp.

RIBEIRO, M.C.; METZGER, J. P.; MARTENSEN, A.C.; PONZONI, F.J.; HIROTA, M.M. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implication for conservation. **Biological Conservation,** v. 142, p. 1141–1153, 2009.

RIBEIRO, K.T.; MADEIRA, J.A.; MONTEIRO, R.F. Does Flooding favour galling insects? **Ecological Entomology,** v. 23, p. 491-494, 1998.

RIES, L.; FLETCHER R. J.; BATTIN J.; SISK, T. D. Ecological Responses to Habitat Edges: Mechanismes, Models, and Variability explained. **Annual Review in Ecology, Evolution and Systematics,** v. 35, p. 491-522, 2004.

SANTOS, B.A.; PERES, C.A.; OLIVEIRA, M.A.; GRILLO, A.; ALVES-COSTA, C.P.; TABARELLI, M. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. **Biological Conservation,** v. 141, p. 249-260, 2008.

SANTOS, J.C.; CARNEIRO, M.A.A.; FERNANDES, G.W. Insetos galhadores neotropicais: diversidade e ecologia evolutiva dos herbívoros mais sofisticados da natureza. pp. 183-

199. In K. Del-Claro and H.M. Torezan-Silingardi (Eds), **Ecologia das interações plantas-animais.** 2012, Technical Books Editora, Rio de Janeiro, Brasil.

SILVA, J.M.C.; TABARELLI, M. Tree species impoverishment and the future of the Atlantic forest of northeast Brazil. **Nature,** v. 404, p. 72-74, 2000.

STOTZ, D.F.; FITZPATRICK, J.W.; PARKER, T.A.; MOSKOVITZ, D.K. **Neotropical Birds: Ecology and Conservation.** Univ. Chicago Press, Chicago, 1996.

TABARELLI, M.; MANTOVANI, W.; PERES, C. A. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. **Biological Conservation**, v. 91, p. 119-127, 1999.

TABARELLI, M.; PERES, C. A. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest fragmentation. **Biological Conservation,** v. 1061, p. 165-176, 2002.

TABARELLI, M.; MANTOVANI, W.; PERES, C.A. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic Forest: implication for Forest regeneration. **Biological Conservation**, v. 91, p. 119-127, 2003.

TABARELLI, M.; GASCON, C. Lessons from fragmentation Research: Improving Management and Policy Guidelines for biodiversity Conservation. **Conservation Biology,** v. 19, p.734-739, 2005.

TABARELLI, M.; AGUIAR, A.V.; GIRÃO, L.C.; PERES, C.; LOPES, A.V. Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. **Conservation Biology,** v. 24, p. 1654-1663, 2010.

TABARELLI, M.; PERES, C.A.; MELO, F.P.L. The “few winners and many losers” paradigm revisited: emerging prospects for tropical forest biodiversity. **Biological Conservation**, v. 155, p. 136-140, 2012.

TERBORGH, J.; WINTER, B. Some causes of extinction. *In*: **Conservation biology: an evolutionary - ecological perspective.** Soulé, M. & Wilcox, B. (eds.). pp 119-133. Sunderland, MA. Sinauer Associations, 1980.

TERBORGH, J.; LOPEZ, L.; NUNEZ V.P.; RAO, M.; SHAHABUDDIN, G.; ORIHUELA, G.; RIVEROS, M.; ASCANIO, R.; ADLER, G.H.; LAMBERT, T.D.; BALBAS, L. Ecological Meltdown in Predator-free forest fragments. **Science,** v. 294, p. 1923- 1925, 2001.

THIES C.; TSCHARNTKE T. Landscape structure and biological control in agroecosystems. **Science,** v. 285, p. 93-95, 1999.

THIES, C.; STEFFAN-DEWENTER, I.; TSCHARNTKE, T. Effects of landscape context on herbivory and parasitism at different spatial scales. **Oikos,** v. 101, p. 18-25, 2003.

THIES, C.; STEFFAN-DEWENTER, I.; TSCHARNTKE, T. Interannual landscape changes influence plant–herbivore–parasitoid interactions. **Agriculture, Ecosystems and Environment,** v. 125, p. 266-268, 2008.

TSCHARNTKE, T.; STEFFAN-DEWENTER, I.; KRUESS, A.; THIES C. Characteristics of insect populations on habitat fragments: A mini review**. Ecological Research**, v. 17, n. 2, p. 229-239, 2002.

TSCHARNTKE, T.; BRANDL, R. Plant-Insect Interactions in Fragmented Landscapes. **Annual Review Entomology,** v. 49, p. 405-430, 2004.

URBAS, P.; ARAÚJO JÚNIOR, M.V.; LEAL, I. R.; WIRTH, R. Cutting more from cut forests - edge effects on foraging and herbivory of leaf-cutting ants. **Biotropica,** v. 39, p. 489-495, 2007.

VALLADARES, G.; SALVO, A.; CAGNOLO, L. Habitat Fragmentation Effects on Trophic Processes of Insect–plant Food Webs. **Conservation Biology**, v. 20, p. 212-217, 2006.

VELOSO, H.P.; RANGEL-FILHO, A.L.L.; LIMA, J.C.A. **Classificação da vegetação brasileira, adaptada a um sistema universal**. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, Brazil, 1991.

WARING, G.L.; PRICE, P.W. Plant water stress and gall formation (Cecidomyiidae: Asphondylia spp) on creosote bush. **Ecological Entomology,** v. 15, p. 87-95, 1990.

WILCOX, B.; MURPHY, D.D. Conservation strategy: the effects of fragmentation on extinction. **American Naturalist,** v. 25, p. 879-887, 1985.

WILCOVE, D.S.; MCLELLAN, C.H.; DOBSON, A.P. Habitat fragmentation in the temperate zone. In **Conservation Biology**, ed. ME Soulé, Sunderland, MA: Sinauer, pp.237-56, 1986.

WIRTH, R.; MEYER, S.T.; ALMEIDA, W.R.; ARAÚJO-JR, M.V.; BARBOSA, V.S.; LEAL, I.R. Living on the edge: drastic increase of leaf-cutting ant (*Atta* spp.) densities at the edge of a Brazilian Atlantic Forest remnant. **Journal of Tropical Ecology,** v. 23, p. 501-505, 2007.

WIRTH, R.; MEYER, S.T.; LEAL, I.R.; TABARELLI, M. Plant–Herbivore Interactions at the Forest Edge. **Progress in Botany,** v. 68, p. 423–448, 2008.

WOODMAN, R.L.; FERNANDES, G.W. Differential mechanical defense: herbivory, evapotranspiration, and leaf-hairs. **Oikos**, v. 60, p. 11-19, 1991.

ZABEL, J.; TSCHARNTKE, T. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? **Oecologia,** v. 116, p. 419-425, 1998.

ZARTMAN, C.E. Forest fragmentation effects on epiphyllous bryophyte communities in central Amazonia. **Ecology,** v. 84, p. 948-954, 2003.

ZEIPEL, H.V.; ERIKSSON, O.; EHRLÉN, J. Host plant population size determines cascading effects in a plant–herbivore–parasitoid system**. Basic and Applied Ecology,** v. 7, p. 191-200, 2006.