UNIVERSIDADE FEDERAL DE PERNAMBUCO

DOUGLAS HENRIQUE ALVES DE MELO

EFEITO DE PERTURBAÇÕES ANTRÓPICAS E ARIDEZ SOBRE A COMUNIDADE DE BORBOLETAS FRUGÍVORAS NA CAATINGA

RECIFE
2021

UNIVERSIDADE FEDERAL DE PERNAMBUCO

DOUGLAS HENRIQUE ALVES DE MELO

EFEITO DE PERTURBAÇÕES ANTRÓPICAS E ARIDEZ SOBRE A COMUNIDADE DE BORBOLETAS FRUGÍVORAS NA CAATINGA

Tese apresentada ao Programa de Pós-graduação em Biologia Animal da Universidade Federal de Pernambuco, Centro de Ciências Biológicas, como requisito para obtenção do título de Doutor em Biologia Animal.

Orientadora: Inara Roberta Leal
Coorientador: Bruno K. Cordeiro Filgueiras

RECIFE
2021

Catalogação na fonte
Bibliotecária Claudina Queiroz, CRB4/1752

Melo, Douglas Henrique Alves de
Efeito de perturbações antrópicas e aridez sobre a comunidade de borboletas frugívoras na Caatinga / Douglas Henrique Alves de Melo - 2021.
146 folhas: il., fig., tab.

Orientadora: Inara Roberta Leal
Coorientador: Bruno K. Cordeiro Filgueiras
Tese (doutorado) – Universidade Federal de Pernambuco, Centro de Biociências. Programa de Pós-Graduação em Biologia Animal. Recife, 2021.

Inclui referências.

1. Nymphalidae 2. Perturbação antrópica 3. Indicadores ecológicos I. Leal, Inara Roberta (orientadora) II. Filgueiras, Bruno K. Cordeiro (coorientador) Título

583.95 CDD (22.ed.) UFPE/CB-2021- 224

DOUGLAS HENRIQUE ALVES DE MELO

EFEITO DE PERTURBAÇÕES ANTRÓPICAS E ARIDEZ SOBRE A COMUNIDADE DE BORBOLETAS FRUGÍVORAS NA CAATINGA

Tese apresentada ao Programa de Pós-graduação em Biologia Animal da Universidade Federal de Pernambuco, Centro de Ciências Biológicas, como requisito para obtenção do título de Doutor em Biologia Animal.

Área de concentração: Biologia Animal

Aprovada em: 27/05/2021

BANCA EXAMINADORA

Dr. Simão Dias Vasconcelos
Universidade Federal de Pernambuco
(Avaliador Interno)

Dr. Cristiano Agra Iserhard
Universidade Federal de Pelotas
(Avaliador Externo)

Dr. Jessie Pereira dos Santos
Universidade Estadual de Campinas
(Avaliador Externo)

Dra. Fernanda M. Pereira de Oliveira
Universidade Federal de Pernambuco
(Avaliador Externo)

Dr. Márcio Zikán Cardoso
Universidade Federal do Rio Grande do Norte
(Avaliador Externo)

Dr. Artur Campos Dália Maia
Universidade Federal de Pernambuco
(Suplente Interno)

Dra. Ariadna V. Freitas e Lopes
Universidade Federal de Pernambuco
(Suplente Externo)

Aos meus pais,
com muito amor e gratidão,
Dedico.

AGRADECIMENTOS

Chega ao fim mais uma etapa importante na minha vida. A quem sou grato por isso? Com certeza a muitas pessoas que ao longo dessa jornada contribuíram com conhecimento, orientações ou simplesmente com suas amizades. Sem dúvida, vocês fazem parte dessa história. Vocês me ajudaram a amadurecer como pessoa e como profissional. Gratidão!

A Deus pela vida e por ser a fonte de toda sabedoria.

A minha família, especialmente aos meus pais (Gabriel e Solange) e ao meu irmão (David). Vocês são os meus melhores amigos. Obrigado por todos esses anos de dedicação e apoio. Amo vocês!

A minha esposa Michele pelo companheirismo, pelo otimismo mesmo nos momentos difíceis e por sempre acreditar na minha capacidade. Você foi fundamental para a conclusão dessa etapa.

À professora Inara Leal por aceitar me orientar no mestrado e agora no doutorado. Obrigado pela dedicação, pelos ensinamentos e pela paciência. Foi um prazer desenvolver projetos com uma profissional competente como você.

Ao meu amigo Bruno Filgueiras pela coorientação desse projeto. Sou grato por toda orientação e ideias trocadas. Sua ajuda foi fundamental! Além da sua contribuição intelectual, és um grande parceiro de campo. Passamos por ótimos momentos em Serra Grande e agora no Catimbau. Você é fera!

Ao professor André Victor Lucci Freitas (Unicamp). Puxa! Sem palavras para expressar o quanto você foi importante na minha jornada até aqui. Abriu as portas para mim ainda na graduação, onde tive o prazer de conhecer pessoas incríveis e de aprofundar meu conhecimento com borboletas. Poderia falar muito aqui, mas só agradeço e parabenizo pelo excelente profissional que és, pois mesmo distante estás sempre pronto para ajudar. Muito obrigado! Que esta pareceria dure por muito tempo.

Ao professor Marcelo Tabarelli pelos debates relacionados a esta pesquisa e por sua importante contribuição nas revisões dos artigos. Sem dúvida, só tive profissional fera ao meu lado. Sem a colaboração de vocês eu não teria alcançado o mesmo êxito!

A CAPES pela bolsa concedida.

Ao PPGBA pela oportunidade de realizar esta pesquisa e toda esquipe de professores que direta ou indiretamente auxiliaram para a melhoria deste projeto. Em especial, agradeço aos professores Artur Maia e Simão Vasconcelos por me acompanhar ao longo das apresentações semestrais, contribuindo com a revisão crítica desta pesquisa e adicionando conteúdo intelectual.

Aos membros da banca de defesa pelas sugestões e revisão crítica de toda a tese.

Aos colegas do LIPA por partilharmos bons momentos de descontração e conhecimento. Obrigado pelo convívio agradável, seja no laboratório, nas confraternizações ou mesmo nas atividades de campo.

Àqueles que se disponibilizaram em me ajudar algumas vezes em campo: Bruno Filgueiras (amigo e coorientador), Michele (esposa presente em todos os momentos), Stien (amigo de longas datas), Cadu (amigo, parceiro de diversos campos e borboleteiro), Isabelle e Ronald (colegas de laboratório) e Myllena e Rafaela (Graduação). Vocês tornaram o campo muito menos cansativo e, além de tudo, agradável e divertido.

Aos amigos e colegas de diversos laboratórios que durantes os 12 meses de campo pude conviver e conhecer no alojamento do Catimbau. Foram ótimas conversas, risadas e conhecimentos trocados. Com vocês eu passei datas importantes, como aniversário e Natal, que jamais esquecerei. Obrigado por partilharmos momentos inesquecíveis.

Cabe ainda agradecer a alguns habitantes do Catimbau que permitiram a realização desta pesquisa em suas respectivas terras.

Por fim, agradeço a todos que de alguma maneira contribuíram para a realização deste projeto ou que simplesmente ficaram na torcida para que este dia chegasse.

"Graças te dou, Criador e Deus, pois tu me concedeste esta alegria
em tua criação e me alegro com as obras de tuas mãos. Vê, pois,
que completei o trabalho para o qual fui chamado. Nele, usei
todos os talentos que tu concedeste ao meu espírito"

Johannes Kepler

RESUMO

Mudanças no uso da terra (i.e. perturbações agudas), remoção de porções de biomassa nas áreas remanescentes dos ecossistemas naturais (i.e. perturbações crônicas) e mudanças climáticas são as principais causas da perda de biodiversidade em todo o globo. Essas perturbações antrópicas causam alterações nas características naturais do ambiente e criam filtros ambientais que atuam reorganizando e homogeneizando as comunidades ecológicas, com perdas de espécies especialistas e proliferação de generalistas (i.e. substituição de perdedores por vencedores). O uso de indicadores ecológicos torna-se viável para monitorar as respostas de diversos grupos biológicos às mudanças nas paisagens naturais devido às perturbações antrópicas e para a seleção de áreas prioritárias para conservação. Nesta tese, examinei (1) como as comunidades de borboletas frugívoras, um dos principais indicadores ecológicos, são afetadas taxonômica e funcionalmente por distúrbios antrópicos crônicos e aumento de aridez em áreas de Caatinga e (2) como se dá a recuperação, também taxonômica e funcional, dessas comunidades ao longo do processo de sucessão secundária em áreas previamente usadas como agricultura de corte e queima, uma das principais perturbações humanas na Caatinga. Adicionalmente, foi examinado o papel que distúrbios crônicos, riqueza de espécies de árvores e biomassa desempenham na recuperação desses insetos durante a regeneração da floresta. No primeiro capítulo da tese verifiquei que aumentos nos distúrbios crônicos e, principalmente, na aridez alteraram os padrões de distribuição de borboletas frugívoras e simplificaram as comunidades taxonômica e funcionalmente. No segundo capítulo, observei que borboletas frugívoras podem se recuperar rapidamente em termos taxonômicos ao longo da trajetória sucessional na Caatinga, mas fatores como riqueza de árvores e distúrbios crônicos afetaram significativamente os atributos taxonômicos e funcionais de borboletas frugívoras. Estes resultados sugerem que a as mudanças ambientais provocadas pelo aumento da aridez e pela intensa exploração de recursos naturais resultam em comunidades de borboletas frugívoras empobrecidas e homogeneizadas em dimensões taxonômicas e funcionais. Embora as florestas primárias continuem sendo vitais para a manutenção da biodiversidade, o resultado desta tese indica que alguns grupos de organismos podem se recuperar destas perturbações agudas e crônicas, sugerindo que florestas secundárias também têm um papel importante para a conservação da biodiversidade e de funções e serviços ecossistêmicos em paisagens modificadas pelo homem, a menos que os distúrbios crônicos permaneçam constantes nesses habitats.

Palavras-chave: conservação; florestas tropicais secas; indicadores ecológicos; Nymphalidae; perturbação antrópica; sucessão secundária

ABSTRACT

Changes in land use (i.e. acute disturbance), removal of a small portion of biomass in remaining areas of natural ecosystems (i.e. chronic disturbance), and climate change are the most important drivers of biodiversity decline worldwide. These anthropogenic disturbances change the structure of natural habitats and create environmental filters reorganizing and homogenizing ecological communities, with losses of specialist species and proliferation of generalists (i.e. winner-loser replacement). The use of ecological indicators becomes feasible to monitor the response of different biological groups to changes in natural landscapes due to anthropogenic disturbances and for the selection of priority areas for conservation. In this thesis, I examined (1) how fruit-feeding butterfly assemblages, one of the main ecological indicators, are affected taxonomically and functionally by increased chronic disturbances and aridity in Caatinga dry forest and (2) how these butterflies recover their taxonomic and functional composition during the secondary succession process after slash and burn agriculture, one of the most common human activities in the Caatinga. Additionally, the role that chronic disturbances, tree species richness, and biomass can play in the recovery of these insects during forest regeneration was examined. In the first chapter of the thesis, I found that increased chronic disturbances and mainly aridity changed the distribution patterns of fruit-feeding butterflies, simplifying the taxonomic and functional community properties. In the second chapter, I observed that fruit-feeding butterflies can recover quickly in terms of taxonomic along the successional trajectory in the Caatinga, but factors such as tree species richness and chronic disturbances significantly affected the taxonomic and functional attributes of fruit-feeding butterflies. These results suggest that the environmental changes promoted by increasing aridity and intense exploitation of natural resources lead to impoverished and homogenized butterfly communities in taxonomic and functional dimensions. Although primary forests remain vital for the maintenance of biodiversity, the results of the thesis indicate that some groups of butterflies can recover from acute and chronic disturbances, suggesting that secondary forests also play an important role in the conservation of biodiversity and ecosystem services in human-modified landscapes, unless chronic disturbances remain constant in these habitats.

Keyword: anthropogenic disturbance; conservation; ecological indicators; Nymphalidae; seasonally dry tropical forests; secondary succession

LISTA DE FIGURAS

ARTIGO 1 – Aridity and chronic anthropogenic disturbance as organizing forces of fruit-feeding butterfly assemblages in a Caatinga dry forest

LISTA DE FIGURAS

ARTIGO 2 – Rapid recovery of fruit-feeding butterfly assemblages in the regeneration of a Caatinga dry forest submitted to shifting cultivation

LISTA DE TABELAS

ARTIGO 1 – Aridity and chronic anthropogenic disturbance as organizing forces of fruit-feeding butterfly assemblages in a Caatinga dry forest

LISTA DE TABELAS

ARTIGO 2 – Rapid recovery of fruit-feeding butterfly assemblages in the regeneration of a Caatinga dry forest submitted to shifting cultivation

SUMÁRIO

1 INTRODUÇÃO

Na medida em que as pressões decorrentes das atividades humanas continuam a ameaçar os ecossistemas naturais, ecólogos e biólogos da conservação têm alertado cada vez mais sobre os efeitos destrutivos das perturbações antrópicas à biodiversidade global. Embora não sejam as únicas forças que atuam modificando os sistemas naturais, sabe-se que, aliados às mudanças climáticas, os distúrbios antrópicos são os principais fatores responsáveis pela perda e homogeneização da biodiversidade no mundo (SALA *et al*., 2000; FAUSET *et al*., 2012; PÜTTKER *et al*., 2020). Apesar da sua grande extensão em regiões tropicais, as florestas secas também estão entre os ecossistemas mais ameaçados por conta das interferências humanas (OATHAM & BOODRAM, 2006). A Caatinga, por exemplo, tem sido exposta às perturbações antrópicas desde a chegada dos Europeus no século XVI (COIMBRA-FILHO & CÂMARA, 1996), pois o meio de subsistência dos que habitam essa região é fortemente dependente do uso de recursos naturais extraídos da floresta, em um típico regime de perturbação antrópica crônica (ou seja, remoção contínua de pequenas porções de biomassa florestal) (SILVA *et al*., 2017; SOUZA *et al*., 2019). Em virtude disso, por muito tempo a Caatinga foi considerada um ecossistema pobre em espécies e endemismo, o que afastou estudos e investimentos conservacionistas para a região e todos os processos que ameaçam a sua biodiversidade foram negligenciados (LEAL *et al*., 2005).

Dada à velocidade com que as florestas tropicais são convertidas em áreas devotadas a atividades humanas e diante da importância de selecionar áreas prioritárias para conservação, é imprescindível entender quais são (e como atuam) os agentes modificadores da biota, além de compreender como áreas abandonadas após o uso antrópico se recompõem ao longo da trajetória sucessional. Contudo, perante essas constantes pressões sobre a biota, apenas a inspeção adequada de organismos, incluindo borboletas (de suas populações ou comunidades), pode fornecer informações valiosas na definição de áreas prioritárias para a conservação antes que tais efeitos sejam irreversíveis. Por uma série de motivos, as borboletas podem fornecer, de maneira rápida e eficiente, um diagnóstico sobre a integridade das paisagens naturais, auxiliando, embasando com informações relevantes a criação de reservas naturais (FREITAS *et al*., 2014, DeVRIES *et al*., 2016). Em florestas tropicais úmidas, vários estudos têm apontado para a sensibilidade desses insetos a condições microclimáticas (RIBEIRO & FREITAS, 2010; CHECA *et al*., 2014) e a alterações no habitat de natureza aguda (por exemplo, perda e fragmentação de habitats, efeito de borda e presença de trilhas) (UEHARA-PRADO *et al*., 2007; RIBEIRO *et al*., 2012, SANT'ANNA *et al*., 2014; FILGUEIRAS *et al*., 2016; MELO *et* *al*., 2019; GUERATTO *et al*., 2020). No entanto, pouco se sabe sobre a resposta desses organismos a perturbações antrópicas crônicas (por exemplo, exploração de produtos florestais madeireiros e não madeireiros, sobrepastoreio de animais domésticos e caça) e fatores abióticos como o aumento de aridez previsto para várias florestas tropicais secas do Globo (MAGRIN *et al*., 2014).

Nesse contexto, torna-se urgente e fundamental saber se (e como) o aumento da aridez e das perturbações antrópicas crônicas exerce pressão sobre as comunidades de borboletas frugívoras e entender como estes insetos se recuperam ao longo do processo de sucessão secundária na Caatinga. Sendo assim, esta tese está estruturada em dois capítulos: no primeiro, *Aridity and chronic anthropogenic disturbance as organizing forces of fruit-feeding butterfly assemblages in a Caatinga dry forest*, investiguei como perturbações antrópicas crônicas e aridez (preditor de mudanças climáticas) influenciam os atributos taxonômicos e funcionais das comunidades de borboletas frugívoras na Caatinga. No segundo, *Rapid recovery of fruit-feeding butterfly assemblages in the regeneration of a Caatinga dry forest submitted to shifting cultivation*, avaliei como se dá a recuperação taxonômica e funcional das comunidades de borboletas frugívoras ao longo de um gradiente de regeneração na Caatinga. Estudos como este, que buscam compreender como a biodiversidade responde a mudança no habitat, podem fornecer subsídios contundentes para a conservação das espécies e suas respectivas funções ecológicas, além de propor diretrizes para manejo de áreas protegidas.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 Distúrbios antrópicos e mudanças climáticas: efeitos sobre a biota

A rápida expansão da população humana e o uso crescente dos recursos naturais continuam ocorrendo em taxas alarmantes, particularmente transformando os habitats naturais em paisagens antrópicas (SALA *et al.*, 2000; LAURANCE *et al.*, 2014). Essas paisagens agora cobrem grandes áreas na maioria das biotas terrestres, existindo poucas florestas verdadeiramente pristinas (LAURANCE *et al.*, 2014). De fato, é estimado que cerca de 70% das áreas florestadas em todo o mundo já foram modificadas por atividades humanas (FAO, 2010). Sem dúvida, as recorrentes pressões humanas representam uma ameaça significativa às paisagens naturais e o fator determinante para o declínio e reorganização da biodiversidade global (SALA *et al.*, 2000; TABARELLI *et al.*, 2010; FAUSET *et al.*, 2012; PÜTTKER *et al.*, 2020).

Entre os tipos de perturbações antrópicas conhecidas, as mudanças no uso da terra são as mais evidentes e foram mais estudadas e divulgadas. Esse tipo de perturbação ocorre com frequência na escala da paisagem, havendo uma completa descaracterização do habitat original por meio de corte raso da vegetação, por isso é chamada de aguda, resultando principalmente em perda e fragmentação de habitats (SINGH, 1998). Embora a perda de espécies seja o principal efeito destrutivo desse distúrbio, as consequências são bem mais amplas e pervasivas. As perturbações agudas alteram fatores abióticos, tais como temperatura, umidade, intensidade luminosa e disponibilidade de nutrientes do solo dentro dos fragmentos de vegetação remanescentes (SANTOS *et al.*, 2009; DANTAS DE PAULA *et al.*, 2011). Em decorrência disso, os padrões de organização biológica podem ser completamente alterados: 1) substituindo espécies especialistas por espécies adaptadas às novas condições do ambiente (SANTOS *et al.*, 2008; TABARELLI *et al.*, 2010; DOHM *et al.*, 2011; LEAL *et al.*, 2012), 2) alterando atributos taxonômicos, funcionais e filogenéticos das comunidades biológicas (OLIVEIRA *et al.*, 2004; TABARELLI *et al.*, 2008; SANTOS *et al.*, 2010; FILGUEIRAS *et al.*, 2011; LEAL *et al.*, 2012; MELO *et al.*, 2019) e 3) simplificando e homogeneizando a biota (ARROYO-RODRÍGUEZ & MANDUJANO, 2006; TABARELLI *et al.*, 2008; LÔBO *et al.*, 2011). De fato, as perturbações agudas são relatadas na literatura como as maiores ameaças atuais que influenciam a persistência da biodiversidade em todo o planeta (CORLETT, 2000; TABARELLI *et al.*, 2004).

Embora os efeitos dos distúrbios agudos na biodiversidade sejam bastantes difundidos, as florestas primárias e os remanescentes florestais secundários também estão sujeitos aos distúrbios antrópicos crônicos, os quais também possuem efeitos negativos sobre a biota (LAURANCE & PERES, 2006). Esses distúrbios ocorrem dentro das florestas, por meio da remoção contínua de pequenas porções de biomassa, sem causar perda e fragmentação de habitats (SINGH, 1998; MARTORELL & PETERS, 2005). Pode-se citar como atividades típicas de perturbações crônicas: a extração seletiva de madeira, as coletas de produtos florestais não madeireiros, a criação extensiva de animais domésticos e a caça, gerando um mosaico de áreas com diferentes intensidades de perturbação (MARTORELL & PETERS, 2005, MAY-TOBIN, 2011). Diferentemente da perda e fragmentação de habitat, as perturbações antrópicas crônicas não causam uma completa descaracterização da vegetação. Na verdade, esses distúrbios operam em pequenas escalas e em baixa intensidade, dando a falsa impressão de que o ecossistema não está sendo impactado, mas o impacto das perturbações crônicas pode ser, também, deletério à biota (MARTORELL & PETERS, 2009).

Os impactos ecológicos resultantes do distúrbio crônico são menos evidentes que os dos agudos, mas a remoção contínua da biomassa florestal pode resultar em hábitats florestais mais abertos, com microclima mais quente e seco (HARDWICK *et al*., 2015; SILVA *et al*., 2019), além de levar ao declínio de espécies mais usadas pelos humanos ou mais sensíveis aos ambientes mais abertos, afetando a estrutura das comunidades ecológicas (LAURANCE & PERES, 2006). Estudos mostram que as perturbações antrópicas crônicas exercem forte pressão sobre a estrutura demográfica de plantas, favorecendo espécies adaptadas a distúrbios em detrimento de espécies sensíveis à perturbação (RIBEIRO *et al*., 2015, 2016). Também já foi observado perda de diversidade taxonômica, filogenética e funcional de plantas e animais e aumento na similaridade da biota, indicando homogeneização das comunidades (RIBEIRO-NETO *et al*., 2016; OLIVEIRA *et al*., 2017; RITO *et al*., 2017, VÁZQUEZ-REYES *et al*., 2017; ARNAN *et al*., 2018). Por fim, existem estudos demonstrando, também, que perturbações antrópicas crônicas podem reduzir os serviços providos pelas formigas às plantas, tais como a dispersão de sementes (LEAL *et al*., 2014; OLIVEIRA *et al*., 2019) e proteção anti-herbivoria (LEAL *et al*., 2015; OLIVEIRA *et al*., 2020).

Ainda que a mudança no uso da terra continue sendo o principal fator contribuindo para a extinção de espécies e perda de habitat (HOFFMANN *et al*., 2010), ela não é a única pressão que atua sobre os sistemas naturais. Projeta-se que as mudanças climáticas se tornem igualmente ou mais importantes nas próximas décadas (JETZ *et al*., 2007; PEREIRA *et al*., 2010). O IPCC (2014) prevê que a superfície terrestre enfrentará um aumento na temperatura média global na ordem de 4.8º C até 2100, o que está intimamente associado às mudanças no regime de precipitação e sua compreensão e influência é vital para projetar mudanças em muitos sistemas naturais (KNAPP *et al*., 2008). Além disso, existe ainda uma preocupação crescente de que as mudanças climáticas intensifiquem os efeitos das perturbações antrópicas, tornando-se um filtro ambiental adicional em áreas perturbadas (HIROTA *et al*., 2011; RITO *et al*., 2017).

Pesquisas de diversos campos de conhecimento revelam que em alguns períodos e regiões as mudanças climáticas passadas eram tão grandes e rápidas quanto às projetadas para o futuro (JACKSON & OVERPECK, 2000; HARRISON & SANCHES GOÑI, 2010). Atualmente, diversos estudos já têm documentado uma variedade de impactos biológicos atribuíveis às mudanças climáticas, tais como: mudanças morfológicas, comportamentais, fenológicas e de distribuição de espécies, além de outros atributos da comunidade (EASTERLING *et al*., 2000; MCMENAMIN *et al*., 2008; PHILLIPS *et al*., 2008; CLARK *et al*., 2016; FADRIQUE *et al*., 2018). Esse fenômeno também é responsável por várias alterações nos ecossistemas naturais (SALAZAR *et al*., 2007; HOEGH-GULDBERG *et al*., 2007; OHLEMULLER *et al*., 2008) e pelo seu papel facilitador da propagação e estabelecimento de espécies invasoras (HELLMANN *et al*., 2008). Por fim, também há uma preocupação crescente de que as mudanças climáticas afetem diversas interações ecológicas essenciais para a manutenção da vida (BERTIN, 2008). Por exemplo, evidências sugerem que incompatibilidades nas respostas fenológicas às mudanças climáticas entre plantas e polinizadores podem afetar significativamente esses parceiros mutualísticos, o que pode levar a dissociação das interações entre flores e polinizadores (GORDO & SANZ, 2005).

2.2 Regeneração florestal e resiliência

Com o avanço das mudanças no uso da terra, vastas extensões de florestas primárias acabam convertidas em campos abandonados, onde as florestas secundárias tornam a crescer e podem contribuir para a persistência da biodiversidade florestal (CHAZDON, 2003). De fato, é apontado que a maioria das florestas tropicais do futuro será constituída por florestas secundárias em processo de regeneração após desmatamento anterior (WRIGHT & MULLER-LANDAU, 2006). No entanto, sabe-se que a perda da biodiversidade associada à diminuição da qualidade dos ecossistemas naturais compromete o funcionamento e a capacidade das florestas fornecerem serviços ecológicos (EWERS & DIDHAM, 2006; LAURANCE *et al*., 2014). Como mencionado anteriormente, os efeitos negativos das perturbações antrópicas podem ser exacerbados pelas mudanças climáticas (por exemplo, aumento de temperatura e escassez de água) (HIROTA *et al*., 2011; RITO *et al*., 2017). Sem dúvida, a interação dessas duas pressões pode comprometer a vitalidade e a capacidade de regeneração das florestas, o que tem aumentado o interesse em sucessão secundária entre ecólogos e biólogos da conservação, embora a extensão dos habitats florestais continua a diminuir em todo o mundo (FAO & UNEP, 2020). Nesse sentido, a restauração ecológica torna-se uma alternativa viável para aumentar a cobertura florestal e conectividade entre os locais remanescentes em um prazo razoável e o estudo de sucessão secundária natural tem exercido uma grande influência na prática de recuperação e manejo da vegetação (QUESADA *et al*., 2009).

Espera-se que o valor de uma floresta secundária aumente com o tempo, à medida que as espécies de florestas maduras se movem e se acumulam nesses remanescentes (CHAZDON *et al*. 2009). Existem estudos que mostram que ao longo da sucessão muitas características estruturais da comunidade de plantas se recuperam (por exemplo, densidade de árvores, riqueza de espécies e área basal) e as características ambientais se tornam mais amenas (por exemplo, nível de luz e temperatura do ar e do solo) (LEBRIJA-TREJOS *et al*., 2010, 2011), favorecendo a recuperação biótica e consequentemente a sucessão ecológica (CHAZDON *et al*., 2009). Nessa perspectiva, as florestas secundárias representam uma alternativa para manter a biodiversidade em paisagens modificadas pelo homem e a compreensão de como essas florestas mudam ao longo da sucessão é importante não apenas para garantir a conservação da biodiversidade, mas também para manter o fornecimento de serviços ecossistêmicos em regiões tropicais (BARLOW *et al*., 2007; CHAZDON *et al*. 2009). No geral, há diversas abordagens propostas para o estudo da sucessão; porém, o curto tempo disponível tem sido uma das principais limitações para a nossa compreensão da sucessão florestal (LEBRIJA-TEJOS *et al*., 2010). Desta forma, o uso de cronosequência, ou seja, um conjunto de áreas que sofreram o mesmo tipo de perturbação, mas com diferentes idades de regeneração, torna-se um caminho para contornar esse problema (LEBRIJA-TEJOS *et al*., 2010) e tem sido um dos métodos mais utilizados para o estudo de sucessão ecológica (CHAZDON *et al*., 2007).

Nos últimos anos, um número crescente de estudos tem monitorado a regeneração florestal e os processos de sucessão ao longo do tempo, combinando cronosequências e abordagens dinâmicas (LEBRIJA-TEJOS *et al*., 2010, MORA *et al*., 2015, NORDEN *et al*., 2011). Vários trabalhos quantitativos mostram que as florestas secundárias são capazes de recuperar níveis de riqueza de plantas e animais semelhantes aos das florestas primárias em poucas décadas após o abandono (DUNN, 2004; MARTIN *et al*., 2013). Por exemplo, a partir de estudos em cronosequência, foi verificado que alguns atributos das comunidades arbóreas (e.g. riqueza de espécies) das florestas úmidas podem alcançar valores equivalentes aos das florestas primárias de forma determinística e dentro de 20-30 anos (GUARIGUATA & OSTERTAG, 2001). Esse fato demonstra a resiliência de algumas florestas frente às pressões externas. Entende-se resiliência como a velocidade em que um ecossistema retorna às suas propriedades físicas e biológicas após perturbações (HOLLING, 1973). Após um período de tempo apropriado, um ecossistema resiliente é capaz de recuperar sua identidade em termos de estruturas básicas, tais como a densidade de indivíduos, riqueza, composição taxonômica, interações ecológicas, funções ecossistêmicas, entre outros atributos (HOLLING, 1973; WALKER & SALT, 2006). A depender da capacidade de lidar com o grau de mudança, as florestas podem responder de diferentes maneiras aos distúrbios. Assim, a composição taxonômica característica, as funções ecológicas e estrutura da vegetação podem ou não ser alteradas (THOMPSON *et al*., 2009). Alguns animais também possuem papéis importantíssimos nos processos que envolvem a organização do ecossistema, por meio da polinização, dispersão de sementes e herbivoria, e a perda dessas espécies pode ter efeitos graves para a resiliência do ecossistema (ELMQVIST *et al*., 2003). De fato, diversos estudos relatam que a resiliência dos ecossistemas está diretamente relacionada à diversidade biológica e à capacidade que ela confere para reter os processos ecossistêmicos (WALKER, 1995; PETERSON *et al*., 1998; HOOPER *et al*., 2005; DREVER *et al*., 2006).

A resiliência (ou seja, a velocidade com que os atributos da floresta secundária se aproximam das florestas primárias) pode mudar de acordo com vários fatores (CHAZDON *et al*., 2009). Por exemplo, em paisagens modificadas pelo homem, o sucesso da recuperação da biota é alto onde a perturbação antrópica após o abandono é baixa, quando florestas antigas estão próximas e quando dispersão de sementes por animais está presente. Por outro lado, em paisagens tropicais com alto nível de perturbação antrópica, baixa presença (ou ausência) de fauna responsável pela dispersão de sementes e distantes de florestas primárias, a taxa de recuperação pode ser baixa ou até ausente (CHAZDON *et al*., 2009). Assim, é essencial compreender e prever os mecanismos associados à resiliência no que se refere às maneiras pelas quais os ecossistemas florestais respondem à degradação, perda de espécies e mudança climática (KINZIG *et al*., 2001).

2.3 Florestas tropicais secas

2.3.1 Distribuição e estado de conservação

As florestas tropicais secas (isto é, *Seasonally Dry Tropical Forests*, sensu MURPHY & LUGO, 1986; PENNINGTON *et al*., 2009) são áreas de florestas singulares para a conservação da biodiversidade. Elas podem ser definidas como florestas que ocorrem em regiões tropicais caracterizadas por acentuada sazonalidade na distribuição de chuvas, resultando em vários meses de seca (MOONEY *et al*., 1995). Essas florestas compreendem um bioma globalmente extenso, representando mais do que 40% das florestas tropicais no mundo, cobrindo grandes áreas na África, Austrália, América Central e Sul, Índia e Sul da Ásia (MURPHY & LUGO, 1986). Embora apresentem alto nível de diversidade e endemismo, as florestas tropicais secas também estão sofrendo as consequências das perturbações impostas pelo homem (por exemplo, fragmentação florestal, conversão para agricultura e incêndios) associadas ao crescimento da população humana e das mudanças climáticas (MILES *et al*., 2006). Consequentemente, as florestas tropicais secas estão entre os biomas mais ameaçados do mundo (MILES *et al*., 2006; OATHAM & BOODRAM, 2006), perdendo anualmente até 2% de sua cobertura vegetal (MAY & STUMPF, 2000) e entre 14 e 40 mil espécies devido à destruição dos habitats florestais (HUGHES *et al*., 1997).

Devido a seu clima atrativo e solo adequando para muitos tipos de agricultura e pecuária (TREJO & DIRZO, 2000), as florestas tropicais secas têm historicamente suportado grandes populações humanas fortemente dependentes da exploração dos recursos florestais (MEHTA *et al*., 2008; SINGH *et al*., 2010), em um típico regime de perturbação antrópica crônica (SINGH, 1998). Além disso, estima-se consistentemente um aumento na evaporação e na temperatura e uma redução na precipitação (ou seja, aumento da aridez) em 2100 em relação ao final do século 20 para as florestas tropicais secas (MAGRIN *et al*., 2014), resultando em períodos mais longos e severos de seca que podem ameaçar a manutenção da biodiversidade. De fato, em muitas regiões, as florestas tropicais secas têm experimentado os efeitos negativos das perturbações antrópicas crônicas e mudanças climáticas (GILLESPIE *et al*., 2000; ARIAS-MEDELLÍN *et al*., 2014; ARNAN *et al*., 2018; OLIVEIRA *et al*., 2019). Infelizmente, este cenário atual de mudança do habitat e aumento da aridez pode reduzir a cobertura vegetal e a produtividade, podendo levar as florestas tropicais secas à desertificação, com impactos irreversíveis sobre a biodiversidade e, consequentemente, aos serviços ecossistêmicos (REYNOLDS *et al*., 2007).

2.3.2 Regeneração florestal em florestas tropicais secas

Estudos sobre sucessão secundária têm sido realizados mais frequentemente em florestas tropicais úmidas, mas os padrões resultantes dos processos que conduzem a sucessão nessas florestas podem não ser aplicáveis às florestas tropicais secas. Alguns dos motivos propostos para essa diferença são estes: (1) limitações sazonais da água como um fator determinante dos processos ecológicos em florestas tropicais secas, enquanto que as florestas tropicais úmidas são mais limitadas pela disponibilidade de luz (EWEL, 1977); (2) dispersão de sementes pela ação do vento (anemocoria) como o modo mais importante em florestas tropicais secas (JANZEN, 2002; VIEIRA & SCARIOT, 2006); (3) reprodução vegetativa por meio da rebrota como um mecanismo de regeneração mais relevante em florestas tropicais secas (EWEL, 1977; VIEIRA & SCARIOT, 2006; MCDONALD *et al*., 2010); e (4) menor importância da dinâmica de clareiras, ou seja, a abertura do dossel como fator importante para a regeneração pode não se aplicar em florestas tropicais secas (QUESADA *et al*., 2009; LEBRIJA-TREJOS *et al*., 2010; LÉVESQUE *et al*., 2011).

Essas características peculiares proporcionam diferentes processos ecológicos e mudanças na estrutura da vegetação ao longo da sucessão em florestas tropicais secas (QUESADA *et al*., 2009; LOHBECK *et al*., 2013). Embora aconteçam mudanças consideráveis nas condições ambientais de estágios iniciais (mais quentes e secos) para estágios tardios (mais sombreados e úmidos) (LEBRIJA-TREJOS *et al*., 2011), a força do gradiente de luz é menor nessas florestas do que em florestas tropicais úmidas, pois as primeiras possuem menores diferenças nas condições de luz entre estágios iniciais e tardios (EWEL, 1977; LETCHER *et al*., 2015). No entanto, os regimes de precipitação são vistos como fortes influenciadores dos processos sucessionais em florestas tropicais secas (MASS & BURGOS, 2011). Alguns estudos já têm apontado a importância da disponibilidade de água para processos como germinação de sementes (DANTAS *et al*., 2020), aumento de biomassa (BECKNELL *et al*., 2012) e crescimento e aptidão individual da planta (ENGELBRECHT *et al*., 2007). Por conta do padrão sazonal no regime de chuvas, o período de tempo mais adequado para diversos processos que envolvem a dinâmica de sucessão em florestas tropicais secas é mais restrito, mas essa sazonalidade gera condições abióticas mais severas e variáveis, tornando os ecossistemas secos mais tolerantes a maiores condições de estresses (CECCON *et al*., 2006).

Quanto à capacidade de recuperação dessas florestas (ou seja, resiliência), os poucos estudos existentes não são suficientes para uma afirmação mais precisa. Embora existam sugestões de que florestas tropicais secas são mais resilientes do que as úmidas (QUESADA *et al*., 2009; ÁLVAREZ-YÉPIZ *et al*., 2018), os poucos trabalhos disponíveis são contraditórios. Enquanto alguns mostram uma alta recuperação das florestas secundárias em termos de riqueza, biomassa e composição de espécies em relação às florestas maduras (LEBRIJAS-TREJOS *et al*., 2010), sugerindo uma alta resiliência, outros não observaram uma recuperação tão frequente (QUESADA *et al*., 2009; BARROS *et al*., 2021). É importante lembrar que a resistência inicial, a trajetória e a extensão em que um sistema retorna às condições originais após uma perturbação vão depender da frequência, intensidade, duração e extensão da perturbação, bem como das propriedades inerentes dos sistemas biológicos (MYERS, 1996; WIILLIG & WALKER, 1999). Além disso, os fortes impactos causados pela pecuária e extração de recursos naturais da floresta podem ter efeitos permanentes na dinâmica de regeneração em florestas tropicais secas (CECCON *et al*., 2006). Assim, a compreensão desses fatores de ameaças associados às características inerentes das comunidades biológicas pode nos ajudar a entender como se dá o processo de regeneração em florestas que ainda não têm recebido muita atenção para pesquisas, como é o caso das florestas tropicais secas (SANCHEZ-AZOFEIFA *et al*., 2005; VIEIRA & SCARIOT, 2006; QUESADA *et al*., 2009). Entender esses fatores é fundamental para a recuperação da biomassa e para a sustentabilidade de ecossistemas secos em geral.

2.3.3 Caatinga e suas ameaças

A Caatinga brasileira é um mosaico de florestas tropicais sazonalmente secas e de vegetação arbustiva esclerófila (PENNINGTON *et al*., 2009) que cobre 912.529 km² do Nordeste do Brasil (SILVA *et al*., 2017). Como em todas as regiões semiáridas, as principais características climáticas desse ecossistema são a curta e concentrada estação chuvosa, onde de 50 a 70% das chuvas são concentradas em três meses consecutivos, seguidos por longos períodos de estiagem (NIMER, 1972, KROL *et al*., 2001, CHIANG & KOUTAVAS, 2004), além da alta radiação solar incidente que causa elevadas temperaturas e déficit hídrico. A precipitação média anual varia entre 240 e 1.000 mm, mas metade da região recebe menos de 750 mm (SAMPAIO, 1995; PRADO, 2003). Essa baixa pluviosidade ainda é acompanhada por uma alta irregularidade anual em sua distribuição (tempo e espaço), o que por vezes resulta em secas severas (NIMER, 1972). Assim, comparada a outros ecossistemas brasileiros, a Caatinga apresenta as características mais extremas dentre as variáveis climáticas, o que levou a evolução de uma vegetação tipicamente xerófila, com adaptações em sua morfologia e fisiologia capazes de tolerar condições climáticas adversas a qual é submetida (LEAL, 2003, 2005; Silva *et al*., 2004). Além disso, a Caatinga é apontada como uma das regiões brasileiras com maior probabilidade de ser afetada pelas mudanças climáticas (MARENGO *et al*., 2017). De fato, em regiões com clima mais seco e sazonal, os efeitos das mudanças climáticas tendem a ser mais severos. Os modelos de mudanças climáticas já apontam uma redução de 40-50% na precipitação e um aumento de 3-5°C até o ano 2100 na Caatinga (SOUZA & MANZI, 2014), o que pode desencadear o processo de desertificação desse ecossistema.

Como outras florestas tropicais secas, a Caatinga também se encontra exposta às perturbações antrópicas (MARTORELL & PETERS, 2009), onde cerca de 63% de sua vegetação original já sofreu conversão extensiva para a agricultura (SILVA & BARBOSA, 2017). Além disso, as áreas remanescentes são exploradas por densas populações humanas (26 habitantes / km²), carentes e altamente dependentes dos recursos florestais para suas necessidades básicas (ALBUQUERQUER *et al*., 2017). Atividades como a coleta de lenha, forragem, exploração de produtos florestais madeireiros e não-madeireiros, criação extensiva de animais domésticos e a caça são frequentes, diminuem a produtividade dessas florestas e contribuem para a modificação de toda a paisagem (RIBEIRO *et al*., 2015; RIBEIRO-NETO *et al*., 2016). O aumento dessas atividades típicas de distúrbio crônico na Caatinga tem transformado florestas maduras em remanescentes de florestas secundárias dominadas por arbustos (RIBEIRO *et al*., 2015), os quais exibem comunidades de plantas e animais funcionalmente e filogeneticamente empobrecidos (RIBEIRO *et al*., 2015, 2016; RIBEIRO-NETO *et al*., 2016). Adicionalmente, as perturbações crônicas também têm reduzido a qualidade das funções e serviços fornecidos pelo ecossistema (LEAL *et al*., 2014, 2015), o que torna a Caatinga o terceiro ecossistema mais ameaçado do Brasil (LEAL *et al*., 2005).

Embora existam muitas evidências sobre os efeitos negativos dos distúrbios crônicos e das mudanças climáticas sobre a biota da Caatinga (ARNAN *et al*., 2018; CÂMARA *et al*., 2019; OLIVEIRA *et al*., 2019; RIBEIRO *et al*., 2019; ANDRADE *et al*., 2020; SILVA *et al*., 2020), ainda há muitas lacunas de conhecimento quanto aos aspectos sucessionais nessa região. No entanto, como em outras florestas secas, estudos sugerem que a regeneração da Caatinga é mediada principalmente pela disponibilidade de água, que o recrutamento de plântulas verdadeiras é baixo e que rebrotas/reprodução vegetativa são o principal mecanismo de regeneração nesse ecossistema (BARROS *et al*., 2021; TRINDADE *et al*., 2020). Como a recuperação de uma floresta seca é fortemente controlada pela disponibilidade de água, anos de seca extrema após a perturbação podem limitar a sua capacidade de recuperação. Assim, compreender os efeitos dessas duas importantes forças (distúrbios antrópicos e climáticos) sobre diferentes grupos ecológicos é crucial à medida que aumenta a frequência de eventos extremos.

2.4 Borboletas frugívoras como bioindicadores: resposta à mudança de habitat e fatores abióticos

A maneira mais eficiente para atrair esforços para a conservação é saber quais os processos que levam às mudanças das paisagens naturais e como tais modificações afetam os organismos (FREITAS *et al*., 2003). Como inventariar toda a biodiversidade de uma região é praticamente impossível, devido à escassez de tempo, dinheiro e número reduzido de especialistas, o uso de indicadores biológicos possibilita, de maneira mais rápida, informar as áreas que possuem maior relevância para conservação. Algumas características são essenciais para a definição ou escolha de bons indicadores biológicos (ver BROWN JR., 1991, 1997). Entre outros insetos, as borboletas têm se destacado com sucesso no monitoramento de áreas naturais, pois respondem bem a praticamente todo tipo e intensidade de alteração no ambiente (FREITAS *et al*., 2003, 2006).

Dentre os motivos que as tornam ótimos bioindicadores, pode-se citar: a diversidade de espécies; o fato de serem encontradas o ano inteiro; o ciclo de vida curto; a facilidade de amostragem, identificação e criação em laboratório; o bom conhecimento a respeito da história natural e diversos aspectos da biologia; e a taxonomia relativamente bem resolvida (BROWN JR., 1991; BROWN JR.; FREITAS, 1999). Muitas espécies de borboletas também estão intimamente ligadas ao ambiente em que vivem e são bastante sensíveis a alterações ambientais, sejam elas naturais ou antrópicas (FREITAS & MARINI-FILHO, 2011). Além disso, o colorido de suas asas e a fácil visualização garantem um forte apreço da população, consequentemente, sendo muito utilizadas como “espécie bandeira” com êxito em programas de monitoramento (POLLARD & YATES, 1993; RAIMUNDO *et al*., 2003). Por esses motivos, as borboletas estão entre os grupos mais usados no mundo com fins de monitorar a integridade das paisagens naturais, tornando-se indicadores biológicos eficazes para esse tipo de diagnóstico ambiental (BROWN JR., 1991; BROWN JR. & FREITAS, 2000).

Com cerca de 3.300 espécies ocorrendo no Brasil (BROWN JR. & FREITAS, 2000), as borboletas podem ser separadas em duas guildas, quando considerada a dieta alimentar dos indivíduos adultos (DeVRIES, 1987): (1) A guilda Nectarívora, composta por espécies que se alimentam de néctar, compreendendo as famílias Papilionidae, Pieridae, Lycaenidae, Riodinidae, Hesperiidae e alguns grupos de Nymphalidae; (2) A guilda Frugívora, que inclui as espécies que se alimentam de frutas fermentadas, reunindo as espécies da família Nymphalidae, especificamente das subfamílias Biblidinae, Charaxinae, Satyrinae e Nymphalinae (apenas tribo Coeini) (WAHLBERG *et al*., 2009). Este grupo também pode se alimentar de fezes de vertebrados, seiva secretada por algumas espécies de plantas e carne em decomposição (DeVRIES, 1987). As borboletas frugívoras apresentam algumas vantagens práticas sobre as nectarívoras para o seu estudo. Elas podem ser amostradas facilmente em armadilhas contendo iscas atrativas, o que possibilita uma amostragem simultânea de duas ou mais áreas (ou meses do ano) com o mesmo esforço amostral (DeVRIES, 1987). A identificação dos indivíduos pode ser feita, em sua maioria, no local de captura, sendo marcadas e posteriormente liberadas, permitindo um estudo não destrutivo e com o mínimo de manipulação. Por fim, por se tratar de um recurso alimentar, o uso de armadilhas com iscas atrativas reduz a possibilidade de capturas ao acaso, presentes em outros métodos (UEHARA-PRADO *et al*., 2007; FREITAS *et al*., 2014).

A guilda frugívora tem sido amplamente utilizada em pesquisas que avaliam como diferentes graus de perturbação afetam o padrão de distribuição de espécies, principalmente na América do Sul (BROWN JR., 1991; 1997; BROWN JR. & FREITAS, 2000; UEHARA-PRADO *et al*., 2007, MELO *et al*., 2019). Em florestas tropicais úmidas, estudos mostram que a perda e fragmentação de habitats podem afetar a distribuição de borboletas frugívoras de diversas maneiras após o distúrbio, porém, mais importantemente, as perturbações antrópicas podem causar alterações significativas na composição de espécies (UEHARA-PRADO *et al*., 2007, RIBEIRO *et al*., 2008, NYAFWONO *et al*., 2014; MELO *et al*., 2019). A comunidade de borboletas frugívoras também difere significativamente em áreas com diferentes idades de regeneração, mostrando padrões interessantes de substituição de espécies ao longo do tempo (SANT’ANNA *et al*., 2014). Além de perturbações antrópicas, borboletas também possuem relação estreita com fatores abióticos, ou seja, com condições microclimáticas (BOGGS & MURPHY, 1997; RIBEIRO & FREITAS, 2010; CHECA *et al*., 2014). As mudanças climáticas também podem alterar uma série de fatores comportamentais, reprodutivos e padrões de distribuição de borboletas (STEFANESCU *et al*., 2003; LEE *et al*., 2020). Por exemplo, eventos prolongados de seca ou chuva podem reduzir o sucesso reprodutivo e o tamanho das populações de borboletas (OLIVER *et al*., 2015). Além disso, mudanças no regime de precipitação e temperatura combinadas com a alteração do habitat podem mudar os padrões de diversidade e abundância de borboletas (FORISTER *et al*., 2010; WEPPRICH *et al*., 2019). No entanto, a maioria dos estudos sobre o efeito de perturbações antrópicas e fatores abióticos sobre comunidade de borboletas frugívoras foram feitos em florestas úmidas e pouco se sabe ainda sobre como esta guilda responde a essas variáveis em florestas tropicais secas (mas ver BEIRÃO *et al*., 2017 e CASAS-PINILLA *et al*., 2017).

Como paisagens dominadas por atividades humanas tendem a continuamente perder espécies e simplificar sua estrutura, em um processo conhecido como “sucessão ecológica retrogressiva” (sensu TABARELLI *et al*., 2008), avaliar como perturbações antrópicas agudas e crônicas e o aumento no nível de aridez afetam a comunidade de borboletas frugívoras, bem como compreender como essa guilda se recompõe ao longo da sucessão secundária são fundamentais para subsidiar legislações e diretrizes para conservação da Caatinga.

ARTIGO 1

Aridity and chronic anthropogenic disturbance as organizing forces of fruit-feeding butterfly assemblages in a Caatinga dry forest

Artigo a ser submetido ao periódico *Journal of Animal Ecology*

Formatado conforme as normas *Journal of Animal Ecology* disponível em: https://besjournals.onlinelibrary.wiley.com/hub/journal/13652656/author-guidelines

Aridity and chronic anthropogenic disturbance as organizing forces of fruit-feeding butterfly assemblages in a Caatinga dry forest

Douglas H. A. Melo[1], André V. L. Freitas[2], Marcelo Tabarelli[3], Bruno K. C. Filgueiras[4], Inara R. Leal[3,*]

[1]Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco, Recife, PE, 50670-901, Brazil

[2]Departamento de Biologia Animal and Museu de Zoologia, Universidade Estadual de Campinas, Campinas, SP, C.P. 6109, 13083-970, Brazil

[3]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, PE, CEP 50670-901, Brazil

[4]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, PE, 50670-901, Brazil

*Corresponding author: Inara R. Leal, e-mail: inara.leal@ufpe.br

Abstract

1. Anthropogenic disturbances and climate change are expected to reorganize biodiversity on multiple ecological levels from populations to ecosystems, especially in arid and semiarid regions due to environmental filtering imposed by water stress.
2. This paper examines the individual and combined effects of chronic anthropogenic disturbance and increased aridity on the structure of fruit-feeding butterfly assemblages in a human-modified landscape of Caatinga dry forest, in the northeast of Brazil. Butterflies were recorded monthly across nine old-growth forest stands and their assemblages were described in terms of taxonomic and functional community-level attributes confronted to different levels of chronic disturbance and aridity.
3. A total of 12,694 butterflies from 21 species were recorded, with a small number of species adapted to arid environments dominating the assemblages. Butterfly assemblages were species-poor but had high species replacement (turnover) along both the chronic disturbance and aridity gradients. We observed a negative effect of aridity on alpha and beta (species turnover) diversity of butterfly assemblages. Butterfly assemblages across forest stands exposed to high levels of chronic disturbance and aridity had a nested structure. Functional diversity (Rao’s Q) and the community-weighted means (CWM) of ocellus-bearing species and monocot-feeding larvae were negatively and positively affected by increased aridity and chronic disturbance, respectively. On the other hand, the CWM of wing size and canopy-inhabitant butterfly were positively and negatively affected by aridity and chronic disturbance, respectively.
4. Our findings suggest that aridity and its combination with chronic disturbance, have a drastic effect on the structure of butterfly assemblages in the Caatinga dry forest. These findings highlight that rainfall and chronic disturbances as major drivers of biological

reorganization in human-modified landscapes. As aridity increases, Caatinga tends to support taxonomically and functionally impoverished and highly distorted assemblages.

Keywords: bioindicators, climate change, conservation, human disturbances, Nymphalidae, seasonally dry forest

Introduction

Community assembly at multiple spatial scales and its drivers are key topics in ecology, and have gained increased attention as levels of human disturbance have increased in natural habitats, particularly in tropical forests (Morris, 2010). Although much attention has been devoted to habitat loss and fragmentation, remnant forests in human-modified landscapes (*sensu* Tabarelli et al., 2012) are also exposed to chronic anthropogenic disturbances; i.e. frequent removal of small portions of biomass such as the collection of firewood, fodder, timber and medicinal plants, as well as grazing by livestock (Singh, 1998; Martorell & Peters, 2005; Arnan, Leal et al., 2018). Additionally, human-modified landscapes are exposed to shifts in climatic variables (e.g. precipitation and drought events) associated with climate change, especially those in Seasonally Dry Tropical Forests (*sensu* Murphy & Lugo, 1986; Pennington et al., 2009) (Miles et al., 2006; Rito, Arroyo-Rodríguez et al., 2017; Arnan, Arcoverde et al., 2018). In this perspective, human disturbance and climate change have been argued to reorganize biodiversity from population to ecosystem level (Filgueiras et al., 2021).

Chronic disturbances have been associated to impoverished and functionally distorted assemblages at the community level (Santos et al., 2011; Ribeiro et al., 2015; Ribeiro-Neto et al., 2016), with negative effects on the taxonomic, phylogenetic and functional diversity of plant and animal assemblages (Ribeiro et al., 2015, 2016, 2019; Ribeiro-Neto, et al., 2016). These changes partially result from the dominance of a few species more adapted to disturbance in contrast to the decline of sensitive species abundance, including those involved in key ecosystem functions and ecological services, such as pollination and seed dispersal provided by insects (Memmott et al., 2007; Tylianakis et al., 2008; Leal et al., 2014). However, research on chronic disturbance has been focused mainly on plants, for which direct effects on the exploited populations or indirect effects from reduced forest biomass and associated microclimate changes may be imposed (Rito, Arroyo-Rodríguez et al., 2017; Souza et al., 2019).

There is an increasing concern that climate change may exacerbate the effects of chronic disturbance through the strengthening of environmental filters such as those associated with higher temperatures, habitat desiccation, and aridity (Hirota et al., 2011; Rito, Arroyo-Rodríguez et al., 2017). In addition to long-lasting changes in temperature and precipitation regimes, climate change is increasing the frequency of severe droughts (e.g. ENSO effects) and CO_2 fertilization, which have drastic effects on community-level organization (Phillips et al., 2010). One example is the proliferation of common and dominant plant species accompanied by the decline of the rare ones across drier habitats, where the adverse microclimatic conditions negatively alter the plant recruitment of species restricted to wet areas (Trindade et al., 2020). Climate change can also impact animal behavior, fecundity, phenology (i.e. reproductive timing) and distribution patterns (i.e. migration rates) (Stefanescu et al., 2003; Todd et al., 2011; Mathewson et al., 2016; Lee et al., 2020). Moreover, chronic disturbance and climate change can synergically affect native assemblages (Rito, Arroyo-Rodríguez et al., 2017; Arnan, Arcoverde et al., 2018). Thus, understanding the isolated and synergic impacts of human land use (i.e. chronic disturbance) and climatic changes (aridity) on the structure and diversity of biological communities is a key topic for community assembly, with implications for biodiversity persistence, ecosystem functioning and the provision of ecosystem services in human-modified landscapes (Filgueiras et al., 2021).

Fruit-feeding butterflies have long been used as bioindicator of human impacts (e.g. habitat loss and fragmentation, edge effects, selective logging, presence of trails and fires), mainly across tropical rainforests (Leidner et al., 2010; Ribeiro et al., 2012; Ribeiro & Freitas, 2012; Filgueiras et al., 2016; Andrade et al., 2017; Melo et al., 2019; Gueratto et al., 2020). Prolonged drought or rainfall can reduce breeding success and reduce population sizes of butterflies, which can have implications for the maintenance of metapopulations across human-modified landscapes, leading to population collapse (Oliver et al., 2015). Additionally, changes in precipitation and temperature combined with habitat alteration (i.e. land-use–climate interactions) can shift patterns of butterfly diversity (Forister et al., 2010) and abundance (Wepprich et al., 2019), with potential effects on key ecosystem services (e.g. pollination). However, studies on the response of fruit-feeding butterflies to chronic disturbance and climate change are rare for dry forests (but see Beirão et al., 2017 and Casas-Pinilla et al., 2017).

The Brazilian Caatinga, the largest block of dry forest globally, has been converted into human-modified landscapes since the European arrival in the 16th century (Silva et al., 2017). The Caatinga region is dominated by vegetation mosaics consisting of crop fields (i.e. mostly shifting cultivation) as well as regenerating and old-growth forest stands — which are distributed along a precipitation gradient (400-900 mm) and exposed to intensive exploitation for forest products such as firewood, as well as from browsing by livestock, particularly by free-ranging goats, and timber exploitation (Silva et al., 2017; Souza et al., 2019). Both changes in precipitation levels and chronic disturbances have been associated with community-level changes in plants, particularly species richness and taxonomic and functional composition (Ribeiro et al., 2015, 2019; Ribeiro-Neto, et al., 2016; Rito, Arroyo-Rodríguez et al., 2017; Sfair et al., 2018), with cascading effects on ecosystem functioning and services (Leal et al., 2014; Schulz et al., 2016; Câmara et al., 2019; Oliveira et al., 2019), suggesting that plant-dependent species, such as butterflies, may also respond to these drivers.

This paper examines both the individual and combined effects of chronic disturbance and aridity on a large set of community-level attributes of fruit-feeding butterflies in a human-modified landscape of the Caatinga dry forest in northeastern Brazil. We refer to attributes covering (i) abundance and dominance patterns, (ii) alpha and beta taxonomic diversity, (iii) functional diversity and (iv) taxonomic and functional composition and their responses to both gradients in rainfall and chronic disturbance. Given that both chronic disturbance and rainfall reductions alter plant assemblages, negatively affecting water-demanding plant species and favoring disturbance-adapted species (Rito, Arroyo-Rodríguez et al., 2017), we expect to find (i) impoverished and nested fruit-feeding butterfly assemblages as chronic disturbance and aridity increase, (ii) reductions in alpha, beta and functional diversity in areas that are both highly disturbed and arid, and (iii) abundance increasing of species and/or groups of species with higher flight capacity, resistance to desiccation and those that feed on non-monocots as chronic disturbance and aridity increase. We discuss the patterns we uncover in the light of both taxonomic and functional reorganization of biological communities inhabiting human-modified landscapes.

Methods

Study area

The study was carried out in the Catimbau National Park (8º24’00’’ and 8º36’35’’ S; 37º09’30’’ and 37º14’40’’ W), in the State of Pernambuco, northeast Brazil (Fig. 1). The Park covers a total area of 607 km² with approximately 70% covered by quartzite sandy soils, but planosols and lithosols are also present (15% each; Siqueira et al., 2017). The climate is predominantly of semi-arid Bsh type, with a transition to the rainy tropical As type, according to the Köppen scale. Annual rainfall is between 480 and 1100 mm, with about 60% to 75% of the rainfall occurring in the period from March/April to June/July (Rito, Arroyo-Rodríguez et al., 2017). Annual average temperature is ca. 23°C, with July being the month with the lowest average temperature, of around 21°C, while December is the hottest month, with an average of ca. 25°C (Rito, Arroyo-Rodríguez et al., 2017). The predominant vegetation type is a small-statured seasonally dry tropical forest, dominated by woody plant species from the Leguminosae, Euphorbiaceae, Boraginaceae and Burseraceae families (Rito, Arroyo-

Rodríguez et al., 2017). This protected area is still home to over 400 families whose livelihoods rely on slash-and-burn agriculture, goat farming and the collection of forest products, such as firewood, timber and fodder (Souza et al., 2019). Accordingly, the Caatinga dry forest in our focal landscape has been converted into a successional mosaic, with both old growth and regenerating forest stands exploited for forest products (Souza et al., 2019).

Chronic anthropogenic disturbance and aridity gradients

Nine 0.1-ha permanent forest plots distributed along independent chronic disturbance and rainfall gradients in our focal landscape were established (Rito, Arroyo-Rodríguez et al., 2017) (Fig. 1, Table S1). All plots were on sandy soil, had similar slope, and supported old-growth vegetation that had not experienced slash-and-burn agriculture for at least 100 years (Rito, Arroyo-Rodríguez et al., 2017). Plots were separated by a minimum of 2 km and occurred within an area of 214.3 km^2 (Rito, Arroyo-Rodríguez et al., 2017).

As described by Arnan, Leal et al. (2018), chronic disturbance intensity was estimated through indices combining several sources of disturbance, as follows: (1) a livestock pressure index (consumption of vegetation, trampling, and other physical damage caused by goats and cattle); (2) a wood extraction index (the extraction of dead and live wood for fuel, fence construction and artisanal use); and (3) extraction of non-timber forest products index (medicinal plants, food items for humans, hunting and livestock fodder). For the livestock pressure index (LPI) and woody extraction index (WEI), we conducted field assessments of goat trail length, goat dung, cattle dung, live wood extraction (stem cuts) and coarse woody debris extraction (litter) within each plot (see Arnan, Leal et al., 2018 for more details). For the extraction of non-timber forest products index (NTFPI), we used two approaches: (1) geographic distances based on remote sensing (i.e. proximity to the nearest house and proximity to the nearest road, using satellite imagery and ArcGIS 10.1 software). Since the distance is inversely related to level of disturbance, we used the inverse of distance as our metric; and (2) interviews with inhabitants of the nearest village to each plot applying informal and semi structured questionnaires to assess the number of people living in each village (see Arnan, Leal et al., 2018 for more details). Index values were calculated using the following formula:

$$I = \frac{\sum_{i=1}^{n} (y_i - y_{min})/(y_{max} - y_{min})}{n} \times 100$$

where I is disturbance intensity; y_i is the observed value for a given disturbance metric in plot i; y_{min} is the minimum observed value for the disturbance metric across all plots; y_{max} is the maximum observed value for the disturbance metric across all plots; and n is the number of individual disturbance metrics incorporated in the index. The values of the three individual indices were standardized between 0 and 1 to make them comparable and to allow them to be integrated into a single chronic disturbance multimetric index (i.e. global chronic disturbance index; GI) (see Arnan, Leal et al., 2018 for methodological details).

To estimate aridity, data on mean annual rainfall were acquired from the WorldClim database (Hijmans et al., 2005). We downloaded the dataset at a resolution of 30 arc seconds (equivalent to 1 km, http://www.worldclim.org), and the mean annual rainfall for each plot was extracted using the *maptools* package **(**Bivand & Lewin-Koh, 2015) in the R software (R Development Core Team, 2017). We then calculated the mean annual climatic water deficit, which is the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET; based on biologically usable energy and water) (Lutz et al., 2010). For each plot, the calculated difference between annual PET and AET was defined as the climatic water deficit value, which we adopted as our aridity index (see Arnan, Leal et al., 2018 for more details). All calculations were performed using ArcGIS 10.1 software.

Fruit-feeding butterfly surveys

Sampling of fruit-feeding butterflies was carried out monthly from May 2018 to April 2019. Each plot had one sampling unit composed of five portable bait traps, totaling 45 traps across our study landscape. The traps were arranged a distance of at least 30 m from each other and suspended at a height of between 1 and 1.5 m above the ground. The traps remained open during seven consecutive days per month and were checked every 48 hours, when baits were replaced. The number of trap-days was considered the sampling effort, i.e., the total number of traps used in the field (45 traps) multiplied by the number of days sampling lasted (84 days), which result in 3,780 trap-days.

The traps used were of the Van Someren-Rydon type (following DeVries, 1997), which consist of cylindrical tubes made with netting (110 cm high × 35 cm in diameter) and an internal cone (30 cm high and 22 cm wide at the opening) at the bottom to prevent butterflies from escaping. The lower part was open and attached to a plywood platform with a distance of 4 cm to allow butterflies to enter the trap. A mixture of banana and sugar cane juice fermented for 48 h was used as bait. Baits were placed inside traps in plastic pots with a perforated cover to prevent butterflies from drowning in the liquid, to avoid feeding by other insects and to reduce evaporation (Hughes et al., 1998; Freitas et al., 2014).

During each visit, all captured individuals were identified, marked and then released. Voucher specimens of all recorded species (up to 10 vouchers per species — about 1% of the number of individuals total sampled) were deposited in the entomological collections of the Universidade Federal de Pernambuco, Recife, PE, Brazil. All butterflies were identified to the specific level and the classification followed Lamas (2004), modified by Wahlberg et al. (2009).

Functional traits

Butterfly species were classified into functional groups based on morphological and ecological attributes (Table S2) (see Iserhard et al., 2019 for more details). We selected four attributes mainly related to flight capacity, mobility, larval diet and habitat requirements (Iserhard et al., 2019). Size of the anterior wing (hereafter wing size) was measured by the length of the costal margin from the joint with the thorax to its apex (for an average of up to five individuals per species). This trait is directly linked to flight capacity and resistance to desiccation (i.e. bigger butterflies are more tolerant to desiccation and can move further through the landscape). Similarly, the use of the canopy by butterfly species (hereafter Canopy), which is also related to tolerance of high temperatures and desiccation, was attributed. The feeding of larvae on monocotyledon plants (hereafter larval monocots) was also included, whose species are generally associated with shaded humid environments where grasses are more likely to grow and persists during long dry periods. Finally, the presence of ocellus (hereafter ocellus), a trait related to deflection of predator attacks and which is partially linked to the use of monocotyledon plants by larvae, was also adopted.

Data analysis

The coverage estimator recommended by Chao & Jost (2012) was adopted to estimate the accuracy of diversity inventories, using iNEXT (Hsieh et al., 2016). To assess changes in fruit-feeding butterfly alpha diversity, we adopted the effective numbers of species (so-called Hill numbers, ^qD) of orders 0 (^0D, species richness), 1 (^1D, exponential Shannon entropy) and 2 (^2D, inverse Simpson concentration) (Jost, 2007). The ^0D order is not sensitive to abundances and so gives disproportionate weight to rare species, while ^1D weights each species according to its abundance in the community, without favoring rare or abundant species (i.e. common species) (Jost, 2007). Finally, ^2D can be interpreted as the number of very abundant or dominant species in the community (Jost, 2006). To examine patterns of species turnover and nestedness we adopted a species partitioning method, employing a multiple-site dissimilarity metrics (Baselga, 2010). The total Sørensen dissimilarity (beta diversity, $\beta_{SØR}$) allow the separation of beta diversity into components of dissimilarity due to species replacements (i.e. turnover; β_{SIM}) and dissimilarity due to nestedness (β_{SNE}). Functional diversity was defined using Rao's quadratic entropy (Rao's Q), while functional community composition was calculated using community-weighted means (CWM). Rao's Q reveals patterns of trait convergence or divergence compared to a random expectation (reviewed in Ricotta & Moretti, 2011), while the CWM summarizes shifts in mean trait values within communities due to environmental selection (supporting in accordance with the mass-ratio hypothesis; Grime, 1998). Since different types of traits were combined (i.e. categorical and continuous), the Gower approach was adopted to calculate a species-dissimilarity matrix (de Bello et al., 2013). Rao's Q and CWM were computed using the FD package (Laliberté et al., 2015) in R (R Development Core Team, 2017).

Generalized Linear Models (GLMs) were used to assess the effects of chronic disturbance (CAD), aridity and their combined effect (CAD + aridity) on the following community-level attributes of fruit-feeding butterfly assemblages: (i) abundance, (ii) taxonomic diversity (alpha — Hill numbers of order 0, 1 and 2; beta diversity — species turnover and nestedness), (iii) functional diversity (Rao's Q) and (iv) functional community composition (CWM_Size, CWM_Canopy, CWM_Larval monocots and CWM_Ocelus). The residuals of all GLMs were examined to evaluate the adequacy of the error distribution and the minimally significant model was selected. Collinearity among predictor variables was assessed with the variance inflation factor (VIF) using the *car* package (Fox & Weisberg, 2011) for R (R Development Core Team, 2017). All VIF values were <2 (ranging from 1.04 to 1.48), suggesting independence (i.e. no collinearity) among predictors (Chatterjee et al., 2000). The performance of GLMs was assessed using Akaike's Information Criterion (AIC). To obtain model-averaged parameter estimates we used Akaike weights (*wi*). We considered an explanatory variable as important when: (i) the variable exhibited a high sum of Akaike weights (i.e. considering each candidate model in which it appeared); and (ii) the model-averaged parameter estimates did not include zero (i.e. the model-averaged unconditional variance was lower than the model averaged parameter estimate) (Burnham & Anderson, 2002). We considered models with a difference in AICc < 2 as compared to the best model (i.e. the one with lowest AICc value; Burnham & Anderson, 2002) as plausible. All models were constructed using the *glmulti* package (Calcagno & Mazancourt, 2010) for R version 3.0.1. The goodness-of-fit of each model was defined as the explained deviance by the complete model / explained deviance by the null model × 100 (Crawley, 2013).

Finally, the correlation between our explanatory variables (chronic disturbance and aridity) and the species composition was examined using a distance-based redundancy analysis (dbRDA) (Legendre & Gallegher, 2001). Scores of fruit-feeding butterfly abundance were square-root transformed to minimize the effect of a few high abundant species, while all species with fewer than 5 individuals were removed before calculating the Bray-Curtis distance among butterfly assemblages. The significance of the relation between explanatory variables and butterfly composition was assessed with permutation tests, using 9999 random permutations. All analyses were performed using R (R Development Core Team, 2017).

Results

Community overview

Bait traps captured a total of 12,694 fruit-feeding butterflies across our nine forest plots, totaling 21 species from four subfamilies: Biblidinae, Charaxinae, Satyrinae and Nymphalinae (tribe Coeini) (Table S3). Biblidinae was the most species-rich subfamily (nine species), followed by Charaxinae (six species), Satyrinae (three species) and Nymphalinae (two species). The most abundant butterfly species were *Hamadryas februa februa* (41% of all individuals), *Fountainea halice moretta* (19%), *Fountainea glycerium cratais* (17%) and *Pharneuptychia* sp.

(11%). Seven species were considered to be rare in the focal landscape (i.e. < 5 individuals), two of which were represented by only one individual: *Historis odius dious* Lamas, 1995 (Nymphalinae) and *Paryphthimoides poltys* (Prittwitz, 1865) (Satyrinae) (Table S3).

Abundance and alpha- and beta-diversity across chronic disturbance and aridity gradients

The abundance of fruit-feeding butterflies was positively related to chronic disturbance (Fig. 2e) and negatively related to aridity (Fig. 2a) and the combined effect of chronic disturbance with aridity (Fig. 2, Table 1). In general, aridity was the most important predictor negatively affecting α diversity measures, especially the total number of species and the number of common species (^{0}D and ^{1}D, respectively), although the combined effect of chronic disturbance with aridity was also negatively related to fruit-feeding butterfly diversity (e.g. the total number of species — ^{0}D) (Fig. 2, Table 1). From this perspective, the effect of chronic disturbance on the total number of species (^{0}D) was most explicit at drier sites (Fig. 3).

Along the whole gradient of chronic disturbance and aridity, total Sørensen dissimilarity was 55% due to species replacement (turnover) and 45% due to nestedness. As expected, in terms of β diversity, aridity was negatively associated with species turnover (β_{SIM}) (Fig. S1, Table S4). The combined effect of chronic disturbance and aridity was positively related to nestedness (β_{SNE}) (Fig. S1, Table S4). Thus, drier forests with high levels of chronic disturbance exhibited nested fruit-feeding butterfly assemblages.

Taxonomic and functional composition across chronic disturbance and aridity gradients

Regarding taxonomic composition, the first dbRDA axis explained 66% of the variation in species composition. This axis was significantly and negatively associated with chronic disturbance, but positively associated with aridity (χ^2=2.73; p=0.01) (Fig. 4). That is, some species (e.g. *F. halice moretta*, *F. glycerium cratais* and *H. februa februa*) with high abundance were positively related to chronic disturbance and mainly to aridity (Fig. 4 and 5), while other species such as *Opsiphanes invirae remoliatus* and *Pharneuptychia* sp. (Satyrinae), were negatively affected by aridity increasing (Fig. 5). Chronic disturbance and aridity significantly affected both functional diversity and composition of fruit-feeding butterfly assemblages. Functional diversity (Rao's Q) and the community-weighted means (CWM) of ocellus-bearing species and those with monocot-feeding larvae were negatively and positively affected by increasing aridity and chronic disturbance, respectively (Fig. 6, Table S5). On the other hand, the CWM of wing size and canopy-inhabitant butterfly species were positively and negatively affected by aridity and chronic disturbance, respectively (Fig. 6, Table S5).

Discussion

Our results suggest that while human-modified landscapes of the Caatinga dry forest support abundant, but species-poor butterfly assemblages at both local and landscape scales, they do exhibit high levels of species turnover among some groups. We found that both chronic disturbance and aridity represent strong drivers of butterfly assemblage structure. Aridity is the most important driver of changes in butterfly assemblages, whereby increased aridity drastically reduces fruit-feeding butterfly abundance along with alpha (^{0}D – species richness and ^{1}D – common species), beta (β_{SIM} - species turnover) and functional diversity, but the combined effect of aridity and chronic disturbance also play a decisive and negative role in terms of alpha and beta diversity. Moreover, we found that butterfly assemblages were nested in forest stands with high levels of chronic disturbance and aridity, with assemblages in the most arid and disturbed plots being nested subsets of those in less arid and disturbed sites. Finally, our results indicate the Caatinga dry forest is undergoing taxonomic and functional reorganization of its fruit-feeding butterfly assemblages, with species and functional groups with traits that confer increased sensitivity to aridity (i.e. ocellus-bearing species and monocot-feeding larvae) decreasing in abundance and more desiccation tolerant species and functional groups (i.e. larger and canopy-inhabitant butterflies) increasing in abundance.

Our findings corroborate previous studies that have demonstrated the adverse effects of chronic disturbance and aridity on butterflies across dry forests. For instance, it was found in a Colombian dry forest that wood extraction have a strong and negative impact on butterfly assemblages, resulting in a loss of diversity as disturbance increases (Casas-Pinilla et al., 2017). The reorganization of butterfly assemblages we report here has also been observed in other ecological groups ─ especially plants, where increasing rainfall has a conspicuous and positive effect on plant diversity (especially rare species) (e.g. Rito, Arroyo-Rodríguez et al., 2017; Ribeiro et al., 2019). Moreover, disturbance and aridity have been shown to limit the distribution of plant species that are sensitive to human use (Ribeiro et al., 2019) or changes in water availability (Rito, Arroyo-Rodríguez et al. 2017), while other species exhibiting morphological and physiological adaptations to open and dry conditions are benefited (Rito, Arroyo-Rodríguez et al., 2017; Sfair et al., 2018; Pinho et al., 2019; Ribeiro et al., 2019). For instance, some plant species are restricted to wetter areas with a nested pattern along water deficit gradients (dry tolerance hypothesis; Esquivel-Muelbert et al., 2017). Moreover, there is clear evidence that increasing aridity intensifies the negative effects of chronic disturbance on butterflies as previously observed for plants (Rito, Arroyo-Rodríguez et al., 2017) and ants (Arnan, Arcoverde et al., 2018).

The strong negative effect of aridity increasing on butterfly assemblages in the present study corroborated our expectation for a dry forest. Water deficit is considered a strong environmental filter in dry forests, influencing species distribution and community organization (Engelbrecht et al., 2007; Mora et al., 2015; Rito, Arroyo-Rodríguez et al., 2017; Arnan, Arcoverde et al., 2018; Souza et al., 2019). Drier forests may provide limited food sources for both larva (leaf) and adult (fleshy fruits) butterflies, which can be further intensified by a large water-deficit, leading to dehydration of host plants and butterflies (especially for low mobility immature stages). In fact, we recorded many dominant and generalist species (e.g. *F. halice moretta*, *F. glycerium cratais* and *H. februa februa*) adapted to arid environments, while very few of the species were dependent on forest or forest edge habitats (e.g. *O. invirae remoliatus* and *Pharneuptychia* sp.), which were negatively impacted by increasing aridity. This may be related to the higher density of pioneer/colonizer species (e.g. Euphorbiaceae) that are more tolerant to disturbance and dryer climatic conditions (Rito, Tabarelli et al., 2017), contributing to a nested pattern due to the proliferation of some fruit-feeding butterflies that use these plants as larval food. In Caatinga dry forests, there is a positive relationship between tree density and butterfly abundance (Beirão et al., 2017), indicating a potential ecological release due to the proliferation of some butterfly species (e.g. *H. februa februa*) and their host plants. Thus, the distribution of fruit-feeding butterflies may be a response to the distribution of their food plants, which are thus constraining the persistence of each butterfly species throughout the chronic disturbance and aridity gradients. Therefore, our results extend the dry tolerance hypothesis to insects, with those fruit-feeding butterfly species most dependent on water-demanding plant species showing restricted distributions in the Caatinga dry forest.

In this perspective, Climate change is driving changes in the functional composition of butterfly assemblages across Caatinga dry forests via environmental filtering, whereby large-bodied and canopy-inhabitant butterflies are dominant and generalist in highly arid areas. In contrast, some species are probably more climate-sensitive, such as some Satyrinae (e.g. *O. invirae remoliatus*, *Pharneuptychia* sp. and *Paryphthimoides poltys*). In fact, several shade-tolerant ecological groups that are typical of closed-canopy tropical rainforests, such as Satyrinae, are underrepresented in the Caatinga. Regarding this functional composition, all sampled Satyrinae presented wing ocelli and their larvae feeds on monocotyledon plants, especially grasses, whose low tolerance to desiccation may contribute to explaining the negative effect of aridity on these butterfly traits. Accordingly, these species can persist in some areas of the landscape where a water deficit is less detrimental to survival for their herbaceous host plants.

In contrast, chronic disturbance in the Caatinga dry forest appears to pose different impacts on butterflies, as it negatively affected large-wing and canopy-inhabitant butterflies and positively affected ocellus-bearing species and monocot-feeding larvae in our focal landscape. Large-bodied insects tend to be more sensitive to unpredictable changes relative to both habitat structure and quality, particularly the seasonal large butterflies (Ribeiro & Freitas, 2011). In addition, disturbances can alter forest structure and reduce canopy cover (Singh, 1998) and favor herbs and grasses, especially if of interest to some livestock (Pereira-Filho et al., 2013), in the Caatinga dry forest. Collectively, canopy collapse or discontinuity and dense herb assemblages could explain both the decline of large-bodied butterflies and the increment of Satyrini (e.g. ocellus-bearing species and monocot-feeding larvae) in the most disturbed areas as documented in our focal landscape.

5. Conclusions

In summary, chronic disturbance and water deficit operate as important drivers of the spatial organization of fruit-feeding butterfly assemblages across human-modified landscapes of the Caatinga dry forest by affecting a large set of community-level attributes. More specifically, we found that abundance, alpha diversity and species turnover of fruit-feeding butterfly assemblages were all highest in wetter areas. Additionally, the chronic disturbances also have a negative effect on the total number of species (${}^{0}D$) of fruit-feeding butterflies. Additionally, we found that fruit-feeding butterfly assemblages exhibited a nested pattern (β_{SNE}), which was greatest in drier areas with high levels of chronic disturbance, indicating the synergistic negative effects of these two factors. In fact, we have shown the effect of increasing aridity is more pronounced in forested areas with high levels of chronic disturbance. In this way, even though aridity has a stronger negative influence on the diversity of fruit-feeding butterflies, chronic disturbance can act as an additional negative factor with the potential to reduce the resilience of Caatinga dry forests. Thus, the potential connections between chronic disturbance, aridity, desiccation, proliferating plant species and their insect attendants as community assembly forces deserves further investigation as both chronic human disturbances and climate change are expected to gain momentum across tropical regions, including arid regions (e.g. the Caatinga and other dry forests). We refer to winner trophic cascades (*sensu* Filgueiras et al., 2021) induced by environmental filtering, which are able to reorganize assemblages taxonomically and functionally (e.g. large-bodied and canopy-inhabitant butterflies), thus redefining the spectrum of biodiversity able to persist in human-modified landscapes and the ecosystem functions and services it is able to provide, as land use and climate change proceed.

Acknowledgments

We thank the ICMBio for allowing us to work in Catimbau National Park. This project was supported by the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq PELD 403770/2012-2 and *Edital Universal* 470480/2013-0) and the *Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco* (FACEPE APQ 0738-2.05/12, APQ 0138-2.05/14, and PRONEX APQ 0138-2.05/14). This study is part of DHAM’s PhD thesis as part of the *Programa de Pós Graduação em Biologia Animal* (PPGBA-UFPE). DHAM acknowledges the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES), Finance Code 001, for a PhD scholarship. BKCF acknowledges the CNPq for a post-doc grant (159106/2018-4) and AVLF, MT and IRL for productivity grants (303834/2015-3, 310228/2016-6 and 305611/2014-3, respectively). AVLF also acknowledges support from the *Fundação de Amaparo à Pesquisa do Estado de São Paulo* (FAPESP 2011/50225-3 and 2013/50297-0) and from the National Science Foundation (NSF DEB-1256742). This publication is part of the *RedeLep – Rede Nacional de Pesquisa e Conservação de Lepidópteros*: SISBIOTA-Brasil/CNPq (Grant 563332/2010-7).

Author’s Contributions

DHAM, BKCF and IRL originally conceived the ideas and designed the experiments; DHAM and BKCF collected the fruit-feeding butterfly data, conduced the statistical analyses and coordinated the writing of the manuscript. AVLF, MT and IRL contributed in the critical revision, adding intellectual content. All authors significantly contributed to the manuscript drafts and gave final approval for submission.

ORCID

D. H. A. Melo: 0000-0002-8607-1373

A. V. L. Melo: 0000-0002-5763-4990

M. Tabarelli: 0000-0001-7573-7216

B. K. C. Filgueiras: 0000-0003-0245-3516

I. R. Leal: 0000-0002-8125-2191

References

Andrade, R. B., Balch, J. K., Carreira, J. Y. O., Brando, P. M., & Freitas, A. V. L. (2017). The impacts of recurrent fires on diversity of fruit-feeding butterflies in a south-eastern Amazon forest. *Journal of Tropical Ecology*, *33*, 22–32. https://doi.org/10.1017/S0266467416000559

Arnan, X., Arcoverde, G. B., Pie, M. R., Ribeiro-Neto, J. D., & Leal, I. R. (2018). Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest. *Science of the Total Environment, 631–632*, 429–438. https://doi.org/10.1016/j.scitotenv.2018.03.037

Arnan, X., Leal, I. R. et al. (2018). A framework for deriving measures of chronic anthropogenic disturbance: Surrogate, direct, single and multi-metric indices in Brazilian Caatinga. *Ecological Indicators*, *94*, 274–282. https://doi.org/10.1016/j.ecolind.2018.07.001

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology Biogeography, 19,* 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Beirão, M. V., Neves, F. S., Penz, C. M., DeVries, P. J., & Fernandes, G. W. (2017). High butterfly beta-diversity between Brazilian Cerrado and Cerrado-Caatinga transition zones. *Journal of Insect Conservation*, *21*, 849–860. https://doi.org/10.1007/s10841-017-0024-x

Bivand, R., & Lewin-Koh, N. (2015). maptools: tools for reading and handling spatial objects. Available online at: http://CRAN.R-project.org/package=maptools

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer.

Calcagno, V., & Mazancourt, C. (2010). glmulti: a R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, *34*, 1–29. https://doi.org/10.18637/jss.v034.i12

Câmara, T., Leal, I. R., Blüthgen, N., Oliveira, F. M. P., & Arnan, X. (2019). Anthropogenic disturbance and rainfall variation threaten the stability of plant-ant interactions in the Brazilian Caatinga. *Ecography*, *42*, 1960–1972. https://doi.org/10.1111/ecog.04531

Casas-Pinilla, L. C., Mahecha-J. O., Dumar-R., J. C., Ríos-Málaver, I. C. (2017). Diversidad de mariposas en un paisaje de bosque seco tropical, en la Mesa de los Santos, Santander, Colombia (Lepidoptera: Papilionoidea). *SHILAP Revista de Lepidopterología*, *45*, 83–108.

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, *93*, 2533–2547. https://doi.org/10.1890/11-1952.1

Chatterjee, S., Hadi, A. S., & Price, B. (2000). Regression Analysis by Example. Wiley.

Crawley, M. J. (2013). The R Book (2nd ed.). John Wiley & Sons.

De Bello, F., Carmona, C. P., Mason, N. W. H., Sebastià, M-T, Lepš J. (2013). Which trait dissimilarity for functional diversity: trait means or trait overlap? *Journal of Vegetation Science*, *24*, 807–819. https://doi.org/10.1111/jvs.12008

DeVries, P. J., Murray, D., Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, *62*, 343–364. https://doi.org/10.1006/bijl.1997.0155

Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., & Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, *447*, 80–82. https://doi.org/10.1038/nature05747

Esquivel-Muelbert, A. et al. (2017). Seasonal drought limits tree species across the Neotropics. *Ecography*, *40*, 618–629. https://doi.org/10.1111/ecog.01904

Filgueiras, B. K. C., Melo, D. H. A., Leal, I. R., Tabarelli, M., Freitas, A. V. L. & Iannuzzi, L. (2016). Fruit-feeding butterflies in edge-dominated habitats: community structure, species persistence and cascade effect. *Journal of Insect Conservation*, *20*, 539–548. https://doi.org/10.1007/s10841-016-9888-4

Filgueiras, B. K. C., Peres, C. A., Melo, F. P. L., Leal, I. R., & Tabarelli, M. (2021). Winner-loser species replacements in human-modified landscapes. *Trends in Ecology and Evolution*. In press.

Forister, M. L., McCall, A. C., Sanders, N. J., Fordyce, J. A., Thorne, J. H., O'Brien, J., Waetjen, D. P., & Shapiro, A. M. (2010). Are secondary forests ready for climate change? It depends on magnitude of climate change, landscape diversity and ecosystem legacies. *PNAS*, *107,* 2088–2092. https://doi.org/10.1073/pnas.0909686107

Fox. J., & Weisberg, S. (2011). An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. Available online at: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Freitas A. V. L., Iserhard C. A., Santos J. P., Carreira J. Y. O., Ribeiro D. B., Melo D. H. A., Rosa A. H. B., Marini-Filho O. J., Accacio G. M., & Uehara-Prado M. (2014). Studies with butterfly bait traps: an overview. *Revista Colombiana de Entomología*, *40,* 209–218.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, *86,* 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Gueratto, P. E., Carreira, J. Y. O., Santos, J. P., Tacioli, A. & Freitas, A. V. L. (2020). Effects of forest trails on the community structure of tropical butterflies. *Journal of Insect Conservation*, *24,* 309–319. https://doi.org/10.1007/s10841-019-00199-x

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25,* 1965–1978. https://doi.org/10.1002/joc.1276

Hirota, M., Holmgren, M., Van Nes, H., & Scheffer, M. (2011). Global resilience of tropical forest and savanna to critical transitions. *Science*, *334,* 232–235. https://doi.org/10.1126/science.1210657

Hsieh T. C., Ma, K. H., Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*, 1451–1456. https://doi.org/10.1111/2041-210X.12613

Hughes J. B., Daily G. C., & Ehrlich P. R. (1998). Use of fruit bait traps for monitoring of butterflies (Lepidotera: Nymphalidae). *Revista de Biología Tropical*, *46*, 697–704. https://doi.org/10.15517/RBT.V46I3.20199

Iserhard, C. A., Duarte, L., Seraphim, N., & Freitas, A. V. L. (2019). How urbanization affects multiple dimensions of biodiversity in tropical butterfly assemblages. *Biodiversity and Conservation*, *28*, 621–638. https://doi.org/10.1007/s10531-018-1678-8

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*, 2427–2439. https://doi.org/10.1890/06-1736.1

Laliberté, E., Legendre, P., & Shipley, B. (2015). Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Package ‘‘FD’’ for version 1.0-12

Lamas, G. (2004). Checklist: Part 4A Hesperioidea – Papilionoidea. In J. B. Heppner (Ed.), *Atlas of Neotropical Lepidoptera* (pp xxxiv + 428). Association of Tropical Lepidoptera.

Leal, L. C., Andersen, A. N., & Leal, I. R. (2014). Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. *Oecologia*, *174*, 173–181. https://doi.org/10.1007/s00442-013-2740-6

Lee, S., Jeon, H., & Kim, M. (2020). Spatial distribution of butterflies in Accordance with climate change in the Korean Peninsula. *Sustainability*, *12*, 1995. https://doi.org/10.3390/su12051995

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia1*, *129*, 271–280. https://doi.org/10.1007/s004420100716

Leidner, A. K., Haddad, N. M., & Lovejoy, T. E. (2010). Does tropical forest fragmentation increase long-term variability of butterfly communities? *PLoS ONE*, *5*, e9534. https://doi.org/10.1371/journal.pone.0009534

Lutz, J.A., van Wagtendonk, J. W., & Franklin, J. F. (2010). Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *Journal of Biogeography*, *37*, 936–950. https://doi.org/10.1111/j.1365-2699.2009.02268.x

Martorell, C., & Peters, E. M. (2005). The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. *Biological Conservation*, *124*, 199–207. https://doi.org/10.1016/j.biocon.2005.01.025

Mathewson, P. D., Moyer-Horner, L., Beever, E. A., Briscoe, N. J., Kearney, M., Yahn, J. M., & Porter, W. P. (2016). Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. *Global Change Biology*, *23*, 1048–1064. https://doi.org/10.1111/gcb.13454

Melo, D. H. A., Filgueiras, B. K. C., Iserhard, C. A., Iannuzzi, L., Freitas, A. V. L, & Leal, I. R. (2019). Effect of habitat loss and fragmentation on fruit-feeding butterflies in the Brazilian Atlantic Forest. *Canadian Journal of Zoology*, *97*, 588–596. https://doi.org/10.1139/cjz-2018-0202

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, *10*, 710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., & Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Mora, F., Martinez-Ramos, M., Ibarra-Manríquez, G., Pérez-Jiménez, A., Trilleras, J., & Balvanera, P. (2015). Testing chronosequences through dynamic approaches: Time and site effects on tropical dry forest succession. *Biotropica*, *47*, 38–48. https://doi.org/10.1111/btp.12187

Morris, R. (2010). Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B*, *365*, 3709–3718. https://doi.org/10.1098/rstb.2010.0273

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*, 67-88. https://doi.org/10.1146/annurev.es.17.110186.000435

Oliveira, F. M. P., Andersen, A. N., Arnan, X., Ribeiro-Neto, J. D., Arcoverde, G. B., & Leal, I. R. (2019). Effects of increasing aridity and chronic anthropogenic disturbance on seed dispersal by ants in Brazilian Caatinga. *Journal of Animal Ecology*, *88*, 870–880. https://doi.org/10.1111/1365-2656.12979

Oliver, T. H., Marshall, H. H., Morecroft, M. D., Brereton, T., Prudhomme, C., & Huntingford, C. (2015). Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, *5*, 941–945. https://doi.org/10.1038/nclimate2746

Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody plant diversity, evolution, and ecology in the tropics: perspectives from Seasonally Dry Tropical Forests. *Annual Review of Ecology, Evolution and Systematics*, *40*, 437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327

Pereira-Filho, J. M., Silva, A. M. A., Cézar, M. F. (2013). Management of the Caatinga for the production of goats and sheep. *Revista Brasileira de Saúde e Produção Animal*, *14*, 77–90. https://doi.org/10.1590/S1519-99402013000100010

Phillips, O. L. et al. (2010). Drought–mortality relationships for tropical forests. *New Phytologist*, *187*, 631–646. https://doi.org/10.1111/j.1469-8137.2010.03359.x

Pinho, B. X., Tabarelli, M., Engelbrecht, B. M. J., Sfair, J., Melo, F. P. L. (2019). Plant functional assembly is mediated by rainfall and soil conditions in a seasonally dry tropical forest. *Basic and Applied Ecology*, *40*, 1–11. https://doi.org/10.1016/j.baae.2019.08.002

R Development Core Team. (2017). R a language and environment for statistical computing. R Foundation for Statistical Computing. Available online at: http://www.R-project.org.

Ribeiro, D. B., Freitas, A. V. L. (2011). Large-sized insects show stronger seasonality than small-sized ones: a case study of fruit-feeding butterflies. *Biological Journal of the Linnean Society*, *104*, 820–827. https://doi.org/10.1111/j.1095-8312.2011.01771.x

Ribeiro D. B., & Freitas A. V. L. (2012). The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. *Journal of Insect Conservation*, *16*, 733–744. https://doi.org/10.1007/s10841-012-9458-3

Ribeiro D. B., Batista R., Prado P. I., Brown Jr. K. S., & Freitas A. V. L. (2012). The importance of small scales to the fruit-feeding butterfly assemblages in a fragmented landscape. *Biodiversity and Conservation*, *21*, 811–827. https://doi.org/10.1007/s10531-011-0222-x

Ribeiro, E. M. S., Arroyo-Rodríguez, V., Santos, B. A., Tabarelli, M., & Leal, I. R. (2015). Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. *Journal of Applied Ecology*, *52*, 611–620. https://doi.org/10.1111/1365-2664.12420

Ribeiro, E. M. S., Lohbeck, M., Santos, B. A., Arroyo-Rodrigues, V., Tabarelli, M., & Leal, I. R. (2019). Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. *Journal of Ecology* 107, 2291-2302. https://doi.org/10.1111/1365-2745.13177

Ribeiro, E. M. S., Santos, B. A., Arroyo-Rodrigues, V., Tabarelli, M., Souza, G., & Leal, I. R. (2016). Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology*, *97*, 1583–1592. https://doi.org/10.1890/15-1122.1

Ribeiro-Neto, J. D., Arnan, X., Tabarelli, M., & Leal, I. R. (2016). Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. *Biodiversity and Conservation*, *25*, 943–956. https://doi.org/10.1007/s10531-016-1099-5

Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, *167*, 181–188. https://doi.org/10.1007/s00442-011-1965-5

Rito, K. F., Arroyo-Rodríguez, V., Queiroz, R. T., Leal, I. R., & Tabarelli, M. (2017). Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. *Journal of Ecology*, *105*, 828–838. https://doi.org/10.1111/1365-2745.12712

Rito, K. F., Tabarelli, M., & Leal, I. R. (2017). Euphorbiaceae responses to chronic anthropogenic disturbances in Caatinga vegetation: From species proliferation to biotic homogenization. *Plant Ecology*, *218*, 749–759. https://doi.org/10.1007/s11258-017-0726-x

Santos, J. C., Leal, I. R., Almeida-Cortez, J. S., Fernandes, G. W., & Tabarelli, M. (2011). Caatinga: the scientific negligence experienced by a dry tropical forest. *Tropical Conservation Science*, *4*, 276-286. https://doi.org/10.1177/194008291100400306

Sfair, J. C., Bello, F., França, T. Q., Baldauf, C., & Tabarelli, M. (2018). Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. *Environmental Research Letters*, *13*, 025005. https://doi.org/10.1088/1748-9326/aa9f5e

Silva, J. M. C., Leal, I. R., & Tabarelli, M. (2017). Caatinga: The Largest Tropical Dry Forest Region in South America. Springer.

Singh, S. P. (1998). Chronic disturbance, a principal cause of environmental degradation in developing countries. *Environmental Conservation*, *25*, 1–2. https://doi.org/10.1017/S0376892998000010

Siqueira, F. F. S., Ribeiro-Neto, J. D., Tabarelli, M., Andersen, A. N., Wirth, R., & Leal, I. R. (2017). Leaf-cutting and populations profit from human disturbances in tropical dry forest in Brazil. *Journal of Tropical Ecology*, *33*, 337–344. https://doi.org/10.1017/S0266467417000311

Souza, D. G., Sfair, J. C., Paula, A. S., Barros, M. F., Rito, K. F., & Tabarelli, M. (2019). Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest. *Forest Ecology and Management*, *435*, 57–65. https://doi.org/10.1016/j.foreco.2018.12.042

Stefanescu, C., Peñuelas, J., & Filella, I. (2003). Effects of climate change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, *9*, 1494–1506. https://doi.org/10.1046/j.1365-2486.2003.00682.x

Tabarelli, M., Aguiar, A. V., Ribeiro, M. Z., & Metzger, J. P. (2012). A conversão da Floresta Atlântica em paisagens antrópicas: lições para a conservação da biodiversidade biológica das florestas tropicais. *Interciencia*, *37*, 88–92.

Todd, B. D., Scott, D. E., Pechmann, J. H. K., & Gibbons, J. W. (2011). Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proceedings of the Royal Society B*, *278*, 2191–2197. https://doi.org/10.1098/rspb.2010.1768

Trindade, D. P. F., Sfair, J. C., Paula, A. S., Barros, M. F., & Tabarelli, M. (2020). Water availability mediates functional shifts across ontogenetic stages in a regenerating seasonally dry tropical forest. *Journal of Vegetation Science*, *31*, 1088–1099. https://doi.org/10.1111/jvs.12896

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*, 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A. V. L. & Brower, A. V. Z. (2009). Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. *Proceedings of the Royal Society B*, *276*, 4295–4302. https://doi.org/10.1098/rspb.2009.1303

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., & Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS ONE*, *14*, e0216270. https://doi.org/10.1371/journal. pone.0216270

Legend for figures

Figure 1. Map of Catimbau National Park, in Pernambuco state, northeastern Brazil (A–B) showing the sampling sites (C). White bars correspond to the global chronic disturbance index across old-growth forests (OF).

Figure 2. Responses of abundance, total species richness (^0D), common species (^1D) and dominant species (^2D) of fruit-feeding butterfly assemblages to aridity and chronic disturbance (CAD) in Catimbau National Park, Pernambuco state, northeastern Brazil. The shaded areas indicate the ranges of 95% confidence intervals.

Figure 3. Contour plots exhibiting the combined effect of aridity and chronic anthropogenic disturbance on fruit-feeding butterfly diversity (^0D) in Catimbau National Park, Pernambuco state, northeastern Brazil.

Figure 4. Distance-based redundancy analysis (dbRDA) showing the relationship between fruit-feeding butterfly composition, aridity, and chronic disturbance (CAD) across old-growth forests (OF) in the Catimbau National Park, in Pernambuco state, northeastern Brazil. Butterfly species: Caso (*Callicore sorana sorana*), Fogl (*Fountainea glycerium cratais*), Foha (*Fountainea halice moretta*), Hafb (*Hamadryas februa februa*), Hyc (*Hypna clytemnestra forbesi*), Phap (*Pharneuptychia* sp.).

Figure 5. Abundance of fruit feeding-butterfly species along an aridity (A) and chronic disturbance (CAD) (B) gradients in Catimbau National Park, Pernambuco state, northeastern Brazil. Rare species (< 2 individuals) were not included due to low abundance.

Figure 6. Responses of community-weighted mean of butterfly traits to aridity and chronic disturbance (CAD) in Catimbau National Park, Pernambuco state, northeastern Brazil. The shaded areas indicate the ranges of 95% confidence intervals. Size (size of the anterior wing), Ocellus (ocellus-bearing species), Canopy (canopy-inhabitant butterflies) and Larval monocots (monocot-feeding larvae).

Table 1. Results of Generalized Linear Models (GLMs), showing the effects of aridity, chronic disturbance (CAD) and their combined effect (aridity + chronic disturbance) on abundance, total species richness (^0D), common species (^1D) and dominant species (^2D) of fruit-feeding butterflies in Catimbau National Park, Pernambuco state, northeastern Brazil. We show the values of model-averaged parameter estimates (β), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model). The sign (+/−) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were most accurate, i.e., those higher than the unconditional variance.

Response variable	**Predictors**	β	**UV**	**Importance**	R^2
Abundance	Aridity	-1.87×10^{-3}	1.46×10^{-5}	0.45	81%
	CAD	8.71×10^{-3}	4.45×10^{-5}	0.84	
	Aridity:CAD	-1.09×10^{-5}	7.71×10^{-9}	0.48	
	Intercept	3.04	1.03×10^{-1}	1.0	
^0D	Aridity	-3.81×10^{-2}	8.06×10^{-4}	0.55	64%
	CAD	-7.52×10^{-3}	1.91×10^{-3}	0.61	
	Aridity:CAD	-3.06×10^{-4}	3.53×10^{-7}	0.79	
	Intercept	13.13	5.54	1.0	
^1D	Aridity	-2.64×10^{-2}	1.53×10^{-4}	0.93	65%
	CAD	1.1×10^{-3}	2.36×10^{-4}	0.3	
	Aridity:CAD	-9.23×10^{-6}	3.95×10^{-8}	0.29	
	Intercept	6.76	1.03	1.0	
	Aridity	-1.59×10^{-2}	1.71×10^{-4}	0.77	63%

$^{2}\boldsymbol{D}$	CAD	4.18×10^{-3}	2.84×10^{-4}	0.48
	Aridity:CAD	3.07×10^{-5}	4.77×10^{-8}	0.46
	Intercept	4.67	1.21	1.0

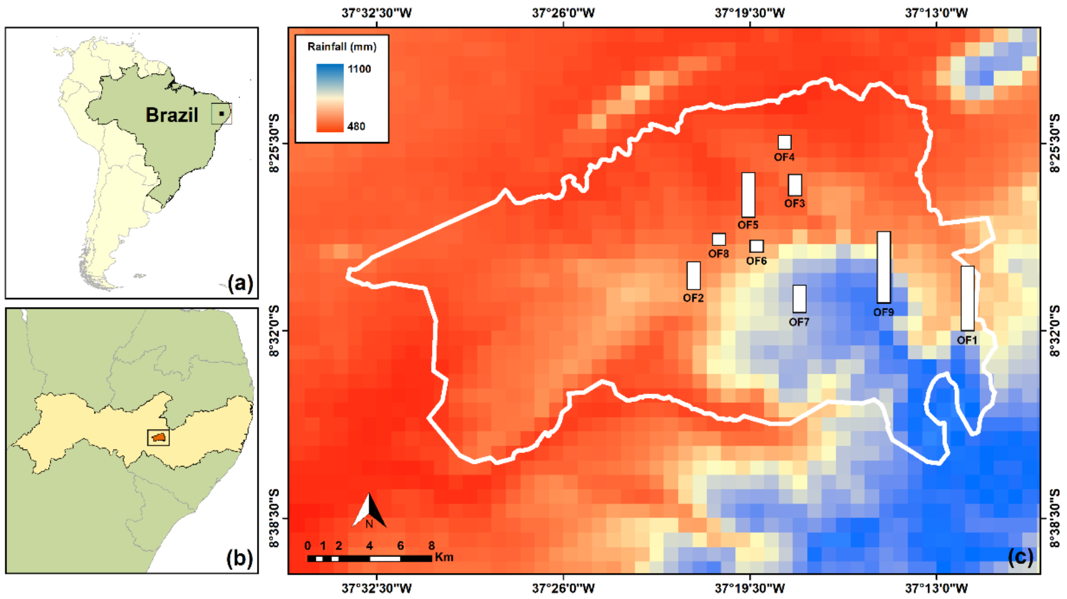

Brazil
(a)
(b)
37°32'30"W
37°26'0"W
37°19'30"W
37°13'0"W
8°25'30"S
8°32'0"S
8°38'30"S
Rainfall (mm)
1100
480
OF4
OF3
OF5
OF8
OF6
OF2
OF7
OF9
OF1
N
0 1 2 4 6 8
Km
(c)

Fig. 1

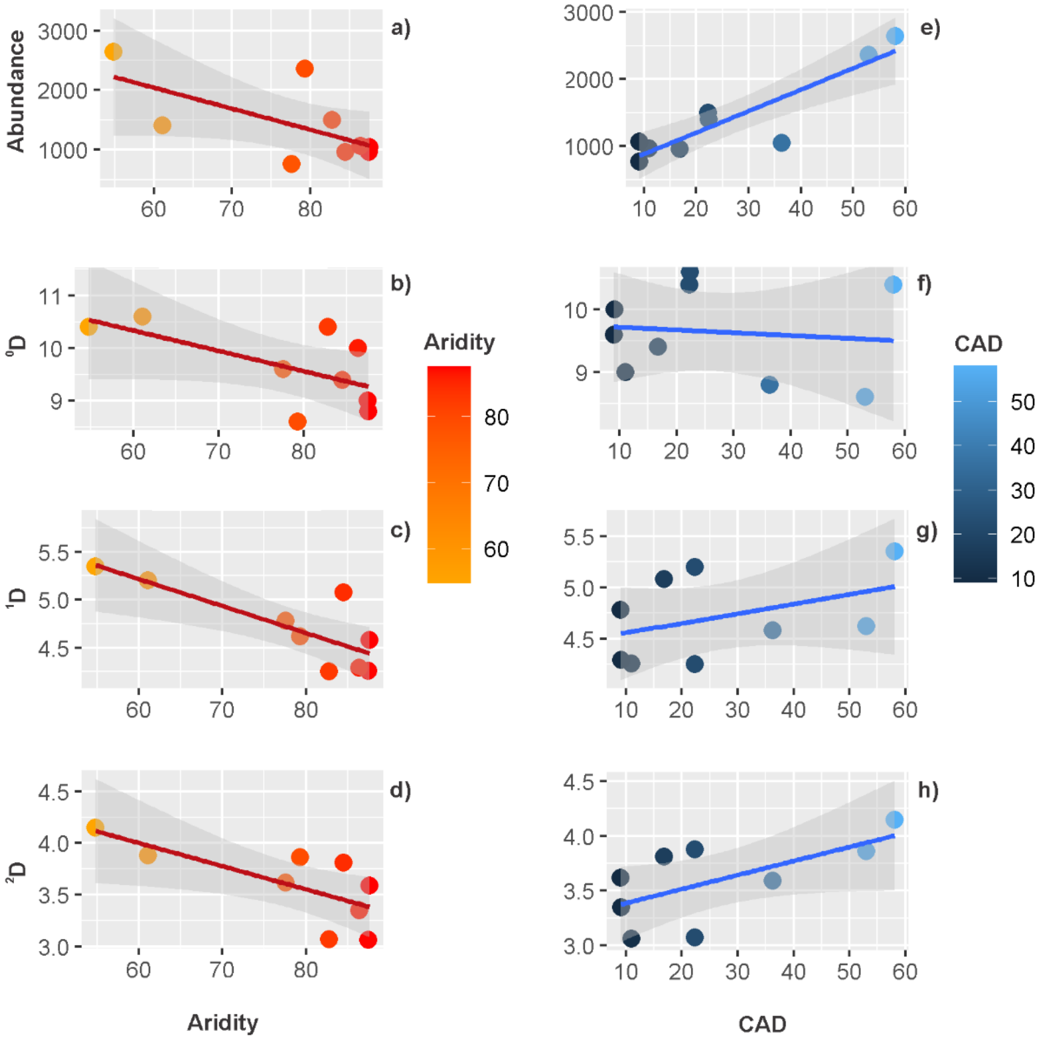

a)
b)
c)
d)
e)
f)
g)
h)
Abundance
3000
2000
1000
^0D
11
10
9
^1D
5.5
5.0
4.5
^2D
4.5
4.0
3.5
3.0
60
70
80
10
20
30
40
50
60
Aridity
80
70
60
CAD
50
40
30
20
10
Aridity
CAD

Fig. 2

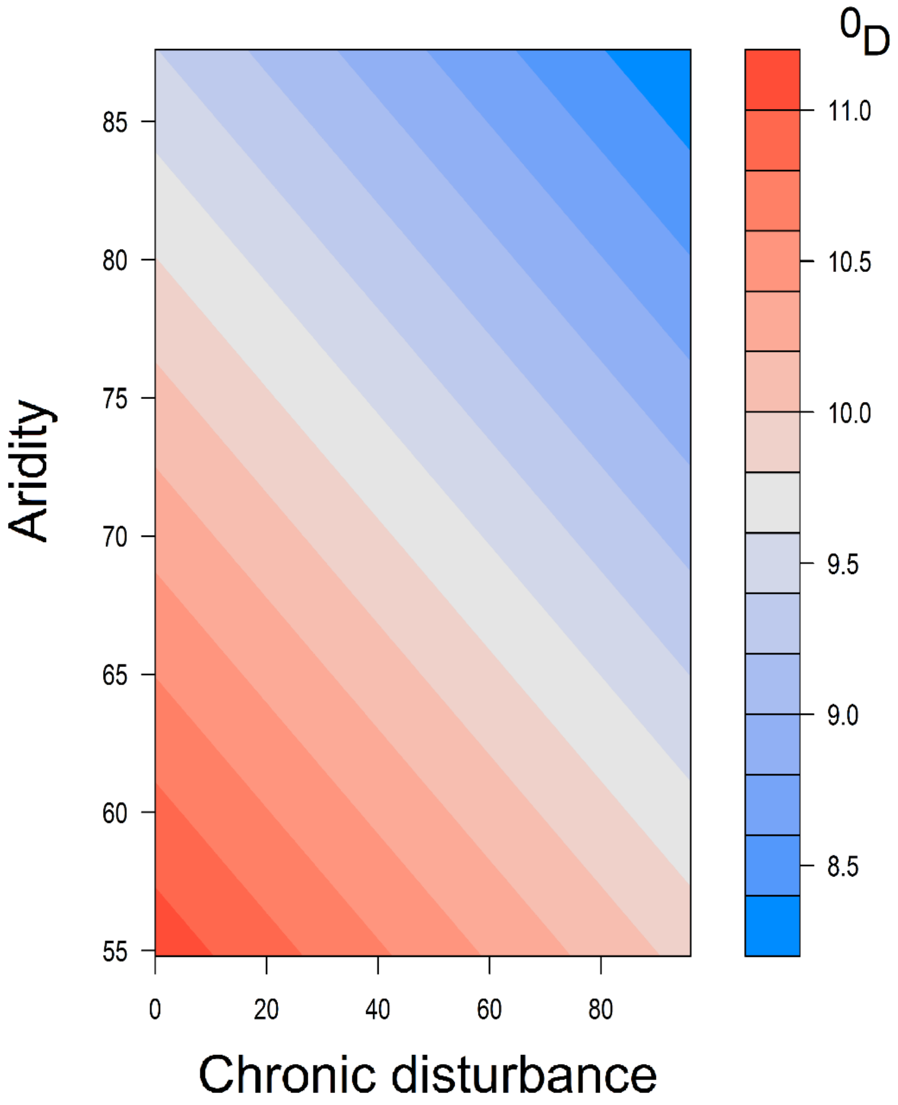

Aridity
85
80
75
70
65
60
55
0
20
40
60
80
Chronic disturbance
0D
11.0
10.5
10.0
9.5
9.0
8.5

Fig. 3

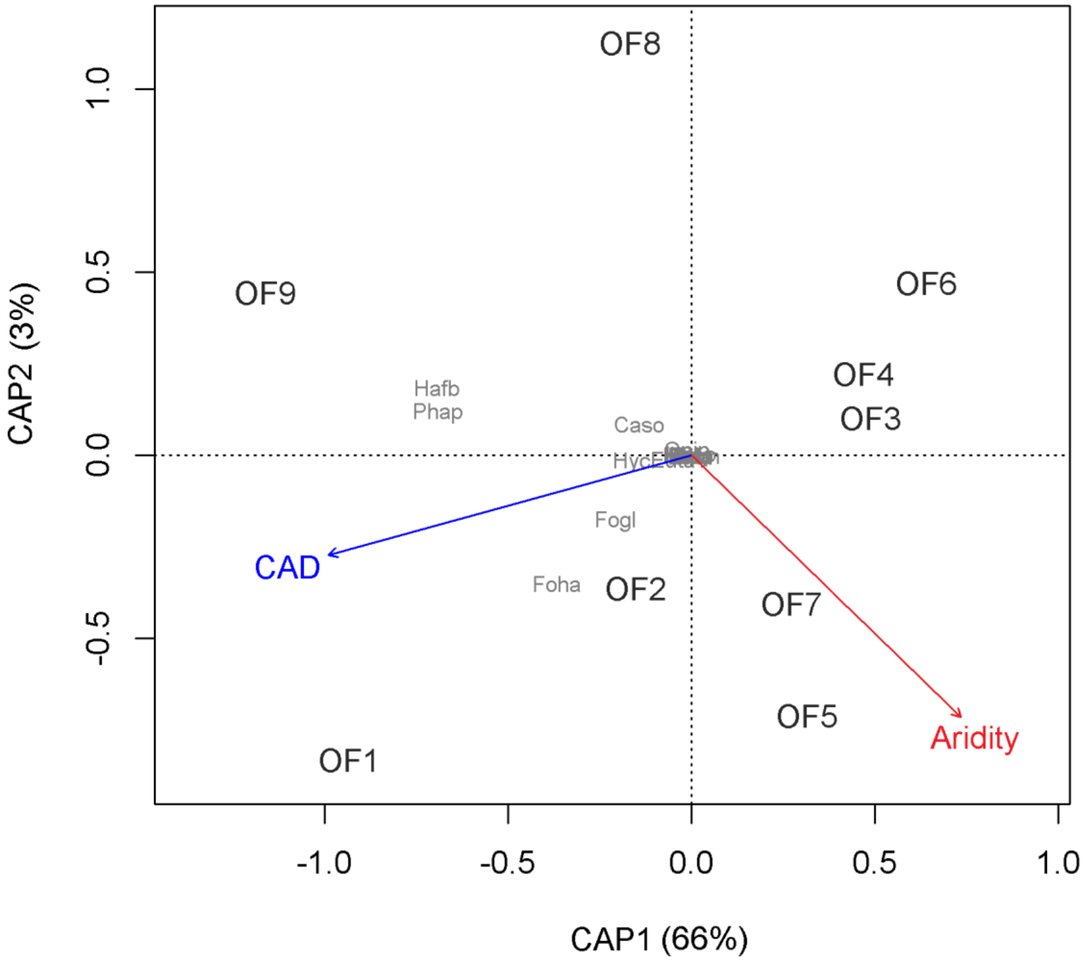

OF8
OF9
OF6
OF4
OF3
Hafb
Phap
Caso
Fogl
CAD
Foha
OF2
OF7
OF5
Aridity
OF1
1.0
0.5
0.0
-0.5
-1.0
CAP2 (3%)
CAP1 (66%)

Fig. 4

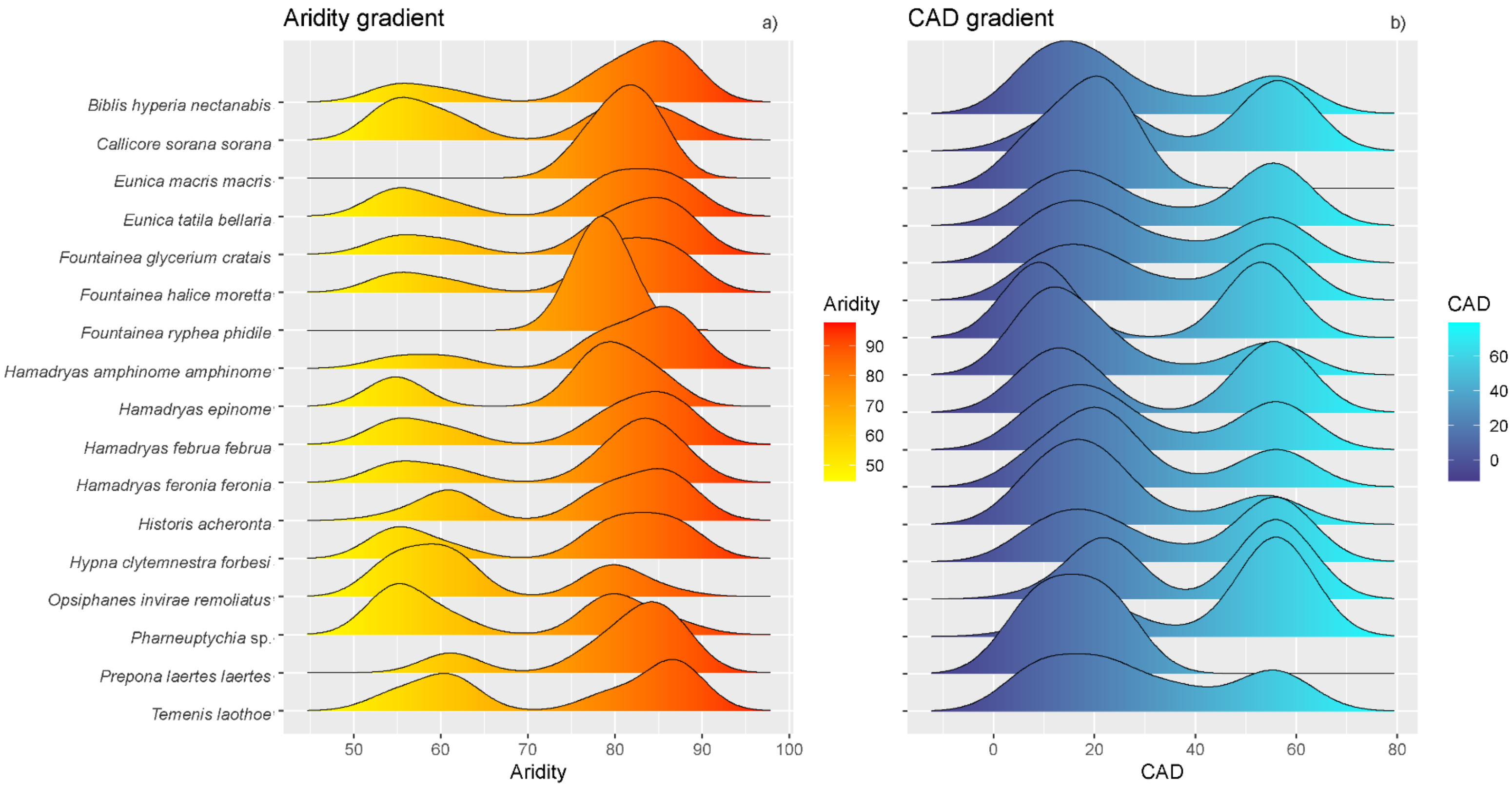

Aridity gradient
a)
Biblis hyperia nectanabis
Callicore sorana sorana
Eunica macris macris
Eunica tatila bellaria
Fountainea glycerium cratais
Fountainea halice moretta
Fountainea ryphea phidile
Hamadryas amphinome amphinome
Hamadryas epinome
Hamadryas februa februa
Hamadryas feronia feronia
Historis acheronta
Hypna clytemnestra forbesi
Opsiphanes invirae remoliatus
Pharneuptychia sp.
Prepona laertes laertes
Temenis laothoe
50
60
70
80
90
100
Aridity
Aridity
90
80
70
60
50
CAD gradient
b)
0
20
40
60
80
CAD
CAD
60
40
20
0

Fig. 5

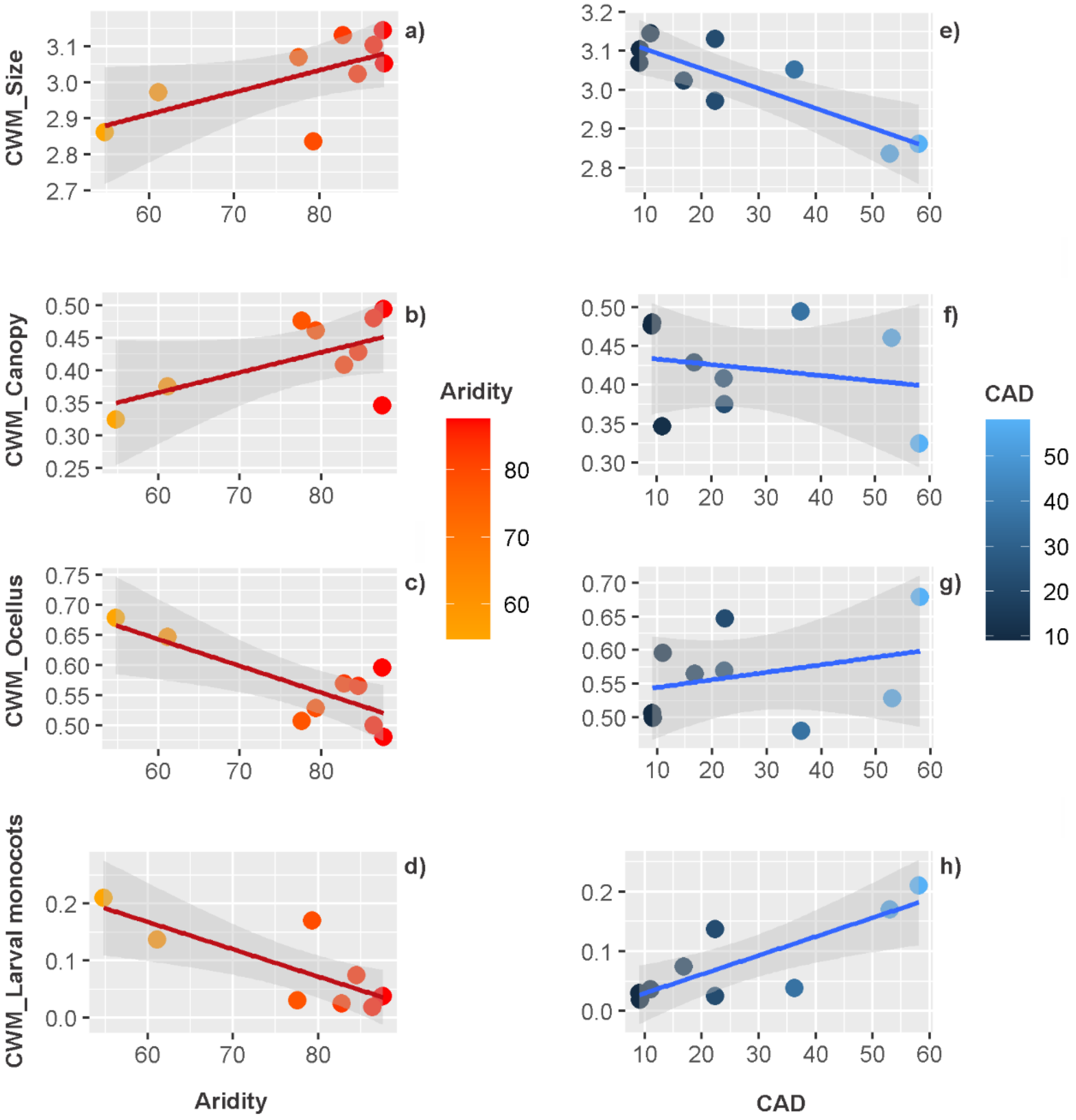

CWM_Size
3.1
3.0
2.9
2.8
2.7
60
70
80
a)
3.2
3.1
3.0
2.9
2.8
10
20
30
40
50
60
e)
CWM_Canopy
0.50
0.45
0.40
0.35
0.30
0.25
60
70
80
b)
Aridity
80
70
60
0.50
0.45
0.40
0.35
0.30
10
20
30
40
50
60
f)
CAD
50
40
30
20
10
CWM_Ocellus
0.75
0.70
0.65
0.60
0.55
0.50
60
70
80
c)
0.70
0.65
0.60
0.55
0.50
10
20
30
40
50
60
g)
CWM_Larval monocots
0.2
0.1
0.0
60
70
80
d)
Aridity
0.2
0.1
0.0
10
20
30
40
50
60
h)
CAD

Fig. 6

Additional Supporting Information for

Aridity and chronic anthropogenic disturbance as organizing forces of fruit-feeding butterfly assemblages in a Caatinga dry forest

Douglas H. A. Melo, André V. L. Freitas, Marcelo Tabarelli, Bruno K. C. Filgueiras, Inara R. Leal

Table S1. Aridity level and chronic disturbance (CAD) of old-growth forests in Catimbau National Park, Pernambuco state, northeastern Brazil. OF1 to OF9 correspond to the nine study plots of old-growth forest.

Table S2. Functional traits of fruit-feeding butterfly sampled in Catimbau National Park, Pernambuco state, northeastern Brazil. Wing size (average of up to five individuals per species). The sign (+/−) represents the present or absent/reduced traits, respectively. Larval plant (D – dicot-feeding larvae; M – monocot-feeding larvae).

Table S3. Abundance of fruit-feeding butterflies sampled in Catimbau National Park, Pernambuco state, northeastern Brazil. OF1 to OF9 correspond to the nine study plots of old-growth forest.

Table S4. Results of Generalized Linear Models (GLMs) showing the effects of aridity, chronic disturbance (CAD) and their combined effect (aridity + chronic disturbance) on species turnover (β_{SIM}) and nestedness (β_{SNE}) of fruit-feeding butterflies in Catimbau National Park, Pernambuco state, northeastern Brazil. We show the values of model-averaged parameter estimates (β), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model). The sign (+/−) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were most accurate, i.e., those higher than the unconditional variance.

Table S5. Results of Generalized Linear Models (GLMs) showing the effects of aridity, chronic disturbance (CAD) and the combined effect (aridity + chronic disturbance) on functional diversity (Rao's Q) and community-weighted means (CWM) of butterfly traits in Catimbau National Park, Pernambuco state, northeastern Brazil. We show the values of model-averaged parameter estimates (*β*), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model). The sign (+/−) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were most accurate, i.e., those higher than the unconditional variance.

Table S1. Aridity level and chronic disturbance (CAD) of old-growth forests in Catimbau National Park, Pernambuco state, northeastern Brazil. OF1 to OF9 correspond to the nine study plots of old-growth forest.

Plot	Aridity	CAD	Coordinates
OF1	66	53.0	8° 31' 52.837"" S and 37° 11' 48.615"" W
OF2	99	22.3	8° 30' 26.070"" S and 37° 21' 18.212"" W
OF3	84	16.8	8° 26' 58.516"" S and 37° 17' 57.634"" W
OF4	94	11.0	8° 25' 40.012"" S and 37° 18' 16.689"" W
OF5	69	36.3	8° 27' 56.877"" S and 37° 19' 33.380"" W
OF6	84	9.07	8° 29' 7.368"" S and 37° 19' 19.942"" W
OF7	84	22.4	8° 31' 15.089"" S and 37° 17' 46.703"" W
OF8	91	9.14	8° 28' 58.984"" S and 37° 20' 34.127"" W
OF9	89	58.06	8° 30' 59.883"" S and 37° 14' 41.796"" W

Table S2. Functional traits of fruit-feeding butterflies sampled in Catimbau National Park, Pernambuco state, northeastern Brazil. Wing size (average of up to five individuals per species). The sign (+/−) represents the present or absent/reduced traits, respectively. Larval plant (D – dicot-feeding larvae; M – monocot-feeding larvae).

Taxon	Size	Ocellus	Canopy	Larval plant
Subfamily Biblidinae				
Biblis hyperia nectanabis (Fruhstorfer, 1909)	3,15	-	-	D
Callicore sorana sorana (Godart, [1824])	2,57	+	+	D
Eunica macris macris (Godart, [1824])	2,54	+	+	D
Eunica tatila bellaria Fruhstorfer, 1908	2,32	+	+	D
Hamadryas amphinome amphinome (Linnaeus, 1767)	3,74	+	-	D
Hamadryas epinome (C. Felder & R. Felder, 1867)	3,22	+	-	D
Hamadryas februa februa (Hübner, [1823])	3,42	+	-	D
Hamadryas feronia feronia (Linnaeus, 1758)	3,51	+	-	D
Temenis laothoe (Cramer, [1777])	2,49	-	+	D
Subfamily Charaxinae				
Fountainea glycerium cratais (Hewitson, 1874)	3,07	-	+	D
Fountainea halice moretta (Druce, 1877)	2,58	-	+	D
Fountainea ryphea phidile (Geyer, 1837)	2,89	-	+	D
Hypna clytemnestra forbesi Godman & Salvin, [1884]	3,55	-	-	D
Prepona laertes laertes (Hübner, [1811])	4,71	+	+	D
Zaretis strigosus (Gmelin, 1790)	2,86	-	+	D
Subfamily Nymphalinae				
Historis acheronta (Fabricius, 1775)	4,19	-	+	D
Historis odius dious Lamas, 1995	7,24	-	+	D

Smyrna blomfildia blomfildia (Fabricius, 1781)	4,43	+	-	D
Subfamily Satyrinae				
Tribe Brassolini				
Opsiphanes invirae remoliatus Fruhstorfer, 1907	3,62	+	+	M
Tribe Satyrini				
Paryphthimoides poltys (Prittwitz, 1865)	1,70	+	-	M
Pharneuptychia sp.	1,75	+	-	M

Table S3. Abundance of fruit-feeding butterflies sampled in Catimbau National Park, Pernambuco state, northeastern Brazil. OF1 to OF9 correspond to the nine study plots of old-growth forest.

Taxon	**Old-growth forests**									
	OF1	**OF2**	**OF3**	**OF4**	**OF5**	**OF6**	**OF7**	**OF8**	**OF9**	**Total**
Subfamily Biblidinae (9)	**870**	**835**	**494**	**553**	**478**	**380**	**732**	**538**	**1265**	**6145**
Biblis hyperia nectanabis (Fruhstorfer, 1909)	23	22	23	15	17	17	16	27	26	186
Callicore sorana sorana (Godart, [1824])	71	36	30	11	21	19	75	20	135	418
Eunica macris macris (Godart, [1824])	0	2	0	0	0	1	0	0	0	3
Eunica tatila bellaria Fruhstorfer, 1908	51	18	23	23	19	16	23	10	52	235
Hamadryas amphinome amphinome (Linnaeus, 1767)	3	1	3	3	1	3	2	4	2	22
Hamadryas epinome (C. Felder & R. Felder, 1867)	1	0	1	0	0	1	0	0	1	4
Hamadryas februa februa (Hübner, [1823])	718	750	413	500	418	322	612	473	1045	5251
Hamadryas feronia feronia (Linnaeus, 1758)	2	6	1	1	1	1	2	2	3	19
Temenis laothoe (Cramer, [1777])	1	0	0	0	1	0	2	2	1	7
Subfamily Charaxinae (6)	**1086**	**623**	**391**	**371**	**523**	**359**	**473**	**504**	**823**	**5153**
Fountainea glycerium cratais (Hewitson, 1874)	373	276	175	144	241	151	211	246	300	2117

Fountainea halice moretta (Druce, 1877)	579	274	180	153	232	172	200	228	361	2379
Fountainea ryphea phidile (Geyer, 1837)	2	0	0	0	0	2	0	0	0	4
Hypna clytemnestra forbesi Godman & Salvin, [1884]	131	70	36	74	50	33	61	28	162	645
Prepona laertes laertes (Hübner, [1811])	0	2	0	0	0	1	1	2	0	6
Zaretis strigosus (Gmelin, 1790)	1	1	0	0	0	0	0	0	0	2
Subfamily Nymphalinae (3)	**4**	**1**	**3**	**2**	**1**	**2**	**5**	**2**	**2**	**22**
Historis acheronta (Fabricius, 1775)	3	1	3	2	1	2	5	2	1	20
Historis odius dious Lamas, 1995	1	0	0	0	0	0	0	0	0	1
Smyrna blomfildia blomfildia (Fabricius, 1781)	0	0	0	0	0	0	0	0	1	1
Subfamily Satyrinae (3)	**401**	**37**	**71**	**35**	**40**	**23**	**192**	**20**	**555**	**1374**
Tribe Brassolini										
Opsiphanes invirae remoliatus Fruhstorfer, 1907	6	1	0	0	0	0	9	1	8	25
Tribe Satyrini										
Paryphthimoides poltys (Prittwitz, 1865)	0	1	0	0	0	0	0	0	0	1
Pharneuptychia sp.	395	35	71	35	40	23	183	19	547	1348
Grand Total	**2361**	**1496**	**959**	**961**	**1042**	**764**	**1402**	**1064**	**2645**	**12694**

Table S4. Results of Generalized Linear Models (GLMs) showing the effects of aridity, chronic disturbance (CAD) and their combined effect (aridity + chronic disturbance) on species turnover (β_{SIM}) and nestedness (β_{SNE}) of fruit-feeding butterflies in Catimbau National Park, Pernambuco state, northeastern Brazil. We show the values of model-averaged parameter estimates (*β*), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model). The sign (+/−) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were most accurate, i.e., those higher than the unconditional variance.

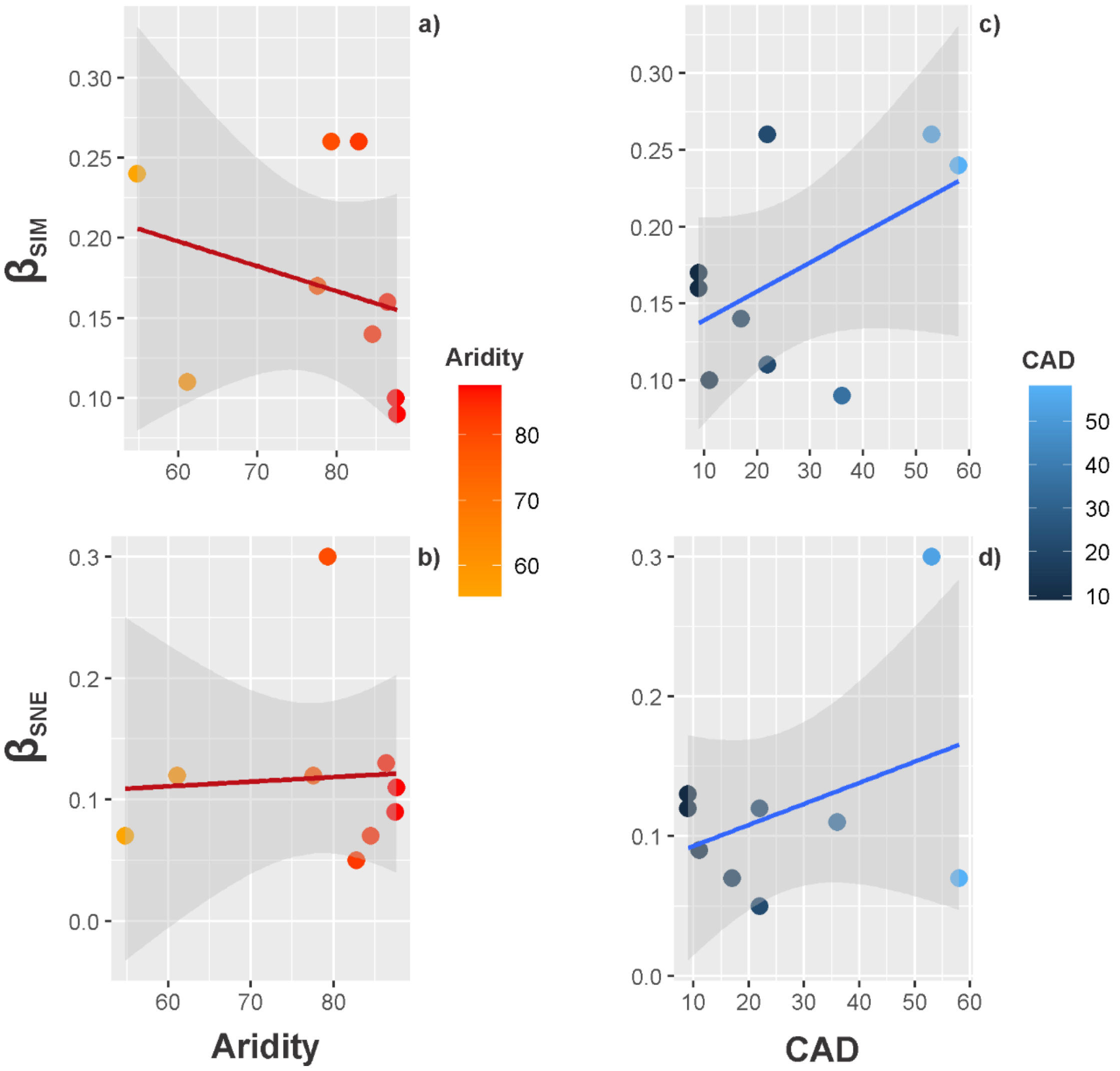
Response variable	**Predictors**	***β***	**UV**	**Importance**	**R^2**
βsim	Aridity	-1.56×10^{-4}	2.67×10^{-6}	0.3	29%
	CAD	1.11×10^{-3}	7.48×10^{-6}	0.48	
	Aridity:CAD	2.99×10^{-6}	1.27×10^{-9}	0.39	
	Intercept	0.146	0.02	1.0	
β_{SNE}	Aridity	1.01×10^{-4}	5.07×10^{-6}	0.33	44%
	CAD	1.32×10^{-3}	2.30×10^{-5}	0.45	
	Aridity:CAD	4.08×10^{-5}	4.64×10^{-9}	0.6	
	Intercept	0.08	0.04	1.0	

Table S5. Results of Generalized Linear Models (GLMs) showing the effects of aridity, chronic disturbance (CAD) and the combined effect (aridity + chronic disturbance) on functional diversity (Rao's Q) and community-weighted means (CWM) of butterfly traits in Catimbau National Park, Pernambuco state, northeastern Brazil. We show the values of model-averaged parameter estimates (*β*), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model). The sign (+/−) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were most accurate, i.e., those higher than the unconditional variance.

Response variable	Predictors	*β*	UV	Importance	R^2
Rao's Q	Aridity	-1.39 x 10-4	3.62 x 10-8	0.59	66%
	CAD	2.22 x 10-5	9.27 x 10-8	0.62	
	Aridity:CAD	2.36 x 10-6	1.58 x 10-11	0.61	
	Intercept	7.32 x 10-2	2.45 x 10-4	1.0	
CWM_Ocellus	Aridity	-3.19 x 10-3	6.51 x 10-6	0.75	68%
	CAD	2.41 x 10-3	1.99 x 10-5	0.47	
	Aridity:CAD	-3.55 x 10-5	3.61 x 10-9	0.49	
	Intercept	0.81	0.04	1.0	
CWM_Canopy	Aridity	1.26 x 10-3	5.85 x 10-6	0.54	52%
	CAD	-3.05 x 10-3	2.22 x 10-5	0.54	
	Aridity:CAD	4.41 x 10-5	4.19 x 10-9	0.55	
	Intercept	0.31	0.04	1.0	
CWM_Larval monocots	Aridity	-3.21 x 10-3	2.92 x 10-6	0.58	87%
	CAD	1.66 x 10-3	6.9 x 10-6	0.63	

	Aridity:CAD	6.38 x 10-6	1.15 x 10-9	0.9	
	Intercept	0.27	0.02	1.0	
CWM_Size	Aridity	3.01 x 10-3	9.72 x 10-6	0.69	80%
	CAD	-2.25 x 10-3	2.08 x 10-5	0.62	
	Aridity:CAD	-2.79 x 10-5	3.48 x 10-9	0.59	
	Intercept	2.89	0.06	1.0	

Figure S1. Responses of species turnover (βsim) and nestedness (βsne) of fruit-feeding butterfly assemblages to aridity and chronic disturbance (CAD) in Catimbau National Park, Pernambuco state, northeastern Brazil. The shaded areas indicate the ranges of 95% confidence intervals.



ARTIGO 2

Rapid recovery of fruit-feeding butterfly assemblages in the regeneration of a Caatinga dry forest submitted to shifting cultivation

Artigo a ser submetido ao periódico *Biodiversity and Conservation*

Formatado conforme as normas *Biodiversity and Conservation* disponível em: https://www.springer.com/journal/10531/submission-guidelines

Rapid recovery of fruit-feeding butterfly assemblages in the regeneration of a Caatinga dry forest submitted to shifting cultivation

Douglas H. A. Melo[1], André V. L. Freitas[2], Marcelo Tabarelli[3], Inara R. Leal[3], Bruno K. C. Filgueiras[4]

[1]Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco, Recife, Pernambuco, 50670-901, Brazil.

[2]Departamento de Biologia Animal and Museu de Zoologia, Universidade Estadual de Campinas, Campinas, São Paulo, 13083-862, Brazil.

[3]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, 50670-901, Brazil.

[4]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, 50670-901, Brazil.

ORCID:

D. H. A. Melo: 0000-0002-8607-1373

A. V. L. Melo: 0000-0002-5763-4990

M. Tabarelli: 0000-0001-7573-7216

I. R. Leal: 0000-0002-8125-2191

B. K. C. Filgueiras: 0000-0003-0245-3516

Abstract

Interest on forest regeneration has increased as secondary forests in regeneration process are cited as the forests of the future. However, the remaining forests are also subject to chronic anthropogenic disturbances, which may reorganize tropical biodiversity. This paper investigates the recovery of fruit-feeding butterfly assemblages after slash-and-burn agriculture in the Caatinga dry forest, including the role that chronic disturbances, tree species richness and biomass can play in their taxonomic and functional recovery during secondary succession across regenerating (4 to 50-yr old) and old-growth forest stands. A total of 20,252 butterflies from 22 species were recorded. There was a high similarity for community-level attributes (e.g. abundance and alpha diversity measures) in different levels of forest regeneration, which indicates a rapid recovery of butterflies along the successional trajectory in the Caatinga dry forest. However, secondary and old-growth forests support relatively distinct assemblages taxonomically and functionally. As expected, chronic disturbance, forest biomass and trees species richness were excellent predictors affecting taxonomic and functional changes. Specifically, large-bodied and canopy-inhabitant butterflies and achieve higher abundance in more disturbed habitats (i.e. higher chronic disturbance), while those ocellus-bearing species that flying in understory and monocot-feeding larvae respond negatively to disturbance, but benefit from increased forest biomass and tree species richness. Our findings suggest that although regenerating secondary forests can recover values of community-level attributes of the fruit-feeding butterflies similar to those of old-growth forests, the presence of chronic disturbance across the landscape can be selecting only some ecological groups more tolerant to adverse conditions. When land used for slash-and-burn agriculture is abandoned, chronic disturbances can delay succession processes, preventing the structure of old-growth forests is reached.

Keywords: anthropogenic disturbance, conservation, ecological indicators, Nymphalidae, seasonally dry tropical forests, secondary succession

Introduction

Tropical forests home significant portions of global biodiversity and are responsible for providing essential ecosystem services for human well-being, such as climate regulation and the provision of forest products (Ferraz et al. 2014). However, human disturbances are reorganizing tropical biodiversity across all levels of ecological organization from population to ecosystem level with tangible impacts on the provision of ecosystem services (Filgueiras et al. 2021). Local disturbances are completely related to the conversion of old-growth forests into human-modified landscapes, through which a myriad of small forest remnants and secondary forest stands of varying ages (regenerating forests) remain embedded within open-habitat matrix as agricultural lands are constantly abandoned (Melo et al. 2013). This is particularly the case of human-modified landscapes devoted to subsistence agriculture via slash-and-burn practices, the predominant land use across several tropical regions (Singh 1998; Laurance and Peres 2006). In this context, secondary forests have been frequently referred as potential source of ecosystem services, including biodiversity (Chazdon et al. 2009), which has led to renewed interest on forest regeneration and its drivers (see Arroyo-Rodriguez et al. 2015).

Whatever the role played by secondary forests in terms of biodiversity retention and provision of ecosystem services, these two targets depend on the speed that secondary forest stands approach the scores supported by the old-growth stands; i.e. recovery rate (Norden et al. 2009). The role of secondary-forest also depends on the successional trajectory or the patterns of species replacement as regeneration proceeds (Poorter et al. 2016). This is an intuitive connection since low recovery rates and successional trajectory marked by the presence of species typical of late successional stages reduce the contribution of early or intermediate secondary forests (see Guarigata and Ostertag, 2001). In this perspective, forest resilience and successional trajectory have been proposed to respond to a myriad of forces operating at multiple scales; from local (e.g. soil degradation) to regional scale such as the available pool of species (Arroyo-Rodriguez et al. 2015). Overall, in the absence of severe degradation imposed by intensive land use (e.g. commercial agriculture and pastures), forest can recovery relatively fast (Dunn 2004; Martin et al. 2013; Guariguata and Ostertag 2001), with the regeneration marked by directional species replacements, from acquisitive towards plant conservative strategies or vice-versa (Lohbeck et al. 2013). This is true for plants, as well as for amphibian and reptile assemblages (Hernández-Ordóñez et al. 2015) and bats (Avila-Cabadilla et al. 2009), but for insect communities changes are less predictable (but see Neves et al. 2010).

Dry forests exposed to slash-and-burn agriculture and chronic disturbances (collection of forest products) during regeneration may exhibit more simple or complex regeneration patterns, including site-dependent resilience and lack of directional species replacement as chronic disturbance favor resprouting species (Barros et al. 2021; Ceccon et al. 2006). Such a resprouting-based resilience (Quesada et al. 2009; Álvarez-Yépiz et al. 2018) probably leads to the occurrence of a common set of host plants across forest regeneration with impacts on the organization of herbivore assemblages. Additionally, the continuous extraction of forest resources (e.g. firewood, fodder, browsing by livestock) during forest regeneration may result in more disturbed forest stands (i.e. light exposure and desiccated stands) and thus benefit disturbance-adapted or generalist plant and insect species (Ribeiro-Neto et al. 2016). Both the presence of resprouting species and chronic disturbances may interfere on patterns of forest resilience and successional trajectory as already documented for plants (Barros et al. 2021). Butterflies constitute a candidate group to examine how insect assemblages recovery or change along forest regeneration, since they comprise ecologically responsive insects (Freitas et al. 2003, 2006) with a diverse fauna depending on plants for larval development and adult feeding.

The Caatinga dry forest in northeast Brazil has been converted into human-modified landscapes by a combination of slash-and-burn agriculture and free-ranging livestock production (Silva et al. 2017). Vegetation mosaics consisting of old-growth and regenerating forest stands of varying age plus agricultural fields comprise the predominant landscapes, through which rural population achieve livelihood by exploiting forest products (Specht et al. 2019). Recent findings have described the Caatinga forest regeneration and dynamics as largely influenced by resprouting species (Barros et al. 2021) with plant assemblages dominated by disturbance-adapted plant species (Ribeiro et al. 2015; Rito et al. 2017a).

Here, we address the recovery rate and the successional trajectory exhibited by fruit-feeding butterfly assemblages as forest regenerate in the context of slash-and-burn agriculture in the Caatinga dry forest. Additionally, the role that chronic disturbances, tree species richness and biomass can play in the recovery of these insects during forest regeneration was examined. We address and contrast a large set of community-level attributes, including ecological composition relative to microhabitat use, predation avoidance and feeding behaviour. Butterflies were recorded across regenerating (i.e. 4-50-yr old) and old-growth forest stands, which covered a small gradient of both precipitation and human-chronic disturbance imposed by locals (e.g. firewood collection and browsing by livestock). Our findings are examined in the light of both patterns and drivers of forest regeneration/resilience in human-modified landscapes marked by intensive use of forest resources.

Material and methods

Study area

The study was carried out in Parque Nacional do Catimbau (Catimbau National Park), a protected area of 607 km² located in the central region of the State of Pernambuco, northeastern Brazil (8º24’00’’ and 8º36’35’’ S; 37º09’30’’ and 37º14’40’’ W) (Fig. 1). The predominant climate in the region is the semi-arid Bsh type, with transition to the rainy tropical As type, according to the Köppen scale. The annual rainfall varies from 480 to 1100 mm, with great irregularity in the interannual regime (Rito et al. 2017b). Generally, about 60% to 75% of rainfall occurs in the period from March/April to June/July (Rito et al. 2017b). The annual average temperature is about 23°C, with July as the coldest month (average temperature of 21°C), and December (average temperature of 25°C) as the hottest month (Rito et al. 2017b). The vegetation consists of a mosaic of arboreal and shrub Caatinga (data obtained from Sociedade Nordestina de Ecologia 2002).

Habitats and fruit-feeding butterfly surveys

We carried out the research in 10 0.1-ha plots already established in areas previously used for slash-and-burn agriculture, which have different regeneration ages since their abandonment (from four to 50 years, defining a chronosequence). In addition, five 0.1-ha plots of old-growth forests with low level of anthropogenic disturbance were selected to serve as control to the regeneration plots (Fig. 1). In order to maintain spatial independence, all plots were selected so that the minimum distance between them was of 1 km. The age of forest stands was established by interviews with local residents. In this way, plots without record of shift cultivation by locals for the last 100 years were considered as old growth forest and arbitrarily set as being 150 years old. Successional stands were previously used for small crops, such as corn, beans and cassava, and were abandoned after lack of financial return and soil nutrient depletion (Souza et al. 2019). All plots were established in areas sharing the same soil type (sandy soils) and similar slope (flat terrain), which indicates a similar history of land use across the landscape.

Each plot received one sampling unit composed of five portable Van Someren-Rydon traps (following DeVries 1997), totaling 75 traps at the study site. These traps consisted of cylindrical tubes made with netting (110 cm of high x 35 cm in diameter) and an internal cone (30 cm high and 22 cm wide at the opening) at the bottom to prevent butterflies from escaping. The lower part was open and attached to a plywood platform with a distance of 4 cm to allow butterflies to enter the trap. A mixture of banana and sugar cane juice fermented for 48 h was used as attractive bait. Baits were placed inside traps in plastic pots with a perforated cover to prevent butterflies from drowning into the liquid, to avoid feeding by other insects, and to reduce evaporation (Hughes et al. 1998; Freitas et al. 2014).

Samplings were carried out monthly from May 2018 to April 2019 and during each visit, all captured individuals were identified, marked and then released. The traps were suspended at a height between 1 – 1.5 m above soil and separated from each other by a distance of 30 m. Monthly traps remained open for seven consecutive days and were revised every 48 hours, when baits were replaced. We used as sampling effort the number of traps-days, i.e., the total number of traps used in the field (75 traps) multiplied by the total days studied (35 days), totaling 6300 traps-days. Voucher specimens of all recorded species (up to 10 vouchers by species – about 1% of the total sampled) were deposited in the entomological collections of the Universidade Federal de Pernambuco, Recife, PE, Brazil. The identification of the butterflies was carried out at the specific level and the classification follows Lamas (2004) modified after Wahlberg et al. (2009).

Functional traits

Fruit-feeding butterflies were characterized into four functional groups based on morphological and ecological attributes correlated to microhabitat, predator avoidance and feeding behavior as follow: wing size and use of the canopy, presence of ocellus and larval host plant (Table S1). Size of the anterior wing (hereafter Size) was measured by the length of the costal margin, from the joint with the thorax to its apex (average of up to five individuals by species). Butterfly wing size is directly linked to flight capacity and resistance to desiccation (i.e. bigger butterflies are more tolerant to desiccation and can move longer through the landscape). Similarly, the use of the canopy by butterfly species (hereafter Canopy) was attributed, which is also related to species tolerance to high temperatures and desiccation. Butterflies were also assigned to the presence of ocellus (hereafter Ocellus), a trait related to deflection of predator attacks and partially linked to the use of monocotyledon plants by larvae. Finally, in terms of larval host plants, the use of larval feeding on monocotyledon plants (hereafter Larval monocots) was also adopted, whose species are basically associated to shaded humid environments where grasses are more likely to grow and persists during the long dry periods. Therefore, in addition to other factors, these attributes are mainly related to flight capacity, mobility, larval diet and habitat requirements (see Iserhard et al. 2019 for more details).

Explanatory variables

We computed the chronic anthropogenic disturbance (hereafter chronic disturbance) considering the three most important sources of these disturbance: (1) descriptors correlated with the disturbance by livestock (Livestock Pressure Index - LPI): animal dung density (goats, sheep, horses and cattle), consumption of vegetation and trampling caused by goats and cattle, (2) descriptors related to firewood and timber collection (Wood Extraction Index - WEI): the extraction of dead and live wood for fuel, fence construction, and artisanal production, and (3) descriptors associated with exploitation of non-timber forest products (i.e. medicinal plants, food items for humans, hunting and livestock fodder) (Non-timber forest products index - NTFPI). For NTFPI, we used geographic distances based on remote sensing (e.g. distance to the farms' headquarters, distance to paved roads (BR-232 or PE-270, two highways at the region), distance to vicinal unpaved roads that give access to the farms and distance to the nearest town) (Ribeiro et al. 2015). These metrics were used as a single chronic disturbance index (i.e. global chronic disturbance index- GI) using a principal component analysis (PCA) in which first axis explained 60 % of data variance (Table S2). For more details about GI please see Arnan et al. (2018).

Finally, we used tree species richness, tree density and biomass (*proxy* of forest age) as vegetation attributes (Table S2). Data on aboveground biomass were obtained for each plot from previous studies (Souza et al. 2019). The tree database available to compute biomass refers to all trees with diameter at soil height (DAS) ≥ 3 cm and total height ≥ 1 m. For more details about tree database please see Rito et al. (2017a, b).

Data analysis

To estimate sample sufficiency, we computed diversity estimates for rarefied and extrapolated samples with sample completeness (as measured by sample coverage) using iNEXT (Hsieh et al. 2016).

To assess changes in fruit-feeding butterfly alpha diversity we used the effective numbers of species (so-called Hill numbers, ${}^{q}D$) of orders 0 (${}^{0}D$, species richness), 1 (${}^{1}D$, exponential Shannon entropy) and 2 (${}^{2}D$, inverse Simpson concentration) (Jost 2007). The ${}^{0}D$ order is not sensitive to abundances and so gives a disproportionate weight to rare species, while ${}^{1}D$ weights each species according to its abundance in the community, without favoring rare or abundant species (i.e. common species) (Jost 2007). Finally, ${}^{2}D$ can be interpreted as the number of 'very abundant' or 'dominant' species in the community (Jost 2006). Rank-abundance distribution plots were examined to compare the most abundant species of fruit-feeding butterflies. In terms of beta diversity, a species partitioning method [i.e. multiple-site dissimilarity metrics; Baselga (2010)] was used to separate total Sørensen dissimilarity (beta diversity, $\beta_{SØR}$) into components of dissimilarity due to species replacements (i.e. turnover; β_{SIM}) and dissimilarity due to nestedness (β_{SNE}). We used analysis of variance (ANOVA) with

Tukey’s post-hoc tests to compare abundance, and taxonomic diversity of fruit-feeding butterfly assemblages in regenerating and old-growth forest stands.

Functional community composition was calculated using community-weighted means (CWM), which summarizes shifts in mean trait values within communities due to environmental selection for certain traits (supporting the mass-ratio hypothesis; Grime 1998). Since different types of traits were combined (i.e. categorical and continuous), the “Gower approach” was adopted to calculate a species-dissimilarity matrix (de Bello et al. 2016). CWMs were computed using the FD package (Laliberté et al. 2015) performed in the R software package (R Development Core Team 2017).

To analyze changes in species and functional composition regarding both regenerating and old-growth forests, a non-metric multidimensional scaling (NMDS) ordination was performed, based on a Bray-Curtis dissimilarity matrix of abundance (Clarke and Gorley 2006). We use ANOSIM (Clarke and Gorley 2006) to test the significance of the relationships between habitat types and species/functional groups similarity. We used SIMPER (PRIMER version 6, Clarke and Gorley 2006) to determine the contribution that individual species and functional groups made toward distinguishing differences in community structure between habitats. NMDS, ANOSIM and SIMPER were done using PRIMER software, version 6 (Clarke and Gorley 2006).

Finally, Generalized Linear Models (GLMs) were employed to analyze the effects of forest vegetation structure (tree density, tree species richness and biomass) and chronic disturbance on abundance, taxonomic diversity (alpha – Hill numbers of order 0, 1 and 2; beta diversity – species turnover and nestedness) and functional community composition (CWM_Ocelus, CWM_Canopy, CWM_Larval monocots and CWM_Size) of fruit-feeding butterfly assemblages. Gaussian error distributions was assumed for all data (Crawley 2013). The residuals of all GLMs were analyzed to evaluate the adequacy of the error distribution and the minimally significant model was selected. A test of the correlation between pairs of predictor variables showed that tree species richness and tree density were significantly correlated ($r = 0.7$; $p < 0.001$). Consequently, we removed the tree density from our models. In addition, collinearity among predictor variables in our models were assesses using the variance inflation factor (VIF) in the “car” package (Fox and Weisberg 2011) for R software (R Core Team 2017). All VIF values were lower than 1.2 (ranging from 1.17 to 1.89), therefore suggesting independence (i.e. no collinearity) among predictors (Chatterjee et al. 2000). We constructed 7 models, which represent all combinations of explanatory variables and the null model (which includes only the intercept).

The relative effect of each predictor variable was assessed using an information-theoretic approach and multi model inference (Burnham and Anderson 2002). For each model, we calculated Akaike's information criterion corrected for small samples (AICc). It was considered that the models with a difference in AICc < 2 when compared to the best model (i.e. the one with lowest AICc value) have similar plausibility (Burnham and Anderson 2002). Akaike weights (*w*i) were used to obtain model-averaged parameter estimates. A given spatial and/or forest attribute was considered an important explanatory variable for a given response variable if: (i) it showed a high sum of Akaike weights (i.e. considering each candidate model in which it appeared); and (ii) the model-averaged parameter estimates did not include zero (i.e. the model-averaged unconditional variance was lower than the model averaged parameter estimate) (Burnham and Anderson 2002; Grueber et al. 2011). All models were built using the package “glmulti” for R version 3.0.1 (Calcagno and Mazancourt 2010). The goodness-of-fit of each model was defined as: (explained deviance by the complete model / explained deviance by the null model) × 100 (Crawley, 2013). All analyses were run using the R software (R Core Team 2017).

Results

A total of 20,252 individuals of fruit-feeding butterflies from 22 species within four subfamilies of Nymphalidae was recorded across the 15 forest stands (Table S3). Biblidinae was the most species-rich and abundant subfamily (nine species and 10,613 individuals), followed by Charaxinae (seven species and 7447 individuals), Satyrinae (four species and 2175 individuals) and Nymphalinae (two species and 17 individuals) (Table S3). Butterfly assemblages were dominated by few species, with three of them, *Hamadryas februa februa* (8971 individuals), *Fountainea halice moretta* (3316 individuals) and *Fountainea glycerium cratais* (2964 individuals) accounting for ca. 75% of all captured individuals (Fig. S1). 15,008 individuals from 19 species were recorded across regenerating forest stands, while 5244 individuals from 19 species were recorded in the old-growth forest (Table S3).

As expected, most butterfly species exhibited higher abundance in late-successional forest stands (Fig. 2). Observed species richness in both regenerating and old-growth forests comprised about 89% and 95% of the estimated richness, but coverage-based sampling curves detected no differences between regenerating and old-growth forest stands (Fig. S2). Butterfly abundances in the local assemblages were very high, but diversity was low and varied little between regenerating and old-growth forest habitats. For instance, regenerating forest stands achieved 1500.8 ± 153.93 butterflies per stands (Mean ± SE), while ${}^{0}D$ achieved only 10.05 ± 0.26 species (Fig. 3). The fruit-feeding butterfly beta diversity was low with most of the variation (74 %) due to species replacement rather than variation on species richness. Interestingly, the early-regenerating stands exhibited the highest values of species turnover (Fig. S3), although old-growth and regenerating forests did not differ relative to either nestedness (ANOVA F = 2.15; $p = 0.16$) or species turnover (ANOVA F = 0.02; $p = 0.82$) (Fig. S3).

Forest habitats were slightly different relative to both taxonomic and functional composition (Fig. 4) as confirmed by ANOSIM tests ($R = 0.55$, $p = 0.001$; $R = 0.34$, $p = 0.02$; respectively) and suggested by abundance changes across particular species along forest regeneration (see Fig. 2). Precisely, average cross-habitat dissimilarity (via SIMPER analysis) indicated a taxonomic and functional segregation of 14% and 12% between regenerating and old-growth forest stands (Table S4, S5). *Opsiphanes invirae remoliatus* (12 %) and *Pharneuptychia* sp. 1 (9 %) were the species that most contributed to habitat taxonomic differentiation (Table S4), while small-bodied butterfly species presenting ocellus and monocot-feeding larvae (26 %) as well as large-bodied and canopy-inhabitant butterflies (17 %) were the functional groups that most contributed to habitat functional differentiation (Table S5).

In addition to forest successional status (i.e. regenerating vs. old-growth forest) chronic disturbance, biomass and tree species richness also affected butterfly assemblages by exhibiting high scores of $\sum_{wi}$ and parameter estimators differing from zero Fig. 5; Fig. S4, Table 1). As expected, biomass and tree species richness (positively) and chronic disturbance (negatively) were excellent predictors affecting abundance, and α diversity scores, particularly the total number of species and common species (^{0}D and ^{1}D, respectively; Fig. 5; Fig. S4; Table 1**)**. Moreover, chronic disturbance was the most important predictor by positively affecting the community-weighted means (CWM) for microhabitat (i.e. canopy-inhabitant butterflies), while CWM for feeding behavior monocot-feeding butterflies were negatively affected (Fig. 6 and S5, Table S6). On the other hand, tree species richness was the predictor that most positively explained the CWM for the ocellus-bearing species (Fig. 6 and S5, Table S6).

Discussion

Our results suggest that fruit-feeding butterfly assemblages can be abundant, but impoverished in human-modified landscapes of the Caatinga dry forest, with a few butterfly species dominating local assemblages and the whole landscape. We refer to impoverished butterfly faunas at multiple spatial scales. Moreover, regenerating and old-growth forest stands support assemblages that are very similar relative to several attributes; i.e. high resilience relative to abundance, species richness and diversity. However, secondary and old-growth forests support relatively distinct assemblages taxonomically and functionally in a great extent due to changes on species abundance along forest regeneration process rather than the replacement of entire taxonomic/ecological groups. Apparently two major groups control assemblage functional profile: large-wing and canopy-inhabitant butterflies that achieve higher abundance in more disturbed habitats (i.e. higher chronic disturbance), while those ocellus-bearing species that fly in understorey and the larvae feed on monocot-plants respond negatively to disturbance, but benefit from increased forest biomass and tree species richness. Therefore, chronic disturbance, forest biomass, trees species richness and forest successional status emerge as key drivers of species assembly and community organization at landscape spatial level including taxonomic and functional directional changes. It implies a successional trajectory marked by predictable changes.

Although the pattern of species richness was not initially considered as our aim, the occurrence of relatively abundant but species-poor assemblages in our focal landscape deserve attention as it probably helps to explain our uncovered patterns relative to assemblage resilience, successional trajectory and community organization. Twenty two species within 20,252 individuals can be considered a higher score as compared to a previous study in the same region (14 species, Nobre et al. 2012), but lower compared to a dry tropical forests in Venezuela (40 species) (Sharabuddin and Terborgh 1999) and other tropical forest ecosystems such as the Atlantic Forest (Uehara-Prado et al. 2007; Santos et al. 2011, 2017; Melo et al.

2019; Gueratto et al. 2020), Amazon (DeVries et al. 1997; DeVries and Walla 2001; Barlow et al. 2007; Ribeiro and Freitas 2012), Pampas (Paz et al. 2014) and Cerrado (Silva et al. 2012; Beirão et al. 2017). Obviously, these comparisons must be considered with caution due to differences in sampling efforts, but 22 species through a year of sampling at landscape-spatial scale do suggest a species-poor fauna.

In terms of recovery/resilience of fruit-feeding butterfly assemblages, some studies indicate high similarity of community-level attributes between secondary/regenerating forests and old-growth forests indicating high resilience (Sáfián et al. 2011; Nyafwono et al. 2014; Sant'Anna et al. 2014). Others refers to contrasting scores, including lower (Barlow et al. 2007) or higher species richness in secondary as compared to old-growth forest (Bobo et al. 2006). Overall, fruit-feeding butterfly assemblages can recover elapsed more than 50 years of land abandonment (Oloya et al. 2021, Sáfián et al. 2011). Our findings suggest the possibility of a faster recovery (i.e. a 4-yr-old forest stand similar to average old-growth forest) for some attributes (e.g. species richness and density), but recovery rate or resilience is apparently site-specific (see Fig. 3). This is because other variables than forest age probably affect butterfly community-level attributes along forest regeneration. Complete recovery, however, is associated to patterns of abundance among particular taxa and ecological groups, and can take decades even considering the impoverished or species-poor fauna supported by our human-modified landscape.

This perspective reinforces the idea that fruit-feeding butterfly assemblages exhibits marked replacement of ecological groups along forest regeneration. However, we can refer that taxonomic/functional successional trajectories reflects not only forest age or successional status (secondary vs. old-growth forest), but also other variables such as biomass, tree species richness and chronic disturbance. In this perspective, the presence of environmental filters (e.g. anthropogenic disturbance) across the landscape can delay succession processes by selecting only some ecological groups more tolerant to adverse conditions, preventing the structure of old-growth forests is reached. The impacts of variables on butterfly community organization have been reported for other tropical ecosystems (Beirão et al. 2017, Akite 2008), but there is little or even no information on dry forests, particularly about chronic disturbances and butterfly resilience/response or community organization across human-modified landscapes.

Although we did not explicitly exam the underlying mechanism for a high resilience but a successional trajectory marked by taxonomic and functional replacements in our focal landscape, we can propose working hypotheses. Precisely, the intense degradation that Caatinga dry forest has experienced (e.g. slash-and-burn agriculture, livestock and charcoal production) since the Europeans arrived in the 16th century (Tabarelli et al. 2018) and harsh natural conditions (i.e. reduced forest biomass and chronic water deficit) can limit species and ecological groups that require more forested and mesic habitats while favors disturbance-adapted species. In fact, in the Caatinga dry forest, human disturbances and low precipitation levels are associated to reduced biomass and more open habitats (Souza et al., 2019; Barros et al. 2011), the proliferation of disturbance-adapted species, including those able to resprout (Barros et al. 2021, Vanderley et al. 2021) and impoverished woody plant assemblages (Ribeiro et al., 2015, 2016; Rito et al. 2017b). Thus, pioneer/colonizer species (e.g. Euphorbiaceae) that are more tolerant to disturbance tend to benefit from habitats that are more open and achieve outstanding biomass (Rito et al. 2017a). It implies microclimatic conditions and composition of host plants that favor disturbance-adapted butterflies (e.g. open habitat specialists) able to oviposite and feed on them; i.e. winner plants supporting winner butterfly species (see Tabarelli et al. 2012, Filgueiras et al. 2021). We refer more generalist, light-demanding or disturbed-adapted butterfly species (e.g. Charaxinae and Biblidinae). These processes allow the small-statured Caatinga dry forest inhabiting sandy soils to support a fauna similar to the canopy of humid tropical forests, dominated by species of sun-loving butterflies.

On the other hand, butterfly species with a more specialized diet during larval phases (e.g. monocot-feeding larvae) and associated with specific habitat conditions (shade tolerance and sensitivity to high temperatures and desiccation) are almost restrict to forest sites with low disturbance levels and with higher forest complexity. We refer to demanding for shaded habitats associated to more structured forests (i.e. understory, canopy and emergent layers) such as Satyrinae – Satyrini, Brassolini and Morphini. This subfamily, with hundreds of species, achieve the highest diversity scores across humid ecosystems such as the tropical rain forests (Lamas, 2004).

In summary, the Caatinga dry forest in human-modified landscapes support relatively impoverished but resilient assemblages in the context of slash-and-burn agriculture. However, secondary forests are not able to support the assemblages of old-growth forests in their taxonomic and functional dimension, particularly due to patterns of species abundance on key ecological groups. Although relatively simple, recovery of butterfly assemblages is affected by a set of variables, including human chronic disturbance. Accordingly, spatio/temporal butterfly assemblage organization is relative predictable (i.e. structured communities) with secondary forests capturing a high proportion of butterfly fauna. As the Caatinga and other dry forests are expected to experience increasing aridity and more intense land use (Magrin et al. 2014), the role played by human disturbance vs natural drivers on the occurrence of impoverished butterfly faunas (e.g. the lack of Satyrinae) deserve further investigation.

Acknowledgments

We thank the ICMBio for allowing us to work in Catimbau National Park and landowners for giving us permission to work on their proprieties. This study was supported by the 'Conselho Nacional de Desenvolvimento Científico e Tecnológico' (CNPq, processes PELD 403770/2012-2 and “Edital Universal” 470480/2013-0) and “Fundação de Amparo à Ciência e

Tecnologia do Estado de Pernambuco” (FACEPE, process APQ-0738-2.05/12, APQ 0138-2.05/14, and PRONEX APQ 0138-2.05/14). This study is part of DHAM PhD thesis at the “Programa de Pós Graduação em Biologia Animal” (PPGBA-UFPE). DHAM acknowledges the “Coordenação de Aperfeiçoamento de Pessoal de Nível Superior” (CAPES, Finance Code 001) for a PhD scholarship. B.K.C. Filgueiras acknowledges CNPq for post-doc grant (process number 159106/2018-4), and A.V.L.F, M.T. and I.R.L. for productivity grants (processes 303834/2015-3, 310228/2016-6 and 305611/2014-3, respectivelly). AVLF also acknowledges support from the “Fundação de Amaparo à Pesquisa do Estado de São Paulo” (FAPESP 2011/50225-3 and 2013/50297-0) and from the National Science Foundation (NSF DEB-1256742). This publication is part of the “RedeLep – Rede Nacional de Pesquisa e Conservação de Lepidópteros”: SISBIOTA-Brasil/CNPq (Grant 563332/2010-7).

References

Álvarez-Yépiz JC, Martínez-Yrízar A, Fredericksen TS (2018) Special issue: Resilience of tropical dry forest to extreme disturbance events. For Ecol Manag 426:1-6. https://doi.org/10.1016/j.foreco.2018.05.067

Akite P (2008) Effects of anthropogenic disturbances on the diversity and composition of the butterfly fauna of sites in the Sango Bay and Iriiri areas, Uganda: implications for conservation. Afr J Ecol 46:3-13. https://doi.org/10.1111/j.1365-2028.2008.00923.x

Arnan X, Leal IR, Tabarelli M, Andrade JF et al (2018) A framework for deriving measures of chronic anthropogenic disturbance: Surrogate, direct, single and multi-metric indices in Brazilian Caatinga. Ecol Indic 94:274-282. https://doi.org/10.1016/j.ecolind.2018.07.001

Arroyo-Rodriguez V, Melo FPL, Martinez-Ramos M, Bongers F, Chazdon RL, Meave JA, Norden N, Santos BA, Leal IR, Tabarelli M (2015) Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. Biol Rev 92:326-340. https://doi.org/10.1111/brv.12231

Avila-Cabadilla LD, Stoner KE, Henry M, Álvarez-Añorve MY (2009) Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. Forest Ecol Manag 258:986–996. https://doi.org/10.1016/j.foreco.2008.12.011

Barlow J, Overal WL, Araujo IS, Gardner TA, Peres CA (2007) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. J Appl Ecol 44:1001-1012. https://doi.org/10.1111/j.1365-2664.2007.01347.x

Barros MF, Ribeiro EMS, Vanderlei RS, De Paula AS, Silva AB, Wirth R, Cianciaruso MV, Tabarelli M (2021) Resprouting drives successional pathways and the resilience of Caatinga dry forest in human-modified landscapes. Forest Ecol Manag, 482:118881. https://doi.org/10.1016/j.foreco.2020.118881

Baselga A (2010). Partitioning the turnover and nestedness components of beta diversity. Glob Ecol Biogeogr 19:134-143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Beirão MV, Neves FS, Penz CM, DeVries PJ, Fernandes GW (2017) High butterfly beta diversity between Brazilian Cerrado and Cerrado-Caatinga transition zones. J Ins Conserv 21:849-860. https://doi.org/10.1007/s10841-017-0024-x

Bobo KS, Waltert M, Fermon H, Njokagbor J, Muhlenberg M (2006) From forest to Ffarmland: butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. J Insect Conserv 10:29-42. https://doi.org/10.1007/s10841-005-8564-x

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Verlag, New York.

Calcagno V, Mazancourt C (2010) glmulti: a R package for easy automated model selection with (generalized) linear models. J Stat Softw 34:1-29. https://doi.org/10.18637/jss.v034.i12

Ceccon E, Huante P, Rincón E (2006) Abiotic factors influencing Tropical Dry Forests regeneration. Braz Arch Biol Technol 49:305-312.

Chatterjee S, Hadi AS, Price B (2000) Regression Analysis by Example. Wiley, New York.

Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Stork NE, Miller SE (2009) The potential for species conservation in tropical secondary forests. Conserv Biol 23:1406-1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. In PRIMER-E. Plymouth.

Crawley MJ (2013) The R Book, second ed. John Wiley and Sons.

De Bello F, Carmona CP, Mason NWH, Sebastià M-T, Lepš J (2013) Which trait dissimilarity for functional diversity: trait means or trait overlap? J Veg Sci, 24:807-819. https://doi.org/10.1111/jvs.12008

DeVries PJ, Murray D, Lande R (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. Biol J Linn Soc 62:343-364. https://doi.org/10.1006/bijl.1997.0155

DeVries PJ, Walla TR (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. Biol J Linn Soc 74:1-15. https://doi.org/10.1006/bijl.2001.0571

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conserv Bio 18:302-309. https://doi.org/10.1111/j.1523-1739.2004.00151.x

Ferraz SFB, Ferraz KMPMB, Cassino CC, Brancalion PHS, Luz DTA, Azevedo TN, Tambosi LR, Metzger JP (2014) How good are tropical forest patches for ecosystem services provisioning? Landsc Ecol 29:187-200. https://doi.org/10.1007/s10980-014-9988-z

Filgueiras BKC, Peres CA, Melo FPL, Leal IR., Tabarelli M (2021) Winner-loser species replacements in human-modified landscapes. Trends Ecol Evol. In press.

Fox J, Weisberg S (2011) An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. Accessed 14 April 2020

Freitas AVL, Francini RB, Brown Jr. KS (2003) Insetos Como Indicadores Ambientais. In: Cullen JRL, Rudran R, Valladares-Pádua C (eds) Métodos de estudos em biologia da conservação e manejo da vida silvestre. Editora da UFPR, Fundação O Boticário de Proteção à Natureza, Curitiba, pp 125-151.

Freitas AVL, Iserhard CA, Santos JP, Carreira JYO, Ribeiro DB, Melo DHA, Rosa AHB, Marini-Filho OJ, Accacio GM, Uehara-Prado M (2014) Studies with butterfly bait traps: an overview. Rev Colomb Entomol 40:209-218.

Freitas AVL, Leal IR, Uehara-Prado M, Iannuzzi L (2006) Insetos Como Indicadores De Conservação Da Paisagem. In: Rocha CFD, Bergallo HG, Van Sluys M, Alves MAS (eds) Biologia da conservação: essências. RiMa Editora, São Carlos, pp 357-384.

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manag 148:185-206. https://doi.org/10.1016/S0378-1127(00)00535-1

Gueratto PE, Carreira JYO, Santos JP, Tacioli A, Freitas AVL (2020) Effects of forest trails on the community structure of tropical butterflies. J Insect Conserv 24:309-319. https://doi.org/10.1007/s10841-019-00199-x

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902-910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699-711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hernández-Ordóñez, O, Urbina-Cardona JN, Martínez-Ramos M (2015) Recovery of amphibian and reptile assemblages during old-field succession of tropical rain forests. Biotropica 47:377-388. https://doi.org/10.1111/btp.12207

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecol Evol 7:1451-1456. https://doi.org/10.1111/2041-210X.12613

Hughes JB, Daily GC, Ehrlich PR (1998) Use of fruit bait traps for monitoring of butterflies (Lepidotera: Nymphalidae). Rev Biol Trop 46:697-704. https://doi.org/10.15517/RBT.V46I3.20199

Iserhard CA, Duarte L, Seraphim N, Freitas AVL (2019) How urbanization affects multiple dimensions of biodiversity in tropical butterfly assemblages. Biodivers Conserv 28:621-638. https://doi.org/10.1007/s10531-018-1678-8

Jost L (2006) Entropy and diversity. Oikos 113:363-375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88:2427-2439. https://doi.org/10.1890/06-1736.1

Laliberté E, Legendre P, Shipley B (2015) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Package ‘‘FD’’ for version 1.0-12

Lamas G (2004) Checklist: Part 4A Hesperioidea – Papilionoidea. In: Heppner JB (ed) Atlas of Neotropical Lepidoptera (pp xxxiv + 428). Association of Tropical Lepidoptera, Gainesville.

Laurance WF, Peres, CA (2006) Emerging threats to tropical forests. University of Chicago Press, Chicago.

Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Paz H, Pérez-García EA, Romero-Pérez IE, Tauro A, Bongers F (2013) Successional changes in functional composition contrast for dry and wet tropical forest. Ecology 94:1211-1216. https://doi.org/10.1890/12-1850.1

Magrin GO, Marengo JA, Boulanger JP, Buckeridge MS, Castellanos E, Poveda G, Scarano FR, Vicuña S (2014) Central and South America. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE (eds) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York, pp 1499-1566.

Martin PA, Newton AC, Bullock JM (2013) Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. P Roy Soc B-Biol Sci 280:20132236. https://doi.org/10.1098/rspb.2013.2236

Melo DHA, Filgueiras BKC, Iserhard CA, Iannuzzi L, Freitas AVL, Leal IR (2019) Effect of habitat loss and fragmentation on fruit-feeding butterflies in the Brazilian Atlantic Forest. Can J Zool 97:588-596. https://doi.org/10.1139/cjz-2018-0202

Melo FPL, Arroyo-Rodríguez V, Fahrig L, Martínez-Ramos M, Tabarelli M (2013) On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol 28:462-468. https://doi.org/10.1016/j.tree.2013.01.001

Neves FS, Oliveira VHF, Espírito-Santo MM, Vaz-De-Mello FZ, Louzada J, Sanchez-Azofeifa A, Fernandes GW (2010) Successional and seasonal changes in a Community of dung beetles (Coleoptera: Scarabaeinae) in a Brazilian Tropical Dry Forest. Nat Conserv 8:160+164. https://doi.org/10.4322/NATCON.00802009

Nobre CEB, Iannuzzi L, Schlindwein C (2012) Seasonality of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in a Brazilian semiarid area. ISRN Zoology 2012:1-8. https://doi.org/10.5402/2012/268159

Norden N, Chazdon RL, Chao A, Jiang Y-H, Vílchez-Alvarado B (2009) Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecol Lett 12:385-94 https://doi.org/10.1111/j.1461-0248.2009.01292.x

Nyafwono M, Valtonen A, Nyeko P, Roininen H (2014) Butterfly Community composition across a successional gradient in a human-disturbed Afro-tropical rain forest. Biotropica 46:210-218. https://doi.org/10.1111/btp.12085

Oloya J, Malinga GM, Nyafwono M, Akite P, Nakadai R, Holm S, Valtonen A (2021) Recovery of fruit-feeding butterfly communities in Budongo Forest Reserve after anthropogenic disturbance. Forest Ecol Manag 491:119087. https://doi.org/10.1016/j.foreco.2021.119087

Paz ALG, Romanowski HP, Morais ABB (2014) Borboletas frugívoras do centro oeste do Rio Grande do Sul, Brasil (Lepidoptera: Nymphalidae). SHILAP Revta Lepd 42:409-422.

Poorter L, Bongers F, Aide TM et al (2016) Biomass resilience of Neotropical secondary forests. Nature 530:211-214. https://doi.org/10.1038/nature16512

Quesada M, Sanchez-Azofeifa GA, Alvarez-Añorve M et al (2009) Succession and management of tropical dry forests in the Americas: review and new perspectives. Forest Ecol Manag 258:1014-1024. https://doi.org/10.1016/j.foreco.2009.06.023

R Development Core Team (2017) R a language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org. Accessed 21 July 2019

Ribeiro DB, Freitas AVL (2012) The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. J Insect Conserv 16:733-744. https://doi.org/10.1007/s10841-012-9458-3

Ribeiro EMS, Arroyo-Rodríguez V, Santos BA, Tabarelli M, Leal IR (2015) Chronic Anthropogenic Disturbance Drives the Biological Impoverishment of the Brazilian Caatinga Vegetation. J App Ecol 52:611-620. https://doi.org/10.1111/1365-2664.12420

Ribeiro EMS, Santos BA, Arroyo-Rodrigues V, Tabarelli M, Souza G, Leal IR (2016b) Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. Ecology 97:1583-1592. https://doi.org/10.1890/15-1122.1

Ribeiro-Neto JD, Arnan X, Tabarelli M, Leal IR (2016) Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. Biodivers Conserv 25:943-956. https://doi.org/10.1007/s10531-016-1099-5

Rito KF, Arroyo-Rodríguez V, Queiroz RT, Leal IR, Tabarelli M (2017b) Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. J Ecol 105:828-838. https://doi.org/10.1111/1365-2745.12712

Rito KF, Tabarelli M, Leal IR (2017a) Euphorbiaceae responses to chronic anthropogenic disturbances in Caatinga vegetation: From species proliferation to biotic homogenization. Plant Ecol 218:749-759. https://doi.org/10.1007/s11258-017-0726-x

Sáfián S, Csontos G, Winkler D (2011) Butterfly community recovery in degraded rainforest habitats in the Upper Guinean Forest Zone (Kakum forest, Ghana). J Insect Conserv 15:351-359. https://doi.org/10.1007/s10841-010-9343-x

Sant'Anna CLB, Ribeiro DB, Garcia LC, Freitas AVL (2014) Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. Restor Ecol 22:480-485. https://doi.org/10.1111/rec.12091

Santos JP, Iserhard CA, Carreira JYO, Freitas AVL (2017) Monitoring fruit-feeding butterfly assemblages in two vertical strata in seasonal Atlantic Forest: temporal species turnover is lower in the canopy. J Trop Ecol 33:345-355. https://doi.org/10.1017/S0266467417000323

Santos JP, Iserhard CA, Texeira MO, Romanowski HP (2011) Fruit-feeding butterflies guide of subtropical Atlantic Forest and Araucaria Moist Forest in State of Rio Grande do Sul, Brazil. Biota Neotrop 11:253-274. https://doi.org/10.1590/S1676-06032011000300022

Shahabuddin G, Terborgh JW (1999) Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and the effects of isolation. J Trop Ecol 15:703-722. https://doi.org/10.1017/S0266467499001121

Silva ARM, Castro CO, Mafia PO, Mendonça MOC, Alves TCC, Beirão MV (2012) Borboletas frugívoras (Lepidoptera: Nymphalidae) de uma área urbana (Área de Proteção Especial Manancial Cercadinho) em Belo Horizonte, Minas Gerais, Brasil. Biota Neotrop 12:292-297. https://doi.org/10.1590/S1676-06032012000300028

Silva JMC, Leal IR, Tabarelli M (2017) Caatinga: The Largest Tropical Dry Forest Region in South America. Springer, Switzerland.

Singh SP (1998) Chronic disturbance, a principal cause of environmental degradation in developing countries. Environ Conserv 25:1-2. https://doi.org/10.1017/S0376892998000010

Sociedade Nordestina de Ecologia (2002) Projeto Técnico para a Criação do Parque Nacional do Catimbau/PE. Secretaria de Ciência, Tecnologia e Meio Ambiente de Penambuco – SECTMA, Recife.

Souza DG, Sfair JC, De Paula AS, Barros MF, Rito KF, Tabarelli M (2019) Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest. For Ecol Manag 435:57-65. https://doi.org/10.1016/j.foreco.2018.12.042

Specht MJ, Santos BA, Marshall N, Melo FPL, Leal IR, Tabarelli M, Baldauf C (2019) Socioeconomic differences among resident, users and neighbour populations of a protected area in the Brazilian dry forest. J Environ Manage 232:607-614. https://doi.org/10.1016/j.jenvman.2018.11.101

Tabarelli, M, Leal IR, Scarano, FR, Silva JMC (2018) Caatinga: legado, trajetória e desafios ruma à sustentabilidade. Ciência e Cultura 70:25-29. http://dx.doi.org/10.21800/2317-66602018000400009

Tabarelli, M, Peres CA, Melo FPL (2012) The ‘few winners and many losers’ paradigm revisited: Emerging prospects for tropical forest biodiversity. Biol Converv 155:136-140. https://doi.org/10.1016/j.biocon.2012.06.020

Uehara-Prado M, Brown Jr. KS, Freitas AVL (2007) Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. Global Ecol Biogeogr 16:43-54. https://doi.org/10.1111/j.1466-8238.2006.00267.x

Wahlberg N, Leneveu J, Kodandaramaiah U, Peña C, Nylin S, Freitas AVL, Brower AVZ (2009) Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. Proc Biol Sci 276:4295-4302. https://doi.org/10.1098/rspb.2009.1303

Table 1 Results of the Generalized Linear Models (GLMs) exhibiting the effects of biomass (BIO), chronic anthropogenic disturbance (CAD) and tree species richness on abundance, total species richness (^0D), common species (^1D) and dominant species (^2D) of fruit-feeding butterflies in the Catimbau National Park, in Pernambuco state, northeastern Brazil. Model-averaged parameter estimates (β), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model) of information-theoretic-based model selection and multi model inference. The sign (+/-) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were more accurate, i.e., those higher than the unconditional variance

Response variable	**Predictors**	β	**UV**	**Importance**	**R^2**
Abundance	BIO	9.79	3.93×10^{2}	0.36	58%
	CAD	-1.10×10^{1}	3.16×10^{2}	0.47	
	TR	2.06×10^{1}	1.45×10^{3}	0.37	
^0D	BIO	1.02×10^{-3}	2.37×10^{-4}	0.18	71%
	CAD	-5.73×10^{-2}	1.28×10^{-3}	0.90	
	TR	3.65×10^{-2}	4.42×10^{-3}	0.46	
^1D	BIO	8.49×10^{-4}	1.44×10^{-4}	0.17	48%
	CAD	-2.16×10^{-2}	6.00×10^{-4}	0.57	
	TR	2.53×10^{-4}	4.81×10^{-4}	0.24	
^2D	BIO	-5.83×10^{-5}	1.06×10^{-4}	0.18	32%
	CAD	-8.81×10^{-4}	1.34×10^{-4}	0.18	
	TR	-4.97×10^{-3}	6.79×10^{-4}	0.19	

Figure captions

Fig. 1 Map of the Catimbau National Park, in Pernambuco state, northeastern Brazil (A-B) showing the sampling sites in old-growth forests (red circles) and regeneration areas (blue circles) (C)

Fig. 2 Abundance of fruit feeding-butterfly species along regenerating forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil

Fig. 3 Relationship between forest age and community-level attributes of fruit-feeding butterflies (including fitted models ± 95% confidence intervals) sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

Fig. 4 NMDS based on fruit-feeding butterfly assemblages in terms of species (A) and functional composition (B) in the Catimbau National Park, in Pernambuco state, northeastern Brazil. Blue circles represent regenerating forest stands and red circles represent old-growth forests

Fig. 5 Responses of abundance, total species richness (^0D), common species (^1D) and dominant species (^2D) of fruit-feeding butterfly assemblages to biomass (BIO), chronic anthropogenic disturbance (CAD) and tree species richness (TR) in the Catimbau National Park, in Pernambuco state, northeastern Brazil. The fitted line and shaded area are the linear trends observed ± 95% confidence intervals, respectively

Fig. 6 Responses of community-weighted mean fruit-feeding butterfly traits to chronic anthropogenic disturbance (CAD) and tree species richness (TR) in the Catimbau National Park, in Pernambuco state, northeastern Brazil. The fitted line and shaded area are the linear trends observed ± 95% confidence intervals, respectively. Butterfly traits (Size – size of the anterior wing, Ocellus – presence of ocellus, Canopy – use of the canopy and Larval monocots – larval feeding on monocotyledon plants)

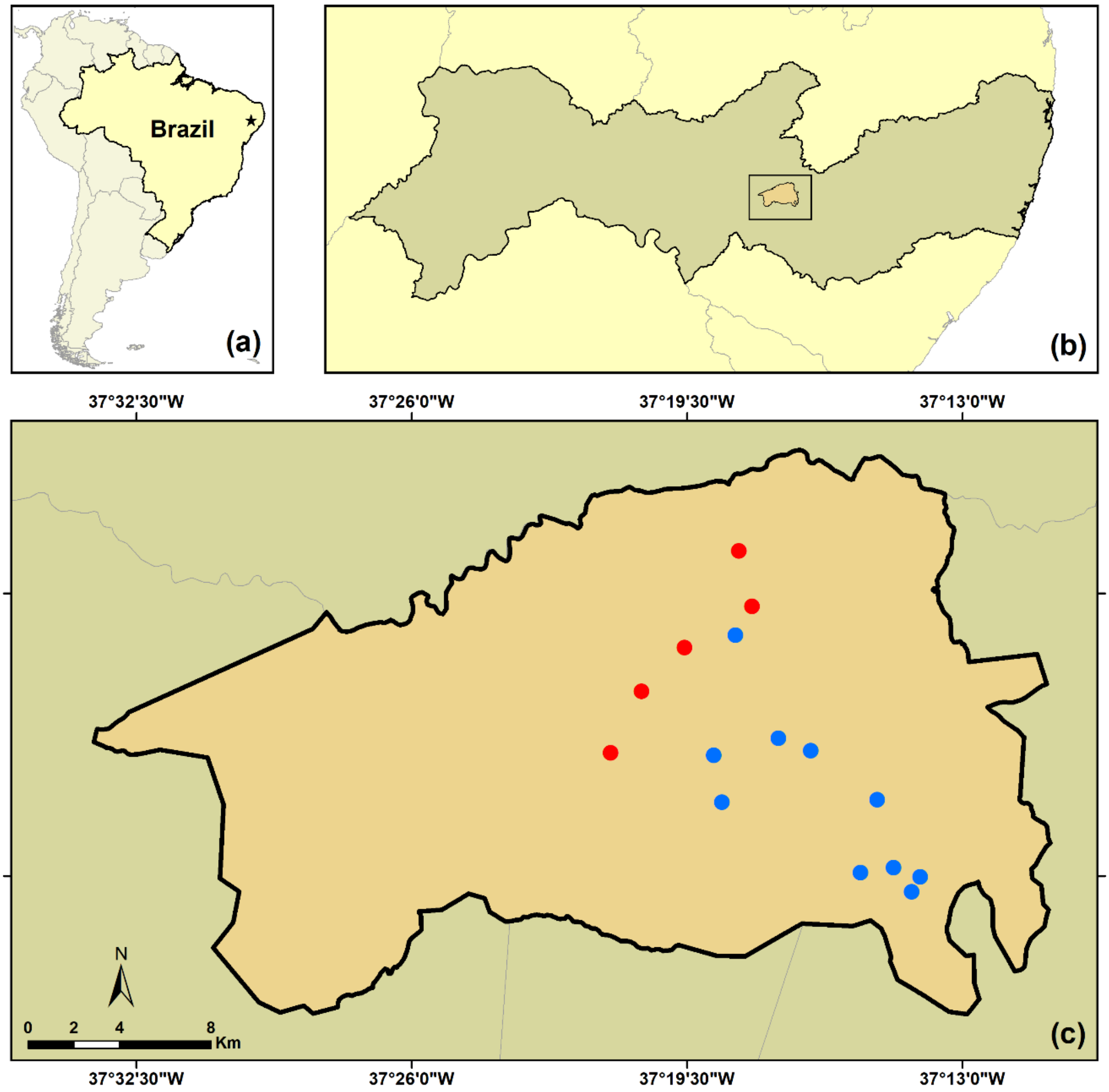

Brazil
(a)
(b)
37°32'30"W
37°26'0"W
37°19'30"W
37°13'0"W
8°26'40"S
8°33'20"S
N
0
2
4
8
Km
(c)

Fig.1

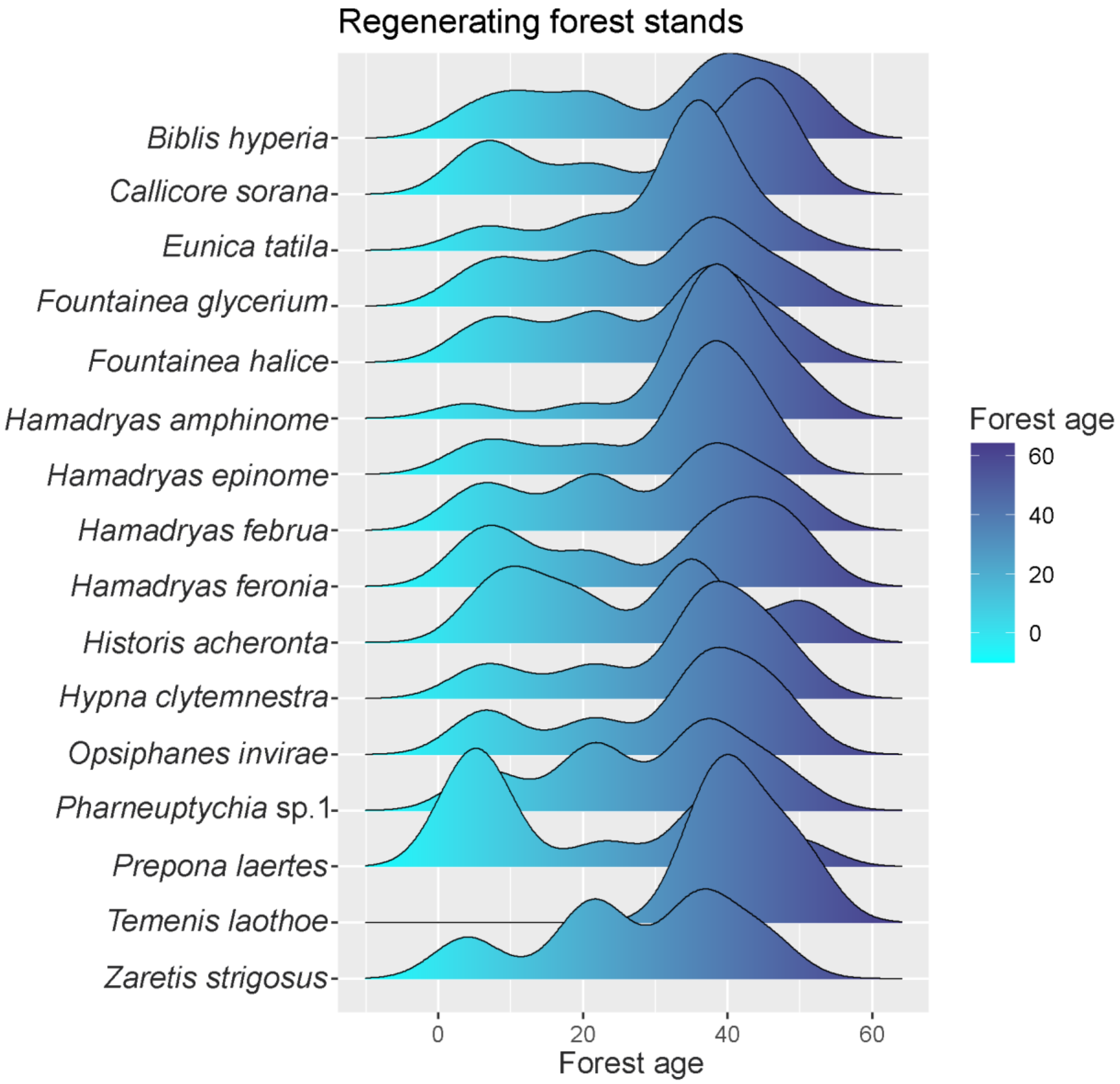

Regenerating forest stands
Biblis hyperia
Callicore sorana
Eunica tatila
Fountainea glycerium
Fountainea halice
Hamadryas amphinome
Hamadryas epinome
Hamadryas februa
Hamadryas feronia
Historis acheronta
Hypna clytemnestra
Opsiphanes invirae
Pharneuptychia sp.1
Prepona laertes
Temenis laothoe
Zaretis strigosus
0
20
40
60
Forest age
Forest age
60
40
20
0

Fig. 2

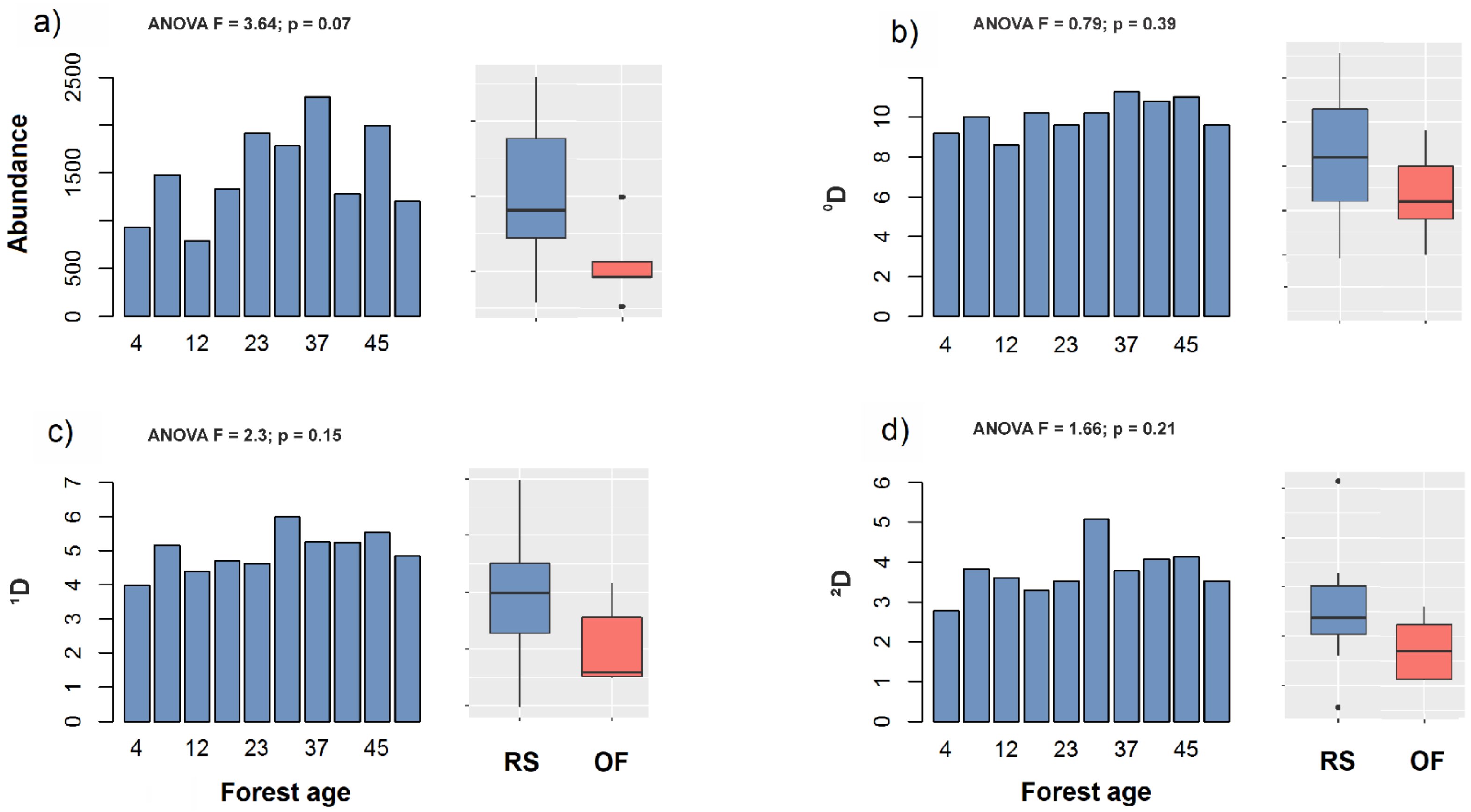

a)
ANOVA F = 3.64; p = 0.07
Abundance
0
500
1500
2500
4
12
23
37
45
b)
ANOVA F = 0.79; p = 0.39
^0D
0
2
4
6
8
10
4
12
23
37
45
c)
ANOVA F = 2.3; p = 0.15
^1D
0
1
2
3
4
5
6
7
4
12
23
37
45
Forest age
RS
OF
d)
ANOVA F = 1.66; p = 0.21
^2D
0
1
2
3
4
5
6
4
12
23
37
45
Forest age
RS
OF

Fig. 3

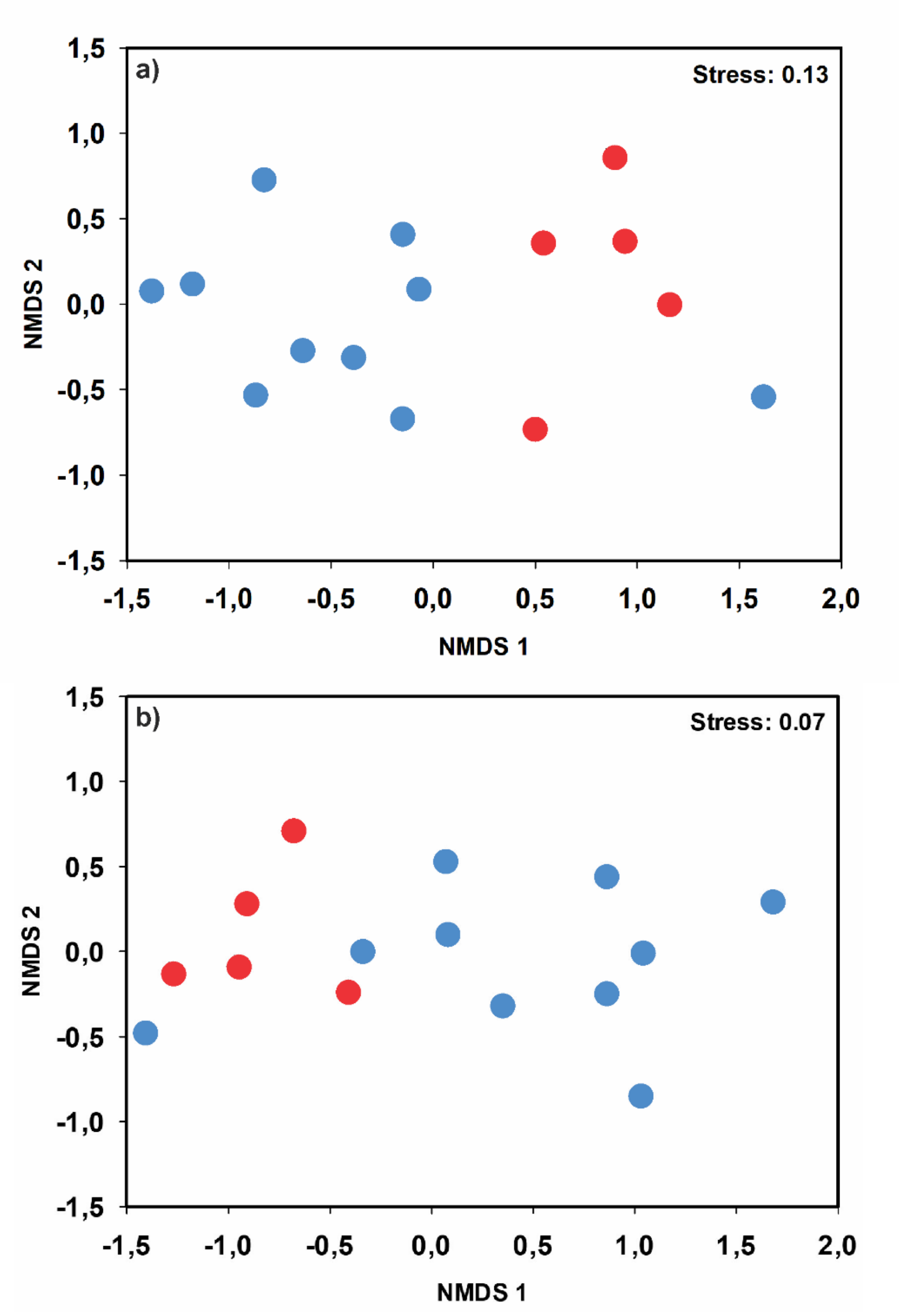

a)
Stress: 0.13
NMDS 2
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-1,5
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0
NMDS 1
b)
Stress: 0.07
NMDS 2
1,5
1,0
0,5
0,0
-0,5
-1,0
-1,5
-1,5
-1,0
-0,5
0,0
0,5
1,0
1,5
2,0
NMDS 1

Fig. 4

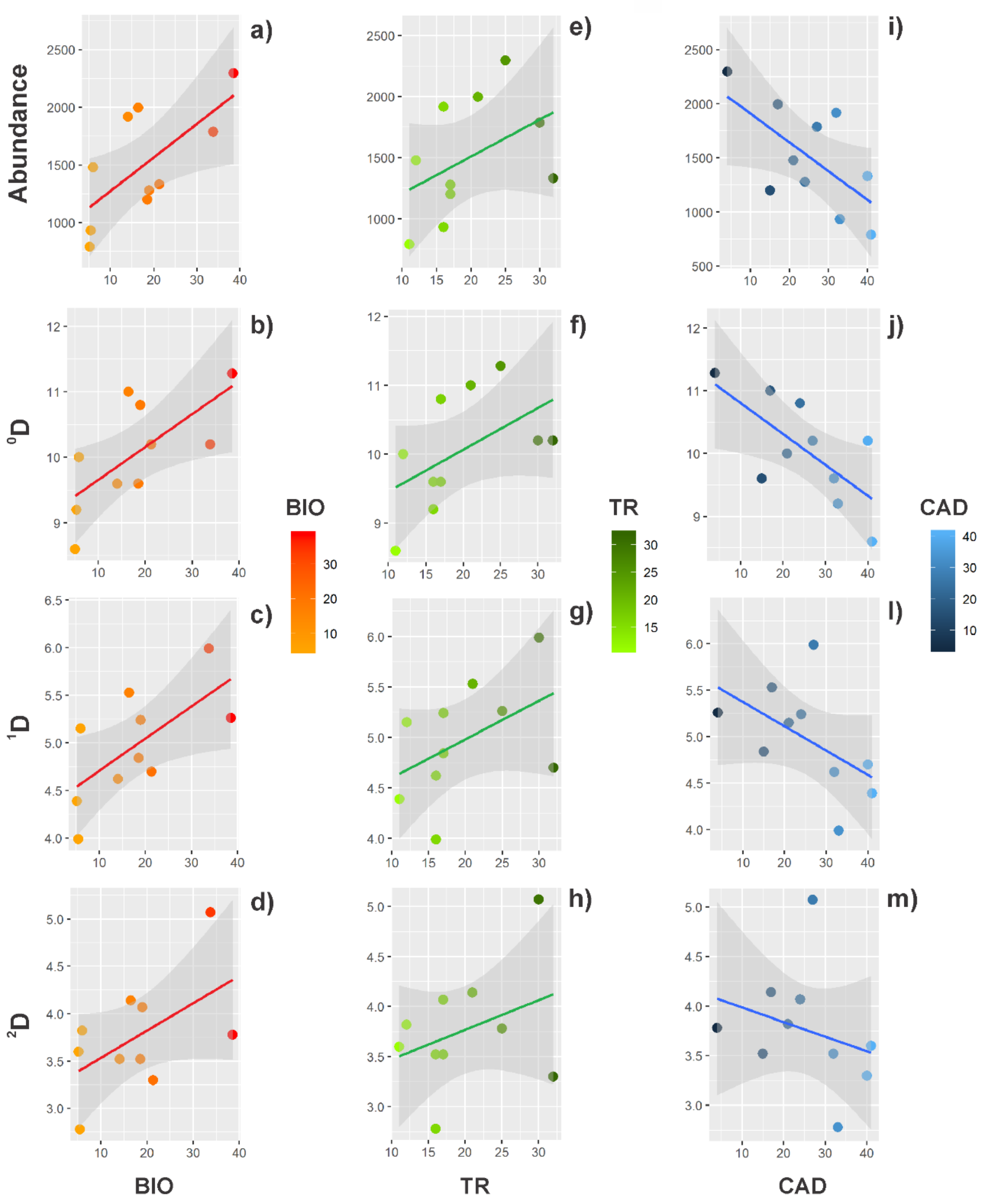

Abundance
^{0}D
^{1}D
^{2}D
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
l)
m)
BIO
TR
CAD
2500
2000
1500
1000
500
12
11
10
9
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
10
15
20
25
30
40

Fig.5

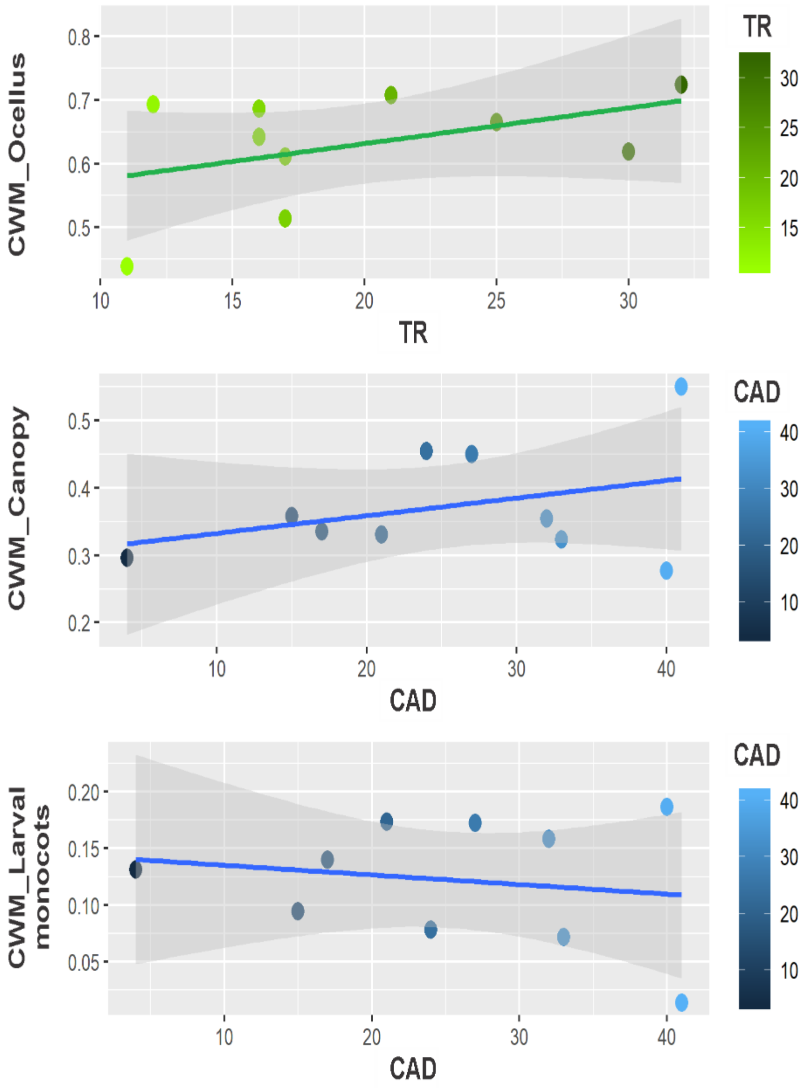

CWM_Ocellus
0.8
0.7
0.6
0.5
10
15
20
25
30
TR
TR
30
25
20
15
CWM_Canopy
0.5
0.4
0.3
0.2
10
20
30
40
CAD
CAD
40
30
20
10
CWM_Larval monocots
0.20
0.15
0.10
0.05
10
20
30
40
CAD
CAD
40
30
20
10

Fig. 6

Additional Supporting Information for

Rapid recovery of fruit-feeding butterfly assemblages in the regeneration of a Caatinga dry forest submitted to shifting cultivation

Douglas H. A. Melo, André V. L. Freitas, Marcelo Tabarelli, Inara R. Leal, Bruno K. C. Filgueiras

Table S1 Functional traits of fruit-feeding butterfly sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil. Size (average of up to five individuals by species). The sign (+/-) represents the present or absent/reduced traits. Microhabitat use (C – canopy-inhabitant butterflies; U – understory-inhabitant butterflies). Larval plant (D – dicot-feeding larval; M – monocot-feeding larval)

Taxon	**Size**	**Ocellus**	**Microhabitat use**	**Larval plant**
Subfamily Biblidinae				
Biblis hyperia nectanabis (Fruhstorfer, 1909)	3,15	-	U	D
Callicore sorana sorana (Godart, [1824])	2,57	+	C	D
Eunica macris macris (Godart, [1824])	2,54	+	C	D
Eunica tatila bellaria Fruhstorfer, 1908	2,32	+	C	D
Hamadryas amphinome amphinome (Linnaeus, 1767)	3,74	+	U	D
Hamadryas epinome (C. Felder & R. Felder, 1867)	3,22	+	U	D
Hamadryas februa februa (Hübner, [1823])	3,42	+	U	D
Hamadryas feronia feronia (Linnaeus, 1758)	3,51	+	U	D
Temenis laothoe (Cramer, [1777])	2,49	-	C	D
Subfamily Charaxinae				
Archaeoprepona demophon thalpius (Hübner, [1814])	5,80	-	C	D
Fountainea glycerium cratais (Hewitson, 1874)	3,07	-	C	D
Fountainea halice moretta (Druce, 1877)	2,58	-	C	D
Fountainea ryphea phidile (Geyer, 1837)	2,89	-	C	D
Hypna clytemnestra forbesi Godman & Salvin, [1884]	3,55	-	U	D
Prepona laertes laertes (Hübner, [1811])	4,71	+	C	D
Zaretis strigosus (Gmelin, 1790)	2,86	-	C	D
Subfamily Nymphalinae				
Historis acheronta (Fabricius, 1775)	4,19	-	C	D
Historis odius dious Lamas, 1995	7,24	-	C	D
Subfamily Satyrinae				
Tribe Brassolini				
Opsiphanes invirae remoliatus Fruhstorfer, 1907	3,62	+	C	M
Tribe Satyrini				
Paryphthimoides poltys (Prittwitz, 1865)	1,70	+	U	M
Pharneuptychia sp.1	1,75	+	U	M
Pharneuptychia sp.2	1,59	+	U	M

Table S2 Forest and vegetation attributes of OF (old-growth forests) and RS (regeneration sites) in the Catimbau National Park, in Pernambuco state, northeastern Brazil

Habitat	**Forest age**	**Forest Biomass**	**Tree species richness**	**Tree density**	**Chronic disturbance***
OF1	~150	39.17	34	36	22
OF2	~150	29.49	16	34	17
OF3	~150	38.85	24	35	11
OF4	~150	25.84	31	31	9
OF5	~150	24.95	23	21	9
RS1	4	61.4	16	21	33
RS2	7	63.6	12	12	21
RS3	12	86.2	11	23	41
RS4	20	58.2	32	35	40
RS5	23	55.5	16	16	32
RS6	35	57.1	30	41	27
RS7	37	54.5	25	29	4
RS8	40	67.1	17	21	24
RS9	45	56.4	21	22	17
RS10	50	68.4	17	11	15

***** Global chronic anthropogenic disturbance index based on livestock pressure, wood extraction and exploitation of non-timber forest products.

Table S3 Abundance of fruit-feeding butterflies sampled at two habitat types in the Catimbau National Park, in Pernambuco state, northeastern Brazil. Total OF corresponds to the total abundance of nine old-growth forests

Taxon	**Regeneration age**										**Total Regenerating forests**	**Old-growth forest**					**Total OF**	**Total**
	4	**7**	**12**	**20**	**23**	**35**	**37**	**40**	**45**	**50**		**OF1**	**OF2**	**OF3**	**OF4**	**OF5**		
Subfamily Biblidinae	**581**	**774**	**356**	**729**	**941**	**807**	**1240**	**586**	**1148**	**651**	**7813**	**835**	**494**	**553**	**380**	**538**	**2800**	**10613**
Biblis hyperia nectanabis (Fruhstorfer, 1909)	11	8	20	14	15	10	15	27	14	30	164	22	23	15	17	27	104	268
Callicore sorana sorana (Godart, [1824])	34	89	27	38	37	36	62	29	232	30	614	36	30	11	19	20	116	730
Eunica macris macris (Godart, [1824])	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	3	3
Eunica tatila bellaria Fruhstorfer, 1908	11	30	7	30	33	187	63	24	41	18	444	18	23	23	16	10	90	534
Hamadryas amphinome amphinome (Linnaeus, 1767)	1	0	0	1	0	4	2	5	2	2	17	1	3	3	3	4	14	31
Hamadryas epinome (C. Felder & R. Felder, 1867)	1	1	1	1	1	3	3	3	3	0	17	0	1	0	1	0	2	19
Hamadryas februa februa (Hübner, [1823])	521	640	299	642	853	566	1088	492	848	564	6513	750	413	500	322	473	2458	8971
Hamadryas feronia feronia (Linnaeus, 1758)	2	6	2	3	2	1	5	3	7	5	36	6	1	1	1	2	11	47
Temenis laothoe (Cramer, [1777])	0	0	0	0	0	0	2	3	1	2	8	0	0	0	0	2	2	10
Subfamily Charaxinae	**283**	**447**	**422**	**353**	**672**	**669**	**755**	**593**	**570**	**435**	**5199**	**623**	**391**	**371**	**359**	**504**	**2248**	**7447**
Archaeoprepona demophon thalpius (Hübner, [1814])	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Fountainea glycerium cratais (Hewitson, 1874)	131	151	205	147	283	258	213	257	138	189	1972	276	175	144	151	246	992	2964
Fountainea halice moretta (Druce, 1877)	118	206	195	146	320	312	322	264	241	185	2309	274	180	153	172	228	1007	3316
Fountainea ryphea phidile (Geyer, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	2
Hypna clytemnestra forbesi Godman & Salvin, [1884]	30	88	22	58	67	98	217	71	190	60	901	70	36	74	33	28	241	1142
Prepona laertes laertes (Hübner, [1811])	3	2	0	0	1	0	2	1	0	1	10	2	0	0	1	2	5	15
Zaretis strigosus (Gmelin, 1790)	1	0	0	1	1	1	1	0	1	0	6	1	0	0	0	0	1	7
Subfamily Nymphalinae	**1**	**1**	**1**	**1**	**0**	**2**	**0**	**0**	**0**	**1**	**7**	**1**	**3**	**2**	**2**	**2**	**10**	**17**
Historis acheronta (Fabricius, 1775)	0	1	1	1	0	2	0	0	0	1	6	1	3	2	2	2	10	16
Historis odius dious Lamas, 1995	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Subfamily Satyrinae	**67**	**257**	**11**	**248**	**304**	**308**	**302**	**100**	**279**	**113**	**1989**	**37**	**71**	**35**	**23**	**20**	**186**	**2175**
Tribe Brassolini																		

Opsiphanes invirae remoliatus Fruhstorfer, 1907	2	10	0	5	5	7	15	3	15	4	66	1	0	0	0	1	2	68
Tribe Satyrini																		
Paryphthimoides poltys (Prittwitz, 1865)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Pharneuptychia sp.1	65	247	11	243	299	301	286	97	264	109	1922	35	71	35	23	19	183	2105
Pharneuptychia sp.2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1
Total	**932**	**1479**	**790**	**1331**	**1917**	**1786**	**2297**	**1279**	**1997**	**1200**	**15008**	**1496**	**959**	**961**	**764**	**1064**	**5244**	**20252**

Table S4 Pairwise dissimilarities of species groups between habitats in the Catimbau National Park, in Pernambuco state, northeastern Brazil

Comparison	**Av. diss (Overall)**	**Species**	**Average abundance**		**Av. Diss**	**Av. diss SD**	**Contrib. (%)**	**Cum. (%)**
			OF	**RS**				
Old-growth forest vs. Regenerating forest stands	14.18 %	*Opsiphanes invirae remoliatus*	0.68	3.93	1,69	2,19	11,92	11,92
		Pharneuptychia sp. 1	9.13	11.35	1,29	1,69	9,12	21,04
		Historis acheronta	2.81	0.93	0,96	1,78	6,8	27,84
		Hamadryas amphinome amphinome	3.38	1,79	0,95	1,48	6,69	34,53
		Fountainea glycerium cratais	13.60	12,28	0,92	1,82	6,49	41,02
		Biblis hyperia nectanabis	7.92	6,54	0,86	1,82	6,07	47,09
		Fountainea halice moretta	13.67	12,57	0,8	2,22	5,61	52,7
		Hamadryas epinome	0.73	2,04	0,76	1,47	5,33	58,02
		Hamadryas februa februa	15.94	14,95	0,71	1,47	4,99	63,02
		Prepona laertes laertes	1.44	1,31	0,68	1,29	4,81	67,83
		Hamadryas feronia feronia	2.59	3,31	0,66	1,7	4,65	72,48
		Eunica tatila bellaria	7.54	7,82	0,63	1,18	4,47	76,94
		Callicore sorana sorana	8.02	8,96	0,63	1,19	4,42	81,37
		Temenis laothoe	0.56	0,93	0,57	0,9	4	85,37
		Hypna Clytemnestra forbesi	9.89	9,87	0,5	1,24	3,52	88,89
		Zaretis strigosus	0.32	0,93	0,44	1,15	3,14	92,02

OF (Old-growth forest); RS (Regenerating forest stands). Average dissimilarity (Av. diss) with standard deviation (SD) and contributions (Cum. %) for all species is explained between habitats.

Table S5 Pairwise dissimilarities of functional groups between habitats in the Catimbau National Park, in Pernambuco state, northeastern Brazil

Comparison	Av. diss (Overall)	Functional Groups	Average abundance		Av. Diss	Av. diss SD	Contrib. (%)	Cum. (%)
			OF	RS				
Old-growth forest vs. Regenerating forest stands	12.19%	1OUM	8,1	13,95	3,21	2	26,32	26,32
		3XCD	19,03	15,77	2,07	1,7	17,02	43,34
		2XCD	19,32	16,8	1,62	1,96	13,31	56,65
		3OUD	30,04	28,06	1,36	1,24	11,16	67,82
		2OCD	8,78	10,48	1,07	0,97	8,74	76,56
		3OCM	0,5	2,42	1,01	2,07	8,27	84,83
		3XUD	11,27	10,85	0,79	1,34	6,5	91,33

Functional groups:

1OUM – 1(size ≤ 2 cm), O (ocellus-bearing species), U (understory-inhabitant butterflies) and M (monocot-feeding larval).

3XCD – 3 (size 3 ≤ 3.99 cm), X (absence of ocellus), C (canopy-inhabitant butterflies) and D (dicot-feeding larval).

2XCD – 2 (size 2 ≤ 2.99 cm), X (absence of ocellus), C (canopy-inhabitant butterflies) and D (dicot-feeding larval).

3OUD – 3 (size 3 ≤ 3.99 cm), O (ocellus-bearing species), U (understory-inhabitant butterflies) and D (dicot-feeding larval).

2OCD – 2 (size 2 ≤ 2.99 cm), O (ocellus-bearing species), C (canopy-inhabitant butterflies) and D (dicot-feeding larval).

3OCM – 3 (size 3 ≤ 3.99 cm), O (ocellus-bearing species), C (canopy-inhabitant butterflies) and M (monocot-feeding larval).

3XUD – 3 (size 3 ≤ 3.99 cm), X (absence of ocellus), U (understory-inhabitant butterflies) and D (dicot-feeding larval).

Table S6 Results of the Generalized Linear Models (GLMs) exhibiting the effects of biomass (BIO), chronic anthropogenic disturbance (CAD) and tree species richness on community-weighted means (CWM) of fruit-feeding butterfly traits in the Catimbau National Park, in Pernambuco state, northeastern Brazil. Model-averaged parameter estimates (*β*), unconditional variance (UV), the importance of variables and the goodness-of-fit of each complete model (R^2) (i.e. the percentage of deviance explained by each complete model) of information-theoretic-based model selection and multi model inference. The sign (+/-) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were more accurate, i.e., those higher than the unconditional variance. Butterfly traits (Size – size of the anterior wing, Ocellus – presence of ocellus, Canopy – use of the canopy and Larval monocots – larval feeding on monocotyledon plants)

Response variable	Predictors	*β*	UV	Importance	R^2
CWM_Size	BIO	-2.58×10^{-4}	2.87×10^{-6}	0.18	28%
	CAD	9.76×10^{-4}	5.71×10^{-6}	0.33	
	TR	4.87×10^{-4}	1.27×10^{-5}	0.22	
CWM_Ocellus	BIO	-8.49×10^{-3}	5.57×10^{-5}	0.67	73%
	CAD	-6.76×10^{-3}	3.17×10^{-5}	0.72	
	TR	1.79×10^{-2}	2.12×10^{-4}	0.73	
CWM_Canopy	BIO	1.62×10^{-3}	1.65×10^{-5}	0.18	61%
	CAD	7.65×10^{-3}	2.77×10^{-5}	0.78	
	TR	-7.38×10^{-3}	1.54×10^{-4}	0.36	
CWM_Larval monocots	BIO	-4.07×10^{-6}	2.32×10^{-6}	0.20	46%
	CAD	-3.14×10^{-3}	1.39×10^{-5}	0.65	
	TR	1.05×10^{-3}	2.24×10^{-5}	0.44	

Fig. S1 Rank-abundance curves of fruit-feeding butterflies sampled in old-growth forests (OF) and regenerating forests (RS) in the Catimbau National Park, in Pernambuco state, northeastern Brazil. The most abundant fruit-feeding butterfly species are labeled: Hafb (*Hamadryas februa februa*), Foha (*Fountainea halice*), Fogl (*Fountainea glycerium cratais*, Phap (*Pharneuptychia* sp.1), Hycl (*Hypna clytemnestra forbesi*) and Caso (*Callicore sorana sorana*)

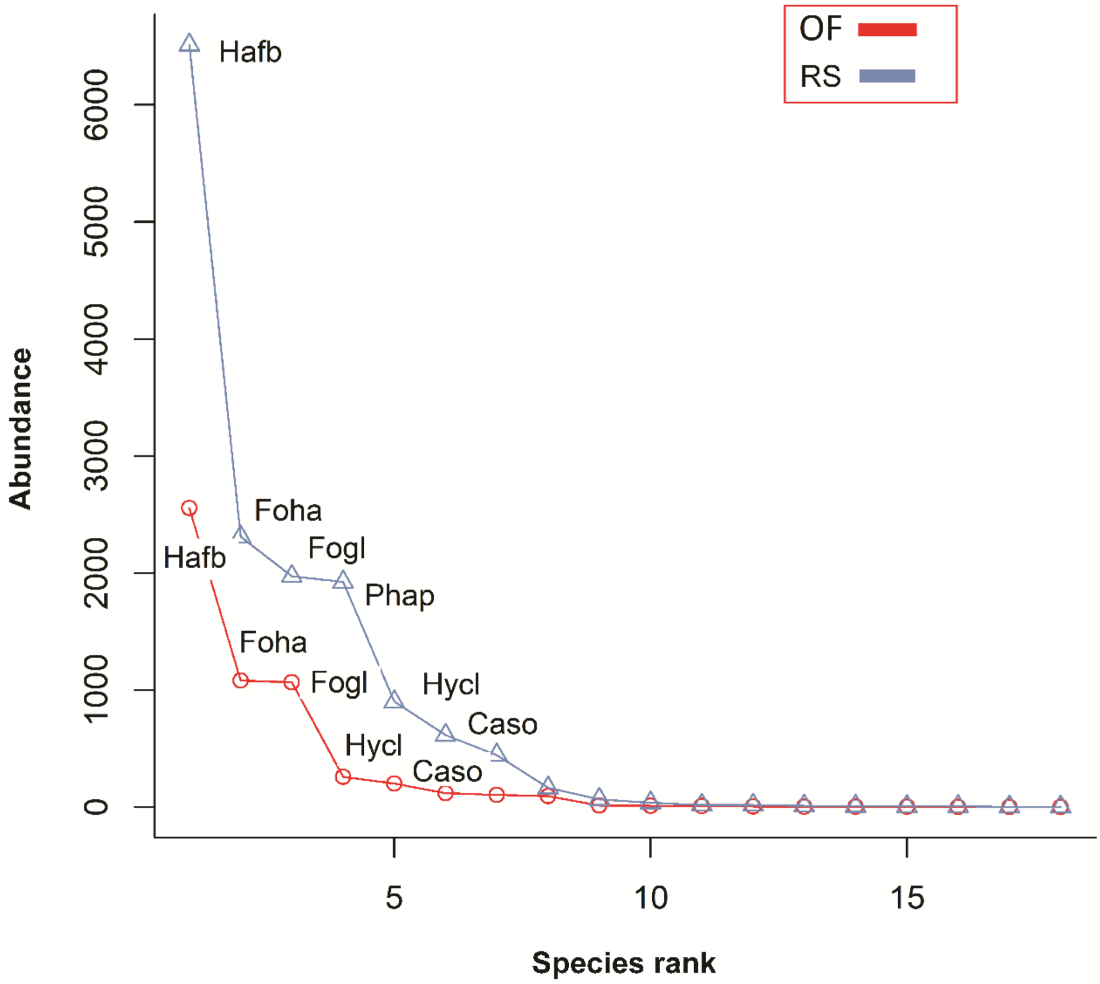


Fig. S2 Sample coverage and the confidence limits of fruit-feeding butterfly assemblages collected in old-growth forests (OF) (red) and regeneration areas (RS) (blue) in the Catimbau National Park, in Pernambuco state, northeastern Brazil

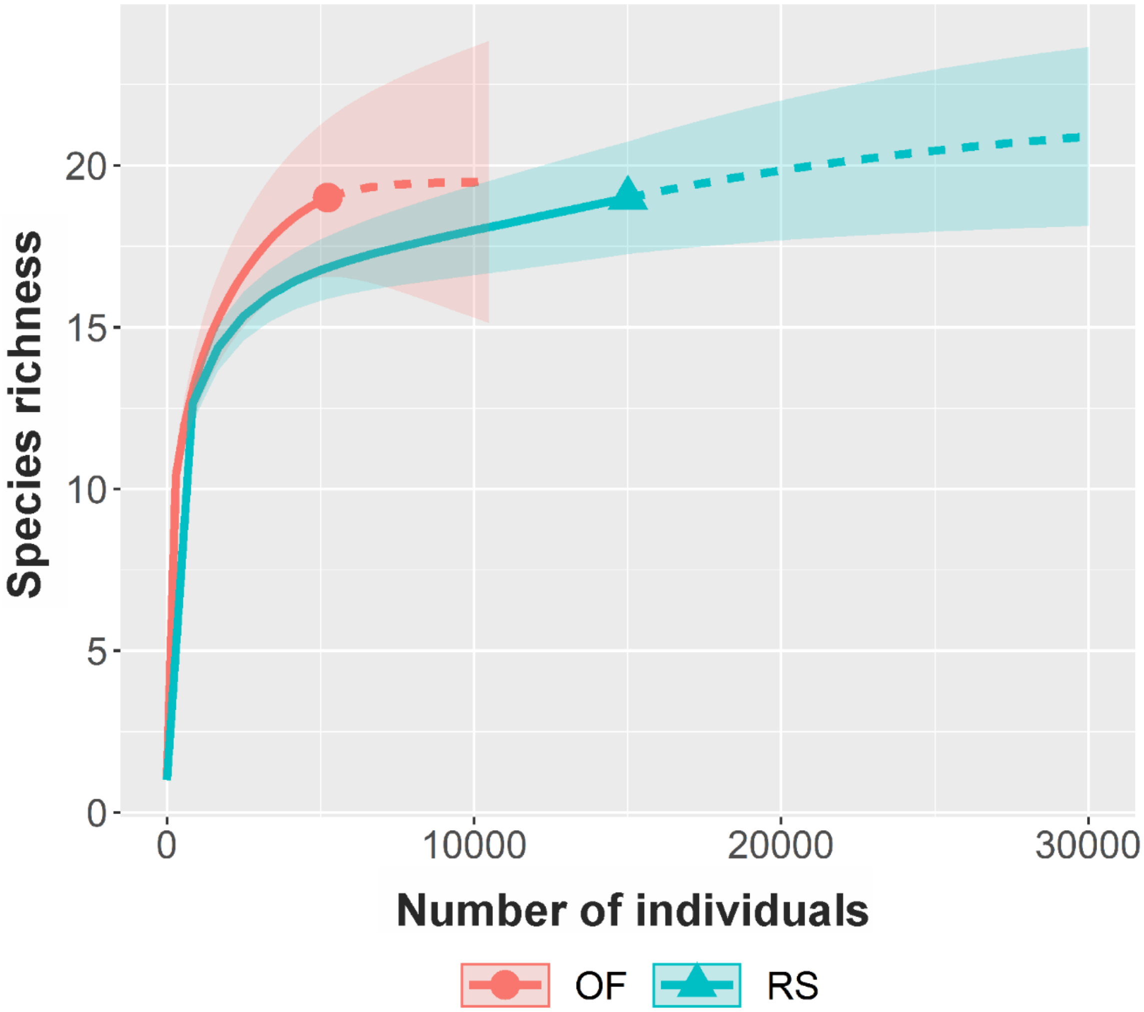


Fig. S3 Fruit-feeding butterfly β diversity regarding β_{SIM} (species turnover) and β_{SNE} (nestedness) across regenerating forest (RS) and old-growth forest stands (OF) in the Catimbau National Park, in Pernambuco state, northeastern Brazil

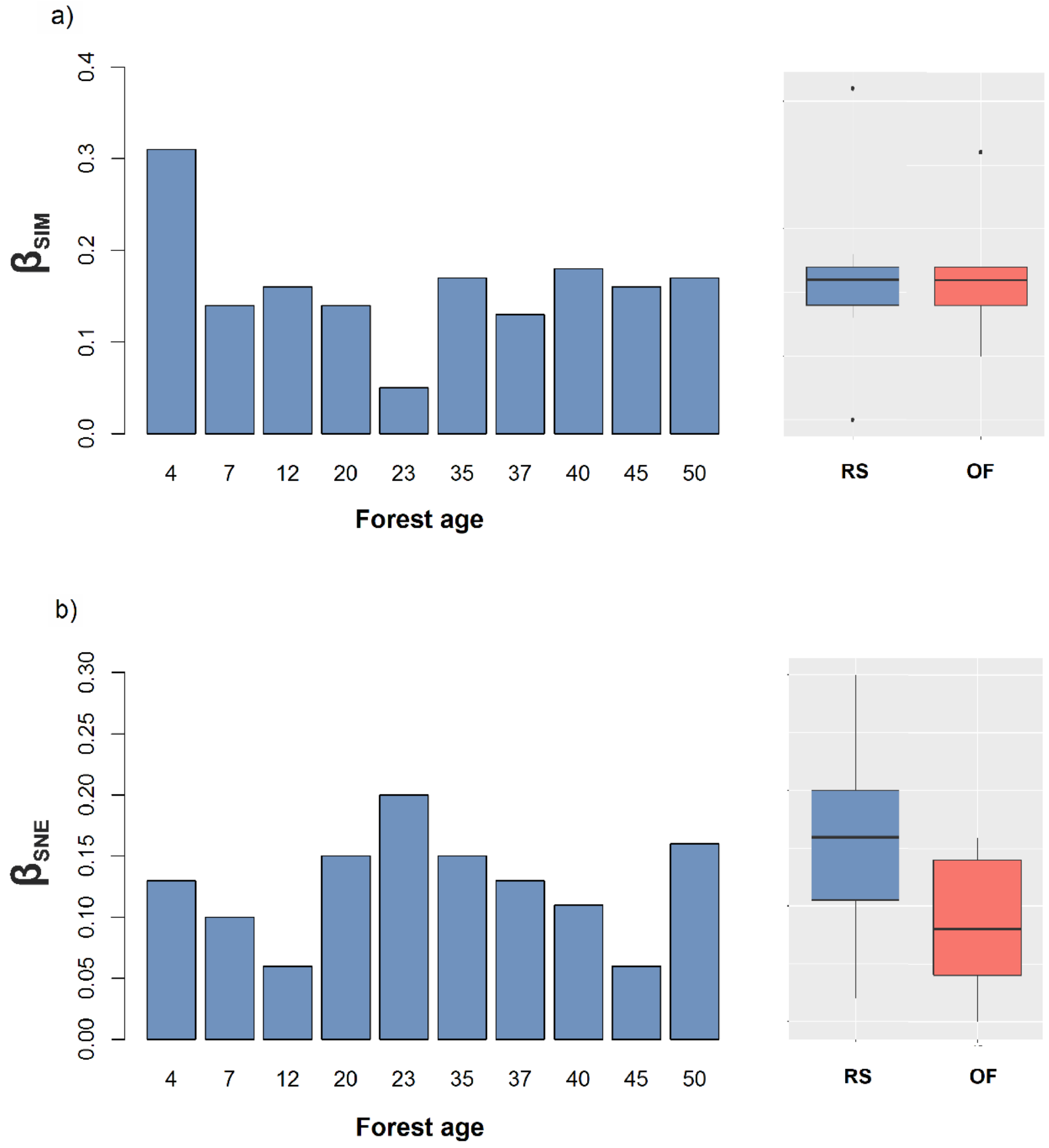


Fig. S4 Predictor variables included in the ΔAICc < 2 set of models for community-level attributes (abundance, ${}^{0}D$ – total species richness, ${}^{1}D$ – common species and ${}^{2}D$ – dominant species) of fruit-feeding butterfly assemblages across regenerating forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil. The sum of Akaike weights (Σwi) shows the importance of each variable. The sign (+/-) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were more accurate, i.e., those higher than the unconditional variance (see parameter estimates and unconditional variances in Table 1). The goodness-of-fit of each complete model (i.e., the percentage of deviance explained by each complete model) is also indicated for each case. Explanatory variables (BIO – biomass, CAD – chronic anthropogenic disturbance and TR – tree species richness)

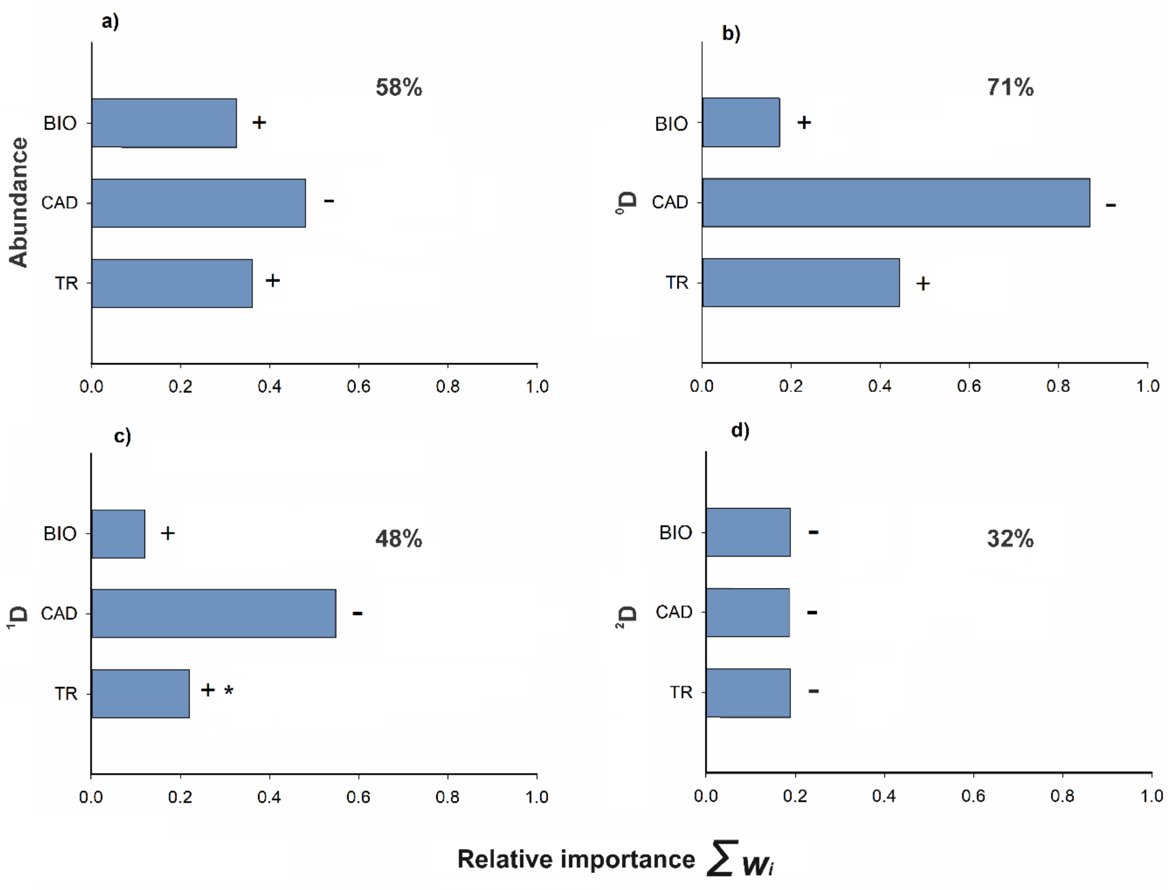


Fig. S5 Predictor variables included in the ΔAICc < 2 set of models for community-weighted mean fruit-feeding butterfly traits across regenerating forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil. The sum of Akaike weights (Σwi) shows the importance of each variable. The sign (+/-) of parameter estimates represents a positive or negative effect of the predictor on the response variable. Our models indicate the parameters that were more accurate, i.e., those higher than the unconditional variance (see parameter estimates and unconditional variances in Table S5). The goodness-of-fit of each complete model (i.e., the percentage of deviance explained by each complete model) is also indicated for each case. Butterfly traits (Size – size of the anterior wing, Ocellus – presence of ocellus, Canopy – use of the canopy and Larval monocots – larval feeding on monocotyledon plants)

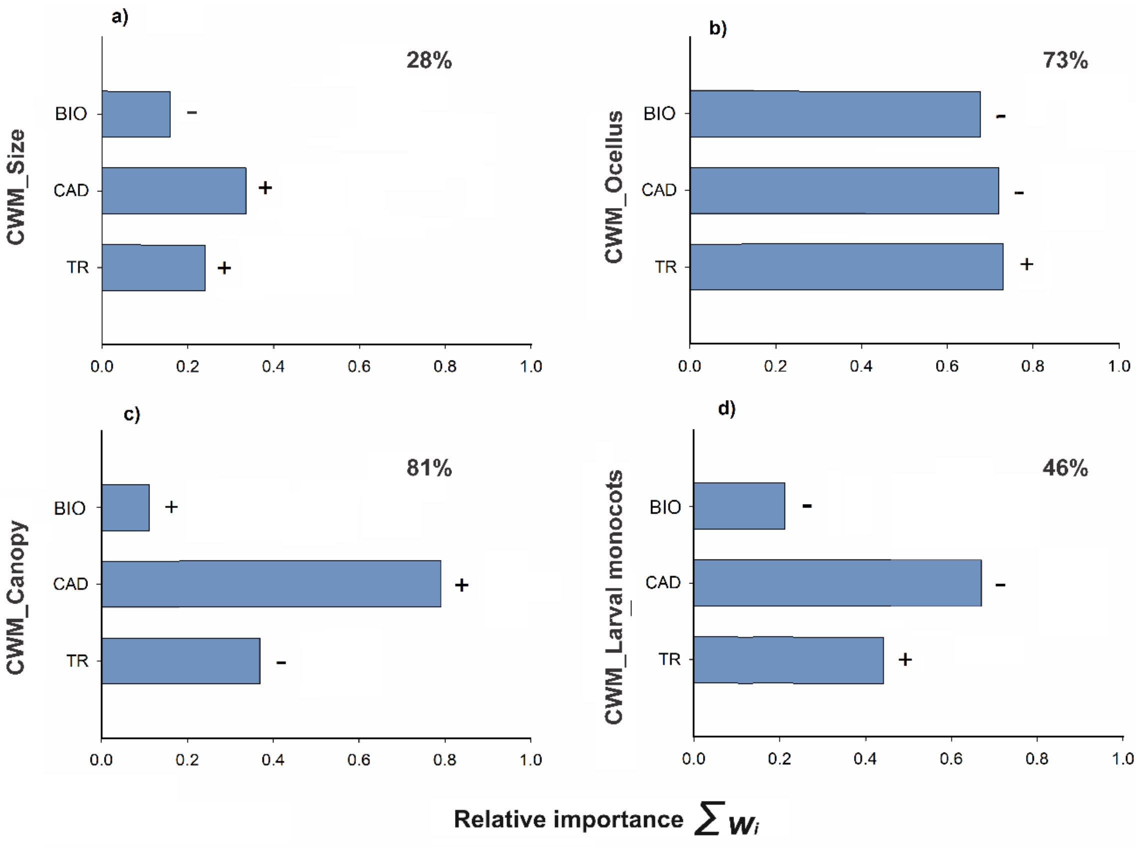
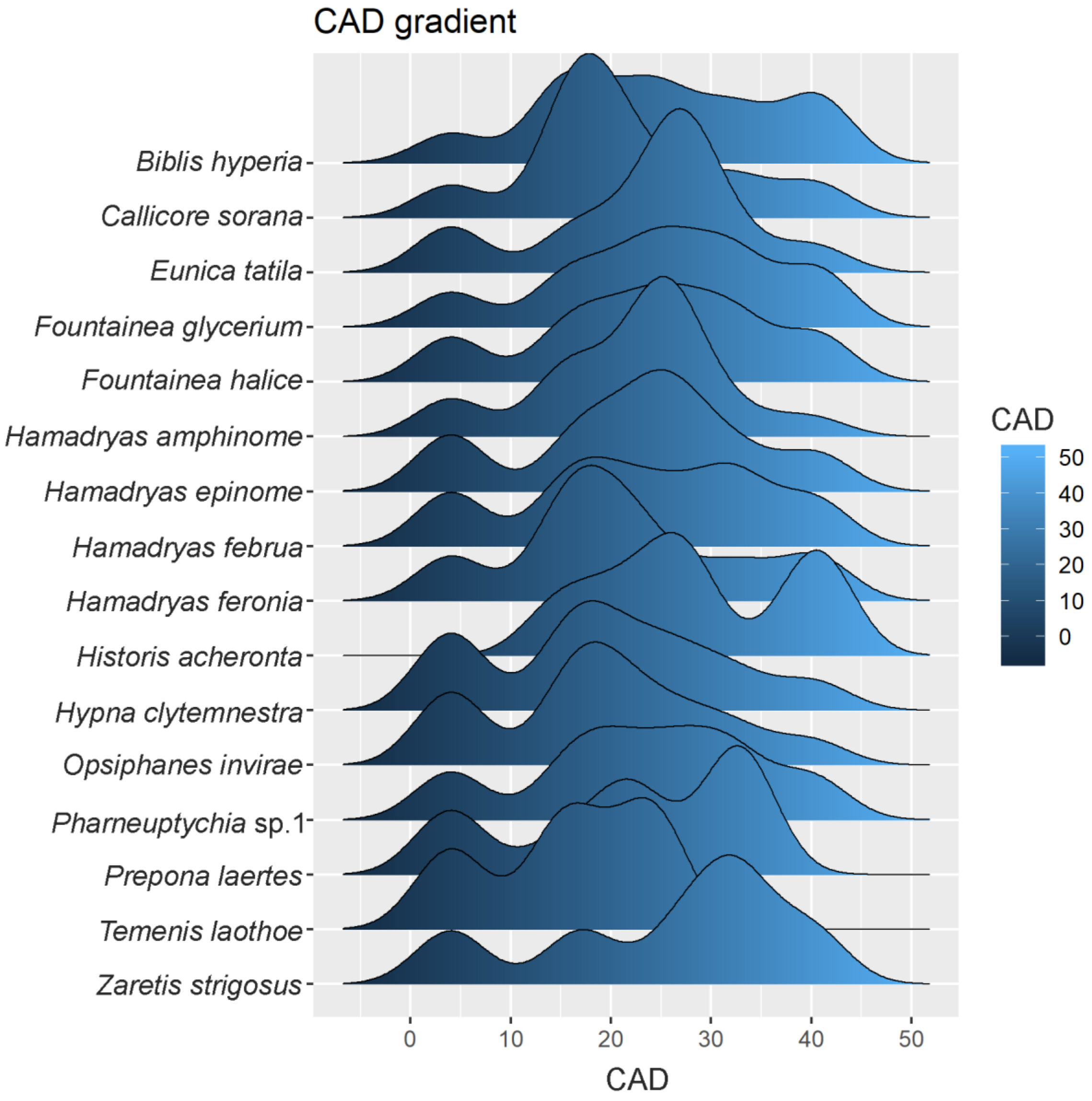


Fig S6 Fruit feeding-butterfly assemblages along regenerating forest stands under different intensities of chronic anthropogenic disturbance (CAD) in the Catimbau National Park, in Pernambuco state, northeastern Brazil



5 CONSIDERAÇÕES FINAIS

Este estudo realizado no Parque Nacional do Catimbau ressalta a importância da implementação de planos de manejo da vegetação e de conservação para biodiversidade, especialmente em um ecossistema como a Caatinga que vem sendo constantemente afetado pela agricultura de corte e queima e distúrbios antrópicos crônicos, o que levou ao status de um dos mais ameaçados do Brasil. A presente tese demonstra que as borboletas frugívoras estão respondendo a mudanças no habitat, ocasionadas por distúrbios crônicos (por exemplo, sobrepastoreio por animais domésticos e extração de madeira) e por variações abióticas (por exemplo, aumento de aridez), o que pode resultar em comunidades taxonomicamente e funcionalmente empobrecidas.

Mais especificamente, essa tese foi constituída por duas abordagens principais: (1) uma avaliação de como as comunidades de borboletas frugívoras são afetadas por distúrbios crônicos e aumento de aridez; e (2) uma análise de como essas comunidades se recompõem ao longo do processo de sucessão secundária natural, incluindo o papel que a riqueza de espécies de árvores, biomassa e distúrbios crônicos podem ter na recuperação desses insetos durante a regeneração da floresta. No primeiro capítulo, os resultados obtidos revelam que as comunidades de borboletas frugívoras exibem um empobrecimento taxonômico e funcional, como também baixos níveis de *turnover* de espécies em áreas extremas do gradiente de déficit hídrico. Além disso, as borboletas frugívoras são aninhadas em florestas com elevados níveis de distúrbio crônico e aridez. Verifica-se ainda que o aumento da aridez causa uma reorganização da comunidade de borboletas frugívoras na Caatinga, onde espécies e grupos funcionais sensíveis à aridez diminuem em abundância, enquanto espécies e grupos funcionais tolerantes à dessecação apresentam elevada abundância. No segundo capítulo, demonstra-se uma rápida recuperação dos atributos da comunidade de borboletas frugívoras (abundância, riqueza de espécies e diversidade) ao longo da trajetória sucessional, mas florestas secundárias e florestas maduras suportam comunidades de borboletas taxonomicamente e funcionalmente distintas. Como previsto, fatores como biomassa e riqueza de espécies de árvores (positivamente) e distúrbios crônicos (negativamente) foram excelentes preditores afetando os atributos taxonômicos das comunidades de borboletas frugívoras. Além disso, os resultados mostram que riqueza de espécies de árvores e distúrbios crônicos também afetam significativamente a composição funcional das comunidades de borboletas frugívoras. Ou seja, grupos ecológicos mais sensíveis a condições adversas aumentam em ambientes mais florestados, mas diminuem com a ação dos distúrbios crônicos que atuam selecionando apenas alguns grupos ecológicos mais tolerantes a ambientes perturbados, levando a homogeneização da biota.

Essas descobertas destacam a precipitação e os distúrbios crônicos como os principais condutores da reorganização de borboletas frugívoras na Caatinga. Quando as terras utilizadas para agricultura de corte e queima são abandonadas, os distúrbios crônicos podem atrasar os processos sucessionais, impedindo que a estrutura de florestas maduras seja alcançada. Uma vez que florestas primárias intactas estão cada vez mais escassas em regiões marcadas por densas populações humanas, programas de manejo ecológico para restaurar e maximizar a regeneração florestal nessas áreas altamente perturbadas podem tornar as florestas secundárias habitáveis e capazes de recuperar parcelas importantes da fauna regional ao longo do tempo. Por outro lado, o descaso pode trazer consequências irreversíveis quanto aos aspectos taxonômicos e funcionais, ocasionado pelos distúrbios crônicos e aumento de aridez, especialmente em florestas que vem sendo sistematicamente devastadas por pressões humanas, como no caso da Caatinga.

6 REFERÊNCIAS

ALBUQUERQUE, U. P.; ARAÚJO, E.; DE CASTRO, C. C.; ALVES, R. R. N. People and Natural Resources in the Caatinga. *In*: SILVA, J. M. C.; LEAL, I. R.; TABARELLI, M. (Eds.). **Caatinga**. Cham: Springer, 2017. p. 303-333.

ÁLVAREZ-YÉPIZ, J. C.; MARTÍNEZ-YRÍZAR, A.; FREDERICKSEN, T. S. Special issue: Resilience of tropical dry forest to extreme disturbance events. **Forest Ecology and Management**, v. 426, p. 1-6, 2018.

ANDRADE, J. F.; ALVARADO, F.; SANTOS, J. C.; SANTOS, B. A. Rainfall reduction increases insect herbivory in tropical herb communities. **Journal of Vegetation Science**, v. 31, p. 487-496, 2020.

ARIAS-MEDELLÍN, L. A.; FLORES-PALACIOS, A.; MARTÍNEZ-GARZA, C. Cacti community structure in a tropical Mexican dry forest under chronic disturbance. **Botanical Sciences**, v. 92, p. 405-415, 2014.

ARNAN, X.; ARCOVERDE, G. B.; PIE, M. R.; RIBEIRO-NETO, J. D.; LEAL, I. R. Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest. **Science of the Total Environment**, v. 631–632, p. 429-438, 2018.

ARROYO-RODRÍGUEZ, V.; MANDUJANO, S. Forest fragmentation modifies habitat quality for *Alouatta palliate*. **International Journal of Primatology**, v. 27, p. 1079-1096. 2006.

BARLOW, J. *et al.* Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. **Proceedings of the National Academy of Sciences USA**, v. 104, p. 18555-18560, 2007.

BARROS, M. F.; RIBEIRO, E. M. S.; VANDERLEI, R. S.; DE PAULA, A. S.; SILVA, A. B.; WIRTH, R.; CIANCIARUSO, M. V.; TABARELLI, M. Resprouting drives successional pathways and the resilience of Caatinga dry forest in human-modified landscapes. **Forest Ecology and Management**, v. 482, p. 118881, 2021.

BECKNELL, J. M.; KUCEK, L. K.; POWERS, J. S. Aboveground biomass in mature and secondary seasonally dry tropical forests: a literature review and global synthesis. **Forest Ecology and Management**, v. 276, p. 88-95, 2012.

BEIRÃO, M. V.; NEVES, F. S.; PENZ, C. M.; DEVRIES, P. J.; FERNANDES, G. W. High butterfly beta-diversity between Brazilian Cerrado and cerrado-caatinga transition zones. **Journal of Insect Conservation**, v. 21, p. 849-860, 2017.

BERTIN, R. I. Plant phenology and distribution in relation to recent climate change. **Journal of the Torrey Botanical Society**, v. 135, p. 126-146, 2008.

BOGGS, C. L.; MURPHY, D. D. Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. **Global Ecology and Biogeography Letters**, v. 6, p. 39-48, 1997.

BROVKIN, V.; CLAUSSEN, M.; PETOUKHOV, V.; GANOPOLSKI, A. On the stability of the atmosphere-vegetation system in the Sahara/Sahel region. **Journal of Geophysical Research Atmosphere**, v. 103, p. 31613-31624, 1998.

BROWN JR., K. S. Conservation of Neotropical environments: insects as indicators. *In*: COLLINS, N. M.; THOMAS, J. A. (Eds.). **The conservation of insects and their habitats**. London: Royal Entomological Society Symposium XV, Academic Press, 1991, p. 349-404.

BROWN JR, K. S. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. **Journal of Insect Conservation**, v. 1, p. 25-42, 1997.

BROWN JR, K. S.; FREITAS, A. V. L. Atlantic Forest butterflies: indicators for landscape conservation. **Biotropica**, v. 32, p. 934-956, 2000.

BROWN JR, K. S.; FREITAS, A. V. L. Lepidoptera. *In*: BRANDÃO, C. R. F.; CANCELLO, E. M. (Eds.). **Biodiversidade do Estado de São Paulo, Brasil: invertebrados terrestres**. São Paulo: FAPESP, 1999, p. 225-245.

CÂMARA, T.; LEAL, I. R.; BLÜTHGEN, N.; OLIVEIRA, F. M. P.; ARNAN, X. Anthropogenic disturbance and rainfall variation threaten the stability of plant-ant interactions in the Brazilian Caatinga. **Ecography**, v. 42, p. 1960-1972, 2019.

CASAS-PINILLA, L. C.; MAHECHA-J. O.; DUMAR-R.; RÍOS-MÁLAVER, I. C. Diversidad de mariposas en un paisaje de bosque seco tropical, en la Mesa de los Santos, Santander, Colombia (Lepidoptera: Papilionoidea). **SHILAP Revista de Lepidopterología**, v. 45, p. 83-108, 2017.

CECCON, E.; HUANTE, P.; RINCÓN, E. Abiotic factors influencing Tropical Dry Forests regeneration. **Brazilian Archives of Biology and Technology**, v. 49, p. 305-312, 2006.

CHAZDON, R. L.; LETCHER, S. G.; VAN BREUGEL, M.; MARTINEZ-RAMOS, M.; BONGERS, F.; FINEGAN, B. Rates of change in tree communities of secondary Neotropical forests following major disturbances. **Philosophical Transaction of the Royal Society B, Biological Sciences**, v. 362, p. 273-289, 2007.

CHAZDON, R. L.; PERES, C. A.; DENT, D.; SHEIL, D.; LUGO, A. E.; LAMB, D.; STORK, N. E.; MILLER, S. E. The potential for species conservation in tropical secondary forests. **Conservation Biology**, v. 23, p. 1406-1417, 2009.

CHAZDON, R. L. Tropical forest recovery: legacies of human impact and natural disturbances. **Perspectives in Plant Ecology, Evolution and Systematics**, v. 6, p. 51-71, 2003.

CHECA, M. F.; RODRIGUEZ, J.; WILLMOTT, K. R.; LIGER, B. Microclimate variability significantly affects the composition, abundance and phenology of butterfly communities in a highly threatened neotropical dry forest. **Florida Entomologist**, v. 97, p. 1-13, 2014.

CHIANG, J. C. H.; KOUTAVAS, A. Climate change: tropical flip-flop connections. **Nature**, v. 432, p. 684-685, 2004.

CLARK, J. S. *et al*. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. **Global Change Biology**, v. 22, p. 2329-2352, 2016.

COIMBRA-FILHO, A. F.; CÂMARA, I. G. **Os limites originais do bioma Mata Atlântica na região Nordeste do Brasil**. Rio de Janeiro: Fundação Brasileira para Conservação da Natureza, 1996. 86 p.

CORLETT, R. T. Environmental heterogeneity and species survival in degraded tropical landscapes. *In*: HUTCHINGS, M. J.; JOHN, E. A.; STEWART, A. J. A. (Eds.) **The ecological consequences of environmental heterogeneity**. Londres: British Ecological Society, 2000, p 333-355.

DANTAS, B. F. *et al*. Rainfall, not soil temperature, will limit the seed germination of dry forest species with climate change. **Oecologia**, v. 192, p. 529-541, 2020.

DANTAS DE PAULA, M.; COSTA, C. P. A.; TABARELLI, M. Carbon storage in a fragmented landscape of Atlantic Forest: the role played by edge-affected habitats and emergent trees. **Tropical Conservation Science**, v. 4, p. 349-358, 2011.

DEVRIES, P. J.; HAMM, C. A.; FORDYCE, J.A. A standardized butterfly sampling protocol: fruit-feeding butterflies (Nymphalidae). *In*: Larsen, T. H. (Ed.) **Core standardized methods for rapid biological field assessment**. Arlington: Conservation International, 2016. p. 139-148.

DEVRIES, P. J. **The butterflies of Costa Rica and their natural history. Vol. I. Papilionidae, Pieridae, and Nymphalidae**. New Jersey: Princeton University Press, 1987. 327 p.

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

DREVER, C. R.; PETERSON, G.; MESSIER, C.; BERGERON, Y.; FLANNIGAN, M. D. Can forests management based on natural disturbances maintain ecological resilience? **Canadian Journal of Forest Research**, v. 36, p. 2285-2299, 2006.

DUNN, R. R. Recovery of faunal communities during tropical forest regeneration. **Conservation Biology**, v. 18, p. 302-309, 2004.

EASTERLING, D. R. *et al*. Climate extremes: observations, modeling, and impacts. **Science**, v. 289, p. 2068-2074, 2000.

ELMQVIST, T.; FOLKE, C.; NYSTRÖM, M.; PETERSON, G.; BENGSTON, J.; WALKER, B.; NORBERG, J. Response diversity and ecosystem resilience. **Frontiers in Ecology and the Environment**, v. 1, p. 488-494, 2003.

ELTAHIR, E. A. B.; BRAS, R. L. Sensitivity of regional climate to deforestation in the Amazon basin. **Advances in Water Resources**, v. 17, p. 101-115, 1994.

ENGELBRECHT, B. M. J. *et al*. Drought sensitivity shapes species distribution patterns in tropical forests. **Nature**, v. 447, p. 80-82, 2007.

EWEL, J. J. Differences between wet and dry successional tropical ecosystems. **International journal of tropical geology, geography and ecology**, v. 1, p. 103-117, 1977.

EWERS, R. M.; DIDHAM, R. K. Confounding factors in the detection of species responses to habitat fragmentation. **Biological Reviews**, v. 81, p. 117-142, 2006.

FADRIQUE, B. *et al*. Widespread but heterogeneous responses of Andean forests to climate change. **Nature**, v. 564, p. 207-212, 2018.

FAUSET, S.; BAKER, T. R.; LEWIS, S. L.; FELDPAUSCH, T. R.; AFFUM-BAFFOE, K.; FOLI, E. G.; HAMER, K. C.; SWAINE, M. D. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. **Ecology Letters**, v.15, p. 1120-1129, 2012.

FILGUEIRAS, B. K. C.; IANNUZZI, L.; LEAL, I. R. Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. **Biological Conservation**, v. 144, p. 362-369, 2011.

FILGUEIRAS, B. K. C.; MELO, D. H. A.; LEAL, I. R.; TABARELLI, M.; FREITAS, A. V. L.; IANNUZZI, L. Fruit-feeding butterflies in edge-dominated habitats: community structure, species persistence and cascade effect. **Journal of Insect Conservation**, v. 20, p. 539-548, 2016.

FAO - Food and Agriculture Organization of the United Nations. **Global Forest Resource Assessment 2010: Key findings**. Roma: FAO Forestry Paper, 2010.

FAO - Food and Agriculture Organization of the United Nations; UNEP - United Nations Environmental Programme. The State of the World's Forests 2020. Forests, biodiversity and people. Rome, 2020. 214 p.

FORISTER, M. L.; MCCALL, A. C.; SANDERS, N. J.; FORDYCE, J. A.; THORNE, J. H.; O'BRIEN, J.; WAETJEN, D. P.; SHAPIRO, A. M. Are secondary forests ready for climate change? It depends on magnitude of climate change, landscape diversity and ecosystem legacies. **PNAS**, v. 107, p. 2088-2092, 2010.

FREITAS, A. V. L.; FRANCINI, R. B.; BROWN JR., K. S. Insetos como indicadores ambientais. *In*: CULLEN, J. R. L.; RUDRAN, R.; VALLADARES-PÁDUA, C. (Eds.). **Métodos de estudos em biologia da conservação e manejo da vida silvestre.** Editora da UFPR, Fundação O Boticário de Proteção à Natureza, 2003. p. 125-151.

FREITAS A. V. L.; ISERHARD C. A.; SANTOS J. P.; CARREIRA J. Y. O.; RIBEIRO D. B.; MELO D. H. A.; ROSA A. H. B.; MARINI-FILHO O. J.; ACCACIO G. M.; UEHARA-PRADO M. Studies with butterfly bait traps: an overview. **Revista Colombiana de Entomología**, v. 40, p. 209-218, 2014.

FREITAS, A. V. L.; LEAL, I. R.; UEHARA-PRADO, M.; IANNUZZI, L. Insetos como indicadores de conservação da paisagem. *In*: ROCHA, C. F. D.; BERGALLO, H. G.; VAN

SLUYS, M.; ALVES, M. A. S. (Eds.). **Biologia da conservação: essências**. São Carlos: RiMa Editora, 2006. p. 357-384.

FREITAS, A. V. L.; MARINI-FILHO, O. J. **Plano de ação nacional para a conservação dos lepidópteros ameaçados de extinção**. Brasília: Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), 2011. 124 p.

GILLESPIE, T. W.; GRIJALVA, A.; FARRIS, C. N. Diversity, composition, and structure of tropical dry forests in Central America. **Plant Ecology**, v. 147, p. 37-47, 2000.

GIULIETTI, A. M.; HARLEY, R. M.; QUEIROZ, L. P.; BARBOSA, M. R. V.; BOCAGE-NETA, A. L.; FIGUEIREDO, M. A. Espécies endêmicas da Caatinga. *In*: SAMPAIO, E. V. S. B.; GIULIETTI, A. M.; VIRGÍNIO, J.; GAMARRA-ROJAS, C. F. L. (Eds.). **Vegetação e Flora da Caatinga. Sampaio**. Recife: Associação Plantas do Nordeste, 2002. p. 103-118.

GORDO, O.; SANZ, J. J. Phenology and climate change: a long-term study in a Mediterranean locality. **Global Change Ecology**, v. 146, p. 484-495, 2005.

GUARIGUATA, M. R.; OSTERTAG, R. Neotropical secondary forest succession: changes in structural and functional characteristics. **Forest Ecology and Management**, v. 148, p. 185-206, 2001.

GUERATTO, P. E.; CARREIRA, J. Y. O.; SANTOS, J. P.; TACIOLI, A.; FREITAS, A. V. L. Effects of forest trails on the community structure of tropical butterflies. **Journal of Insect Conservation**, v. 24, p. 309-319, 2020.

HARDWICH, S. R.; TOUMI, R.; PFEIFER, M.; TURNER, E. C.; NILUS, R.; EWERS, R. M. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. **Agricultural and Forest Meteorology**, v. 201, p. 187-195, 2005.

HARRISON, S. P.; SANCHES GOÑI, M. F. Global patterns of vegetation response to millennial-scale variability and rapid climate change during the last glacial period. **Quaternary Science Reviews**, v. 29, p. 2957-2980, 2010.

HELLMANN, J. J.; BYERS, J. E.; BIERWAGEN, B. G.; DUKES, J. S. Five potential consequences of climate change for invasive species. **Conservation Biology**, v. 22, p. 534-543, 2008.

HIROTA, M.; HOLMGREN, M.; VAN NES, E. H.; SCHEFFER, M. Global resilience of tropical forest and savanna to critical transitions. **Science**, v. 334, p. 232-235, 2011.

HOEGH-GULDBERG, O. *et al.* Coral reefs under rapid climate change and ocean acidification. **Science**, v. 318, p. 7737-1742, 2007.

HOFFMANN, M. *et al.* The impact of conservation on the status of the world’s vertebrates. **Science**, v. 330, p. 1503-1509, 2010.

HOLLING, C. S. Resilience and stability of ecosystems. **Annual Review of Ecology and Systematics**, v. 4, p. 1-23, 1973.

HOOPER, D. U. *et al*. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. **Ecological Monographs**, v. 75, p. 3-35, 2005.

HUGHES, J. B.; DAILY, G. C.; EHRLICH, P.R. Population diversity: its extent and extinction. **Science**, v. 278, p. 689-692, 1997.

IPCC. **Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change**. PACHAURI, R. K.; MEYER, L. A. (Eds.). Switzerland: Geneva, 2014. 151 p.

JACKSON, S. T.; OVERPECK, J. T. Responses of plant populations and communities to environmental changes of the late Quaternary. **The Paleontological Society**, v. 26, p. 194-220, 2000.

JANZEN, D. H. Tropical dry forest: Area de Conservación Guanacaste, northwestern Costa Rica. *In*: PERROW, M. R.; DAVY, A. J. (Eds.). **Handbook of ecological restoration, volume 2, restoration in practice**. Cambridge: Cambridge University Press, 2002. p. 559-583.

JETZ, W.; WILCOVE, D. S.; DOBSON, A. P. Projected impacts of climate and land-use change on the global diversity of birds. **PLoS Biology**, v. 5, p. e157, 2007.

KINZIG, A. P.; PACALA, S. W.; TILMAN, D. **The functional consequences of biodiversity: empirical progress and theoretical extensions**. Princeton: Princeton University Press, 2001. 392 p.

KNAPP, A. K. *et al*. Consequences of more extreme precipitation regimes for terrestrial ecosystems. **Bioscience**, v. 58, p. 811-821, 2008.

KROL, M. S.; JAEGAR, A.; BRONSTERT, A.; KRYWKOW, J. The semiarid integrated model (SDIM), a regional integrated model assessing water availability, vulnerability of ecosystems and society in NE-Brazil. **Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere**, v. 26, p. 529-533, 2001.

LAURANCE, W. F.; PERES, C. A. **Emerging threats to tropical forests**. Chicago: University of Chicago Press, 2006. 520 p.

LAURANCE, W. F.; SAYER, J.; CASSMAN, K. G. Agricultural expansion and its impacts on tropical nature. **Trends in Ecology and Evolution**, v. 29, p. 107-116, 2014.

LEAL, L. C.; ANDERSEN, A. N.; LEAL, I. R. Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. **Oecologia**, v. 174, p. 173-181, 2014.

LEAL, L. C.; ANDERSEN, A. N.; LEAL, I. R. Disturbance Winners or Losers? Plants Bearing Extrafloral Nectaries in Brazilian Caatinga. **Biotropica**, v. 47, p. 468-474, 2015.

LEAL, I. R.; FILGUEIRAS, B. K. C.; GOMES, J. P.; IANNUZZI, L.; ANDERSEN, A. N. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic Forest. **Biodiversity and Conservation**, v. 21, p. 1687-1701, 2012.

LEAL, I. R.; TABARELLI, M.; SILVA, J. M. C. **Ecologia e conservação da Caatinga**. Recife: Editora Universitária, Universidade Federal de Pernambuco, 2003. 828 p.

LEAL, I. R.; TABARELLI, M.; SILVA, J. M. C.; LARCHER, T. E. Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. **Conservation Biology**, v.19, p. 701-706, 2005.

LEBRIJA-TREJOS, E.; MEAVE, J. A.; POORTER, L.; PÉREZ-GARCÍA, E. A.; BONGERS, F. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. **Perspectives in Plant Ecology, Evolution and Systematics**, v. 12, p. 267-275, 2010.

LEBRIJA-TREJOS, E.; PÉREZ-GARCÍA, E. A.; MEAVE, J. A.; POORTER, L.; BONGERS, F. Environmental changes during secondary succession in a tropical dry forest in Mexico. **Journal of Tropical Ecology**, v. 27, p. 477-489, 2011.

LEE, S.; JEON, H.; KIM, M. Spatial distribution of butterflies in Accordance with climate change in the Korean Peninsula. **Sustainability**, v. 12, p. 1995, 2020.

LETCHER, S. G. *et al*. Environmental gradients and the evolution of successional habitat specialization: a test case with 14 Neotropical forest sites. **Journal of Ecology**, v. 103, p. 1276-1290, 2015.

LÉVESQUE, M.; MCLAREN, K. P.; MCDONALD, M. A. Recovery and dynamics of a primary tropical dry forest in Jamaica, 10 years after human disturbance. **Forest Ecology and Management**, v. 262, p. 817-826, 2011.

LOHBECK, M. *et al*. Successional changes in functional composition contrast for dry and wet tropical forest. **Ecology**, v. 94, p. 1211-1216, 2013.

LÔBO, D.; LEÃO, T.; MELO, F. P. L.; SANTOS, A. M. M.; TABARELLI, M. Forest fragmentation drives Atlantic Forest of northeastern Brazil to biotic homogenization. **Diversity and Distributions**, v. 17, p. 287-296, 2011.

MAGRIN, G. O.; MARENGO, J. A.; BOULANGER, J. P.; BUCKERIDGE, M. S.; CASTELLANOS, E.; POVEDA, G.; SCARANO, F. R.; VICUÑA, S. (2014). Central and South America. *In*: BARROS, V. R.; FIELD, C. B.; DOKKEN, D. J.; MASTRANDREA, M. D.; MACH, K. J.; BILIR, T. E. (Eds.). **Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change**. Cambridge and New York: Cambridge University Press, 2014. p. 1499-1566.

MARENGO, J. A.; TORRES, R. R.; ALVES, L. M. Drought in Northeast Brazil—past, present, and future. **Theoretical and Applied Climatology**, v. 129, p. 1189-1200, 2017.

MARTORELL, C.; PETERS, E. M. Disturbance-response analysis: a method for rapid assessment of the threat to species in disturbed areas. **Conservation Biology**, v. 23, p. 377-387, 2009.

MARTORELL, C.; PETERS, E. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. **Biological Conservation**, v. 124, p. 199-207, 2005.

MARTIN, P. A.; NEWTON, A. C.; BULLOCK, J. M. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. **Proceedings of the Royal Society B: Biological Sciences**, v. 280, p. 20132236, 2013.

MASS, J. M.; BURGOS, A. Water dynamics at the ecosystem level in seasonally dry tropical forests. *In*: DIRZO, R.; YOUNG, H. S.; MOONEY, H. A.; CEBALLOS, G. (Eds.). **Seasonally dry tropical forests: ecology and conservation**. Washington: Island Press, p. 141-156, 2011.

MAY, R. M.; STUMPF, M. P. H. Species-Area relations in tropical forests. **Science**, v. 290, p. 2084-2086, 2000.

MAY-TOBIN, C. Wood for fuel. *In*: BOUCHER, D.; PIPA, E.; LININGER, K.; MAYTOBIN, C.; ROQUEMORE, S.; SAXON, E. (Eds.). **The root of the problem: what is driving tropical deforestation today?** Malden: Blackwell, 2011, p. 367-383.

MCDONALD, M. A.; MCLAREN, K. P.; NEWTON, A. C. (2010). What are the mechanisms of regeneration post-disturbance in tropical dry forest? **Environmental Evidence**. Disponível em: www.environmentalevidence.org/SR37.html. Acesso em: 21 ago. 2020.

MCMENAMIN, S. K.; HADLY, E. A.; WRIGHT, C. K. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. **Proceedings of the National Academy of Sciences**, v. 105, p. 16988-16993, 2008.

MEHTA, V. K.; SULLIVAN, P. J.; WALTER, M. T.; KRISHNASWAMY J.; DEGLORIA. S. D. Ecosystem impacts of disturbance in a dry tropical forest in southern India. **Ecohydrology**, v. 1, p. 149-160, 2008.

MELO, D. H.; FILGUEIRAS, B. K. C.; ISERHARD, C. A.; IANNUZZI, L.; FREITAS, A. V. L.; LEAL, I. R. Effect of habitat loss and fragmentation on fruit-feeding butterflies in the Brazilian Atlantic Forest. **Canadian Journal of Zoology**, v. 97, p. 588-596, 2019.

MILES, L.; NEWTON, A. C.; DEFRIES, R. S.; RAVILIOUS, C.; MAY, I.; BLYTH, S.; KAPOS, V.; GORDON, J. E. A global overview of the conservation status of tropical dry forests. **Journal of Biogeography**, v. 33, p. 491–505, 2006.

MOONEY, H. A.; BULLOCK, S. H.; MEDINA, E. Introduction, *In:* BULLOCK, S. H.; MOONEY, H. A.; MEDINA, E. (Eds.). **Seasonally Dry Tropical Forests.** Cambridge: Cambridge University Press, 1995. p. 146-194.

MORA, F.; MARTINEZ-RAMOS, M.; IBARRA-MANRIQUEZ, G.; PEREZ-JIMENEZ, A.; TRILLERAS, J.; BALVANERA, P. Testing chronosequences through dynamic approaches: Time and site effects on tropical dry forest succession. **Biotropica**, v. 47, p. 38-48, 2015.

MURPHY, P. G.; LUGO, A. E. Ecology of tropical dry forest. **Annual Review of Ecology and Systematics**, v. 17, p. 67-88, 1986.

MYERS, N. Two key challenges for biodiversity: Discontinuities and synergisms. **Biodiversity and Conservation**, v. 5, p. 1024-1034, 1996.

NIMER, E. Climatologia da região Nordeste do Brasil. Introdução à climatologia dinâmica. **Revista Brasileira de Geografia**, v. 34, p. 3-51, 1972.

NORDEN, N.; MESQUITA, R. C. G.; BENTOS, T. V.; CHAZDON, R. L.; WILLIAMSON, G. B. Contrasting community compensatory trends in alternative successional pathways in central Amazonia. **Oikos**, v. 120, p. 143-151, 2011.

NYAFWONO, M.; VALTONEN, A.; NYEKO, P.; ROININEN, H. Butterfly Community composition across a successional gradient in a human-disturbed Afro-tropical rain forest. **Biotropica**, v. 4, p. 210–218, 2014.

OATHAM, M.; BOODRAM, N. Gap analysis of neotropical dry forests in protected areas using geographical information systems and global datasets. **Tropical Ecology**, v. 47, p. 271-278, 2006.

OHLEMULLER, R. *et al*. The coincidence of climatic and species rarity: high risk to small-range species from climate change. **Biology Letters**, v. 4, p. 568-572, 2008.

OLIVEIRA, F. M. P.; ANDERSEN, A. N.; ARNAN, X.; RIBEIRO-NETO, J. D.; ARCOVERDE, G. B.; LEAL, I. R. Effects of increasing aridity and chronic anthropogenic disturbance on seed dispersal by ants in Brazilian Caatinga. **Journal of Animal Ecology**, v. 88, p. 870-880, 2019.

OLIVEIRA, F. M. P.; CÂMARA, T.; DURVAL, J. I. F.; OLIVEIRA, C. L. S.; ARNAN, X.; ANDERSEN, A. N.; RIBEIRO, E. M. S.; LEAL, I. R. Plant protection services mediated by extrafloral nectaries decline with aridity but are not influenced by chronic anthropogenic disturbance in Brazilian Caatinga. **Journal of Ecology**, v. 109, p. 260-272, 2020.

OLIVEIRA, F. M. P.; RIBEIRO-NETO, J. D.; ANDERSEN, A. N.; LEAL, I. R. Chronic anthropogenic disturbance as a secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga. **Environmental Conservation**, v. 44, p. 115-123, 2017.

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

OLIVER, T. H.; MARSHALL, H. H.; MORECROFT, M. D.; BRERETON, T.; PRUDHOMME, C.; HUNTINGFORD, C. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. **Nature Climate Change**, v. 5, p. 941-945, 2015.

PENNINGTON, R. T.; LAVIN, M.; OLIVEIRA-FILHO, A. Woody plant diversity, evolution, and ecology in the tropics: perspectives from Seasonally Dry Tropical Forests. **Annual Review of Ecology, Evolution and Systematics**, v. 40, p. 437-457, 2009.

PEREIRA, H. M. *et al.* Scenarios for global biodiversity in the 21st century. **Science**, v. 330, p. 1496-1501, 2010.

PETERSON, G.; ALLEN, C. R.; HOLLING, C. S. Ecological resilience, biodiversity and scale. **Ecosystems**, v. 1, p. 6-18, 1998.

PHILLIPS, O. L.; LEWIS, S. L.; BAKER, T. R.; CHAO, K. J.; HIGUCHI, N. The changing Amazon forest. **Philosophical Transactions of the Royal Society B-Biological Sciences**, v. 363, p. 1819-1827, 2008.

POLLARD, E.; YATES, T. J. **Monitoring butterflies for ecology and conservation**. London: Chapman & Hall, 1993. 274 p.

PRADO, D. As caatingas da América do Sul. *In*: LEAL, I. R.; TABARELLI, M.; SILVA, J. M. C. (Eds.). **Ecologia e conservação da Caatinga**. Recife: Editora Universitária - Universidade Federal de Pernambuco, 2003. p. 3-73

PÜTTKER, T. *et al.* Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. **Biological Conservation**, v. 241, p. 108368, 2020.

QUESADA, M. *et al*. Succession and management of tropical dry forests in the Americas: review and new perspectives. **Forest Ecology and Management**, v. 258, p. 1014-1024, 2009.

RAIMUNDO, R. L. G.; FREITAS, A. V. L.; COSTA, R. N. S.; OLIVEIRA, J. B. F.; MELO, A. B.; BROWN JR., K. S. **Manual de monitoramento ambiental usando borboletas e libélulas - Reserva Extrativista do Alto Juruá**. Série Pesquisa e Monitoramento Participativo em Áreas de Conservação Gerenciadas por Populações Tradicionais, Volume 1. Campinas: CERES/Laboratório de Antropologia e Ambiente, 2003.

REYNOLDS, J. F. *et al*. Global desertification: building a science for dryland development. **Science**, v. 316, p. 847-51, 2007.

RIBEIRO, D. B.; BATISTA, R.; PRADO, P. I.; BROWN JR., K. S.; FREITAS, A. V. L. The importance of small scales to the fruit-feeding butterfly assemblages in a fragmented landscape. **Biodiversity Conservation**, v. 21, p. 811-827, 2012.

RIBEIRO, D. B.; FREITAS, A. V. L. Differences in thermal responses in a fragmented landscape: temperature affects the sampling of diurnal, but not nocturnal fruit-deeding Lepidoptera. **Journal of Research on the Lepidoptera**, v. 42, p. 1-4, 2010.

RIBEIRO, D. B.; PRADO, P. I.; BROWN JR., K. S.; FREITAS, A. V. L. Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. **Diversity and Distributions**, v. 14, p. 961-968, 2008.

RIBEIRO, E. M. S.; ARROYO-RODRIGUEZ, V.; SANTOS, B. A.; TABARELLI, M.; LEAL, I. R. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. **Journal of Applied Ecology**, v. 52, p. 611-620, 2015.

RIBEIRO, E. M. S.; LOHBECK, M.; SANTOS, B. A.; ARROYO-RODRIGUES, V.; TABARELLI, M.; LEAL, I. R. Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. **Journal of Ecology**, v. 107, p. 2291-2302, 2019.

RIBEIRO, E. M. S.; SANTOS, B. A.; ARROYO-RODRIGUES, V.; TABARELLI, M.; SOUZA, G.; LEAL, I. R. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. **Ecology**, v. 97, p. 1583-1592, 2016.

RIBEIRO-NETO, J. D.; ARNAN, X.; TABARELLI, M.; LEAL, I. R. Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. **Biodiversity and Conservation**, v. 25, p. 943–956, 2016.

RITO, K. F.; ARROYO-RODRÍGUEZ, V.; QUEIROZ, R. T.; LEAL, I. R.; TABARELLI, M. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. **Journal of Ecology**, v. 105, p. 828-838, 2017.

SALA, O. E. *et al*. Global biodiversity scenarios for the year 2100. **Science**, v. 287, p. 1770-1774, 2000.

SALAZAR, L. F.; NOBRE, C. A.; OYAMA, M. D. Climate change consequences on the biome distribution in tropical South America. **Geophysical Research Letters**, 34, L09708, 2007.

SAMPAIO, E. V. S. B. Overview of the Brazilian Caatinga. *In*: BULLOCK, S. H.; MOONEY, H. A.; MEDINA, E. (Eds.). **Seasonally dry forests**. Cambridge: Cambridge University Press, 1995. P. 35-58.

SANCHEZ-AZOFEIFA, G. A. *et al*. Research priorities for neotropical dry forests. **Biotropica**, v. 37, p. 477- 485, 2005.

SANT'ANNA, C. L.; RIBEIRO, D. B.; GARCIA, L. C.; FREITAS, A. V. L. Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. **Restoration Ecology**, v. 22, p. 480-485, 2014.

SANTOS, B. A.; ARROYO-RODRÍGUEZ, V.; MORENO, C. E.; TABARELLI, M. Edge-related loss of tree phylogenetic diversity in severely fragmented Brazilian Atlantic Forest. **PLoS ONE**, v. 5, e12325, 2010.

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 Coservation**, v. 141, p. 249-260, 2008.

SANTOS, M. F. A. V.; GUERRA, T. N. F.; SOTERO, M. C.; SANTOS, J. I. N. Diversidade e densidade de espécies vegetais da Caatinga com diferentes graus de degradação no município de floresta, Pernambuco, Brasil. **Rodriguésia**, v. 60, p. 389-402, 2009.

SILVA, I. L. H.; LEAL, I. R.; RIBEIRO-NETO, J. D.; ARNAN, X. Spatiotemporal responses of ant communities across a disturbance gradient: the role of behavioral traits. **Insectes Sociaux**, v. 66, p. 623-635, 2019.

SILVA, J. M. C.; BARBOSA, L. C. F. Impact of Human Activities on the Caatinga. *In*: SILVA, J. M. C.; LEAL, I. R.; TABARELLI, M. (Eds.). **Caatinga**. Cham: Springer, 2017. p. 359-368.

SILVA, J. M. C.; LEAL, I. R.; TABARELLI, M. **Caatinga: The Largest Tropical Dry Forest Region in South America**. Switzerland: Springer, 2017. 506 p.

SILVA, J. M. C.; TABARELLI, M.; FONSECA, M. T.; LINS, L. **Biodiversidade da Caatinga: áreas e ações prioritárias para a conservação**. Brasília: Ministério do Meio Ambiente, 2004. 382 p.

SILVA, J. V. C. L.; HIRSCHFELD, M. N. C.; CARES, J. E.; ESTEVES, A. M. Land use, soil properties and climate variables influence the nematode communities in the Caatinga dry forest. **Applied Soil Ecology**, v. 150, p. 103474, 2020.

SINGH, G.; RAWAT, G. S.; VERMA, D. Comparative study of fuelwood consumption by villagers and seasonal "Dhaba owners" in the tourist affected regions of Garhwal Himalaya, India. **Energy Policy**, v. 38, p. 1895-1899, 2010.

SINGH, S. P. Chronic disturbance, a principal cause of environmental degradation in developing countries. **Environmental Conservation**, v. 25, p. 1-2, 1998.

SOUZA, D. G.; SFAIR, J. C.; PAULA, A. S.; BARROS, M. F.; RITO, K. F.; TABARELLI, M. Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest. **Forest Ecology and Management**, v. 435, p. 57-65, 2019.

SOUZA, E. B.; MANZI, A. O. Mudanças ambientais de curto e longo prazo: projeções, reversibilidade e atribuição. *In*: AMBRIZZI, T.; ARAUJO, M. (Eds.). **Base científica das mudanças climáticas. Contribuição do Grupo de Trabalho 1 do Painel Brasileiro de Mudanças Climáticas ao Primeiro Relatório da Avaliação Nacional sobre Mudanças Climáticas**. Rio de Janeiro: COPPE-UFRJ, 2014. p. 320-351.

STEFANESCU, C.; PEÑUELAS, J.; FILELLA, I. Effects of climate change on the phenology of butterflies in the northwest Mediterranean Basin. **Global Change Biology**, v. 9, p. 1494-1506, 2003.

SUAZO-ORTUÑO, I.; ALVARADO-DÍAZ, J.; MARTÍNEZ-RAMOS, M. Effects of conversion of dry tropical forest to agricultural mosaic on herpetofaunal assemblages. **Conservation Biology**, v. 22, p. 362-374, 2008.

TABARELLI, M.; AGUIAR, A. V.; RIBEIRO, M. C.; METZGER, J. P.; PERES, C. A. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. **Biological Conservation**, v. 143, p. 2328-2340, 2010.

TABARELLI, M.; LOPES, A. V.; PERES, C. A. Edge-effects drive tropical forest fragments towards an early-successional system. **Biotropica**, v. 40, p. 657-661, 2008.

TABARELLI, M.; SILVA, J. M. C.; GASCON, C. Forest fragmentation, synergisms and the impoverishment of Neotropical forests. **Biodiversity and Conservation**, v. 13, p. 1419-1425, 2004.

THOMPSON, I.; MACKEY, B.; MCNULTY, S.; MOSSELER, A. **Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems**. Montreal: Secretariat of the Convention on Biological Diversity, 2009. p. 67.

TREJO, I.; DIRZO, R. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. **Biological Conservation**, v. 94, p. 133-142, 2000.

UEHARA-PRADO, M.; BROWN JR., K. S.; FREITAS, A. V. L. Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. **Global Ecology and Biogeography**, v. 16, p. 43-54, 2007.

VÁZQUEZ-REYES, L. D.; ARIZMENDI, M. C.; GODÍNEZ-ÁLVAREZ, H. O.; NAVARRO-SIGÜENZA, A. G. Directional effects of biotic homogenization of bird communities in Mexican seasonal forests. **Condor**, v. 119, p. 275-288, 2017.

VIEIRA, D. L. M.; SCARIOT, A. Principles of natural regeneration of tropical dry forests for restoration. **Restoration Ecology**, v. 14, p. 11-20, 2006.

WAHLBERG, N.; LENEVEU, J.; KODANDARAMAIAH, U.; PEÑA, C.; NYLIN, S.; FREITAS, A. V. L.; BROWER, A. V. Z. Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. **Proceedings of the Royal Society B**, v. 276, p. 4295-4302, 2009.

WALKER, B. Conserving biological diversity through ecosystem resilience. **Conservation Biology**, v. 9, p. 747-752, 1995.

WALKER, B.; SALT, D. 2006. **Resilience thinking: sustaining ecosystems and people in a changing world**. Washington, D.C.: Island Press. 174 p.

WEPPRICH, T.; ADRION, J. R.; RIES, L.; WIEDMANN, J.; HADDAD, N. M. Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. **PLoS ONE**, v. 14, p. e0216270, 2019.

WILLIG, M. R.; WALKER, L. R. Disturbance in terrestrial ecosystems: Salient themes synthesis, and future directions. *In*: WALKER, L. R. (Ed.). **Ecology of Disturbed Ground**. Amsterdam: Elsevier Science, 1999. p. 747-767.

WRIGHT, S. J.; MULLER-LANDAU, H. C. The future of tropical forest species. **Biotropica**, 38, p. 287-301, 2006.