**UNIVERSIDADE ESTADUAL DE SANTA CRUZ**
**PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO**
**PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE**

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# DIVERSIDADE DE BORBOLETAS EM PAISAGENS DE FLORESTAS TROPICAIS:
## RESPOSTAS A PERTURBAÇÕES ANTRÓPICAS

**ILHÉUS - BAHIA**
**2025**

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## RESPOSTAS A PERTURBAÇÕES ANTRÓPICAS

Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutora em Ecologia e Conservação da Biodiversidade. Área de concentração: Ecologia e Conservação da Biodiversidade

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**ILHÉUS - BAHIA**
**2025**

P436 Pereira, Geanne Carla Novais.

Diversidade de borboletas em paisagens de florestas tropicais: respostas a perturbações antrópicas / Geanne Carla Novais Pereira. – Ilhéus, BA: UESC, 2025.

143 f. : il.

Orientadora: Eliana Cazetta.

Tese (doutorado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade.

Inclui referências.

1. Florestas tropicais. 2. Mata Atlântica. 3. Borboletas. 4. Fragmentação florestal. 5. Perturbações antrópicas. I.Título.

CDD 577.3

Ficha catalográfica elaborada por: Maria José Serrão Nunes – CRB 5/1643

**Agradecimentos**

Primeiramente, agradeço à minha família, que sempre me apoiou e incentivou a seguir meus objetivos. Agradeço por acreditarem muito mais no meu potencial do que eu mesma, e por sempre estarem disponíveis para me ajudar e apoiar. Em especial, agradeço aos meus pais, Maria Antonia Novais Pereira e Nelson Tobias Pereira, que além de tudo ainda ficaram confinados comigo durante a pandemia, e por mais difícil que tenha sido esse momento, estar com vocês foi sempre agradável, reconfortante e feliz. Aos meus irmãos, Kelly Novais Pereira, Dener Nelson Novais Pereira e Tanna Paula Novais Pereira, e meus sobrinhos Sofia Novais Pereira Alves, Vitória Espíndola Pereira e Nicolas Novais Pereira Alves, minha imensa gratidão por fazerem parte desta família maravilhosa e acolhedora.

Agradeço ao Jorge Mario Herrera Lopera, que se mostrou a pessoa mais maravilhosa que o universo poderia colocar em meu caminho. Obrigada com todo meu coração por todo amor, carinho, paciência e cuidado que você tem comigo desde que nos conhecemos. Essa tese é também um pouco sua, não só por ser coautor de dois capítulos, mas principalmente por todo apoio que me deu para que eu pudesse executar e concluir meu projeto. Sempre preocupado com meu bem-estar, você foi e é o suporte que me permitiu trilhar e terminar este percurso, que muitas vezes parecia não ter fim. E por ter incluído na minha vida meus dois amores, Goya e Baleia, que são os seres mais fofos capazes de deixar cada dia mais gostoso de viver.

Todo agradecimento a minha querida orientadora Eliana Cazetta, por toda paciência, incentivo e carinho demonstrados em todo o percurso. Por tentar me ensinar a fazer tudo com calma, a me divertir e vivenciar o processo. Eu tentei aprender, e sei que vou levar suas lições para a vida! À minha coorientadora Marina do Vale Beirão, que me inseriu no universo acadêmico das borboletas e desde então tem sido, além de uma grande amiga, meu suporte "borboletal".

Sou imensamente grata todo os amigos, que me toleraram e apoiaram nessa jornada, proporcionando momentos felizes, agradáveis, divertidos, sem os quais não seria possível sobreviver e terminar esta tese. Em especial, agradeço a Ana Rúbia Rossi e Jéssica Sato, que foram incrivelmente pacientes, principalmente no período da qualificação, e a Paloma Resende, Victória Paz, José Victor Ferreira, Ana Flávia do Nascimento, Amanda Sabino, Alejandra Rivillas, Maria Vetorin e Sebastián Bustamante.

A todos os membros e amigos do Laboratório de Ecologia Aplicado à Conservação (LEAC) e do Laboratório de Interações Ecológicas e Plantas Tropicais (Labint), em especial a Leiza Soares, Milena Gama e Júlia Angeli, e os ic's que tanto trabalharam nesse projeto, Hillary Azevedo, Bruno Mangabinha, Júlia Santos, Laysa Sá Schat e Gabrielly Silva.

Um agradecimento especial para às amigas que mesmo longe se fizeram presente compartilhando essa batalha, Isabela Oliveira, que teve até que revisar identificação de borboletas, e a Érica Rievrs, ou melhor, Eriquê, que mesmo longe sempre se fez presente. Agradeço também ao Fernando Pinho, que me apoiou à sua maneira e me ajudou muito no início dessa jornada.

Agradeço aos novos amigos que o período de sanduíche na Espanha me deu, pessoas que me fizeram sentir em casa, me acolheram e apoiaram: Alexsandro Bezerra, Marta Correa, Borja Buades, Fernanda Hernandez, Pau Luque, e especialmente a Anna Traveset que me aceitou e acolheu em seu laboratório e me ensinou muito.

Agradeço a todos que me ajudaram nos campos eternos: os mateiros Adson (Bii) e Jovelino (Seu Jovem), Mayana, Mario Herrera, Lucca, Júlia Angeli, Ana Flávia, Antonio, Milena, Hillary, Bruno, Jéssica Sato, Eliana Cazetta, Vladimir, Lays e Manu. E as pessoas de Santa Maria Eterna, que sempre nos receberam tão bem, em especial a Késsia. Aos motoristas da UESC, principalmente ao Marcos. E a todos os proprietários que participaram do projeto Rede SisBiota Una e permitiram realização do nosso trabalho.

Sou muito grata ao professor André Victor Freitas e a todos os membros do Labbor que me receberam tão bem, me auxiliaram todo o tempo que estive por lá e depois, nas trocas de e-mails e mensagens. Agradeço especialmente aos que me ajudaram com a identificação: André Victor (Nymphalidae), Augusto Rosa (Satyrini, Pieridae), Eduardo Barbosa (Satyrini), Luisa Mota (Riodinidae e Lycaenidae), Ricardo Siewert (Hesperiidae) e Diogo Dolibaina (Hesperiidae). E a Tiago Oliveira e Larissa pela montagem de algumas borboletas e Ana Carolina Tamiossi pelas fotos de borboletas montadas.

Agradeço também a Marco Dorea, Paula Calaça e Fernanda Figueiredo por dedicarem tempo pra me ensinar e ajudar sobre pólen. O aprendizado não será perdido, e continuaremos o trabalho depois da defesa.

Agradeço aos professores do PPG Ecologia e Conservação da Biodiversidade, em especial a Larissa Rocha pela ajuda com os dados de vegetação além das caronas e momentos de descontração; Camila Cassano; Ricardo Bovendorp; Mirco Solé pela imensa consideração e disponibilização de equipamentos e do espaço do Laboratório de Herpetologia Tropical; Marcelo Mielke pelo empréstimo de equipamentos importantes para o trabalho de campo. Às Secretárias Amábille Kruschewsky e Mayra Honorato, que sempre foram muito solicitas e amáveis.

Agradeço à Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) pela bolsa de doutorado e à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de doutorado sanduiche. Agradeço também às instituições que acreditaram e financiaram este projeto: Fundo Brasileiro para a Biodiversidade e Instituto Humanize (Bolsa Funbio nº 025/2023), *The Rufford Foundation* (nº 36969-1) e Pró-Reitoria de Pesquisa e Pós-Graduação da Universidade Estadual de Santa Cruz (073.11010.2023.0028633-11).

E finalmente, agradeço à banca examinadora por todo o tempo dedicado a avaliação deste trabalho. Muito obrigado à Tatiana Garabini Cornelissen, Márcio Zikán Cardoso, Jhonathan de Oliveira Silva, Jessie Pereira dos Santos e as suplentes Camila Cassano e Isabela Freitas Oliveira.

**Sumário**

## Resumo

As regiões tropicais abrigam a maioria das espécies de borboletas do mundo, mas também enfrentam as maiores taxas de desmatamento e mudanças no uso da terra. Essas perturbações alteram a paisagem, resultando em perda e fragmentação de habitat, que reduzem o tamanho e a conectividade dos remanescentes, levando a mudanças na estrutura local e, consequentemente, impactos negativos na biodiversidade. Com o objetivo de entender esses efeitos na diversidade de borboletas em florestas tropicais, esta tese foi dividida em 3 capítulos. No primeiro capítulo uma metanálise foi realizada, onde foram encontrados 47 estudos relatando 221 efeitos dos impactos antrópicos na riqueza e abundância de borboletas em florestas tropicais. No segundo capítulo, a comunidade de borboletas foi amostrada em 17 paisagens de Mata Atlântica em um gradiente de cobertura florestal, com o objetivo de avaliar como a perda e a fragmentação da floresta, juntamente com a estrutura do habitat local, afetam a diversidade de borboletas. No último capítulo, foram avaliados os efeitos da perda de floresta e da fragmentação *per se* sobre a diversidade de borboletas da família Nymphalidae, discriminando as guildas tróficas (nectarívora vs. frugívora) e a preferência de habitat (espécies dependente de floresta vs. adaptada a perturbações). A metanálise revelou que o efeito das perturbações antrópicas sobre a diversidade de borboletas é negativo, levando a redução da riqueza, principalmente em resposta à diminuição do tamanho dos fragmentos, urbanização e degradação florestal. A abundância, no entanto, aumentou particularmente em resposta aos efeitos de borda e mudanças no uso da terra, sugerindo a proliferação de espécies generalistas. Já a urbanização teve um impacto negativo tanto na riqueza quanto na abundância. No segundo capítulo, foram registrados, 2.515 indivíduos de 281 espécies de borboletas. A fragmentação, medida pelo número de fragmentos, levou a um aumento na abundância, aumento na dominância, e diminuição da diversidade de tribos, resultando em mudanças na composição de espécies entre os fragmentos. No terceiro capítulo, vimos que a perda de floresta afetou positivamente a riqueza e diversidade de espécies nectarívoras e adaptadas a perturbações. A fragmentação *per se* influenciou positivamente a abundância, exceto de espécies dependentes de floresta, cuja riqueza foi afetada negativamente pelo efeito de borda. Nossos resultados demonstram que as perturbações antrópicas em geral têm efeito negativo na diversidade de borboletas em florestas tropicais, mesmo quando a abundância total aumenta. Esse padrão reflete uma mudança na composição das comunidades, com a dominância de espécies adaptadas a perturbações, e resulta em comunidades menos diversas. Os resultados destacam a necessidade de considerar a perda e a fragmentação do habitat, bem como múltiplas dimensões ecológicas, ao planejar estratégias de conservação para garantir a manutenção das comunidades de borboletas e suas funções ecológicas essenciais. Ressaltamos também a importância dos remanescentes florestais em paisagens altamente modificadas, mesmo aquelas com baixa cobertura florestal, para a manutenção de comunidades ricas e abundantes de borboletas.

**Palavras-chave:** Floresta tropical, fragmentação *per se*, Mata Atlântica, mudança no uso da terra, perda de floresta, quantidade de habitat.

## Abstract

Tropical regions, home to most of the world's butterfly species, also face the highest rates of deforestation and land-use change. These disturbances change the landscape, leading to habitat loss and fragmentation, which reduce the size and connectivity of remnants, resulting in local structural changes and negative impacts on biodiversity. To understand these effects on butterfly diversity, this thesis is divided into three chapters. Chapter 1 presents a meta-analysis of 47 studies reporting 221 effect sizes of anthropogenic impacts on butterfly richness and abundance in tropical forests. In Chapter 2, we sampled butterflies in 17 Atlantic Forest landscapes across a forest cover gradient to evaluate how forest loss and fragmentation, along with local habitat structure, affect butterfly diversity. In Chapter 3, we assessed the effects of forest loss and fragmentation *per se* on the diversity of Nymphalidae butterflies, discriminating by trophic guilds (nectar-feeding vs. fruit-feeding) and habitat preference (forest-dependent vs. disturbance-adapted species). The meta-analysis revealed that anthropogenic disturbances generally have a negative effect on butterfly diversity, leading to a reduction in richness, particularly in response to declining patch size, urbanization, and forest degradation. Abundance, however, increased in response to edge effects and land-use changes, suggesting a proliferation of generalist species. Urbanization had a negative impact on both richness and abundance. In Chapter 2, we recorded 2,515 individuals of 281 butterfly species. Fragmentation, measured by the number of forest fragments, led to an increase in abundance, but also an increase in dominance and a decrease in tribe diversity, resulting in changes in tribes composition among fragments. In Chapter 3, we found that forest loss positively affected the richness and diversity of nectar-feeding and disturbance-adapted species. Fragmentation *per se* positively influenced abundance, except for forest-dependent species, whose richness were negatively affected by edge effects. Our results demonstrate that anthropogenic disturbances generally have a negative effect on butterfly diversity in tropical forests, even when total abundance increases. This pattern reflects a shift in community composition toward the dominance of disturbance-adapted species, resulting in less diverse communities. Our findings highlight the need to consider habitat loss and fragmentation, as well as multiple ecological dimensions, when planning conservation strategies to ensure the maintenance of butterfly communities and their essential ecological functions. We also emphasize the importance of forest remnants in highly modified landscapes, even those with low forest cover, for the maintenance of rich and abundant butterfly communities.

**Keywords:** Tropical forest, fragmentation *per se*, Atlantic Forest, land-use change, forest loss, habitat amount.

## Introdução geral

As mudanças no uso da terra, impulsionadas principalmente pela agricultura intensiva e pela urbanização, estão entre as principais causas da perda global de biodiversidade (Jaureguiberry et al. 2022). Essas mudanças são especialmente graves nas regiões tropicais, onde as taxas de desmatamento são mais elevadas (Curtis et al. 2018) e onde se concentra a maior parte da biodiversidade do planeta, incluindo a maioria dos *hotspots* globais (Mittermeier et al. 2004). Estima-se que as florestas tropicais abriguem pelo menos metade das espécies descritas até agora (Myers 1988; Lewis et al. 2015), e entre essas, aproximadamente 82% das espécies florestais listadas como ameaçadas na Lista Vermelha da IUCN (2025). Somente em 2024, 6,7 milhões de hectares de floresta tropical primária foram perdidos (Global Forest Watch 2025). A perda de floresta geralmente resulta em paisagens altamente fragmentadas, onde as florestas são reduzidas a pequenos remanescentes isolados (Haddad et al. 2015; Taubert et al. 2018), que sofrem uma série de efeitos em cascata, levando a mudanças estruturais e ecológicas, como o aumento nos efeitos de borda, isolamento, redução da qualidade da floresta e perda de árvores altas e grandes (Tabarelli et al. 2004; Oliveira et al. 2008). Além disso, a perda de habitat pode promover a homogeneização biótica (McKinney e Lockwood 1999; Maurenza et al. 2025), em que espécies generalistas proliferam e especialistas desaparecem ou persistem em densidades extremamente baixas, que ameaçam sua viabilidade a longo prazo (Filgueiras et al. 2019, 2021). Essas transformações comprometem gravemente a integridade dos ecossistemas tropicais e a persistência dabiodiversidade. Além de comprometer serviços ecossistêmicos essenciais para o bem-estar humano, como a polinização, ciclagem de nutrientes, dispersão de sementes e controle biológico de pragas, entre outros (Millennium Ecosystem Assessment 2005; Díaz et al. 2006).

Dentre os muitos táxons afetados pelas perturbações antrópicas (Murphy e Romanuk 2012, 2014; Dirzo et al. 2014), encontram-se os insetos, sendo Lepidoptera uma das ordens mais afetadas (Sánchez-Bayo e Wyckhuys 2019). Dentro desse grupo, as borboletas são amplamente reconhecidas como importantes bioindicadores devido à sua sensibilidade às mudanças ambientais, incluindo alterações no microclima, na estrutura da vegetação e na disponibilidade de plantas hospedeiras (Brown 1997; Freitas et al. 2003; Uehara-Prado et al. 2009; Bonebrake et al. 2010; Ferrer-Paris et al. 2013; Beirão et al. 2020). As borboletas também servem de alimento para vertebrados e invertebrados, controlam o crescimento das plantas e participam da ciclagem de nutrientes (Iserhard et al. 2017). As borboletas são classificadas em sete famílias: Hedylidae, Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae e Riodinidae (Espeland et al. 2018). E podem ser divididas em duas guildas, nectarívoras e frugívoras. Nectarívoras em geral visitam as flores, enquanto as frugívoras se alimentam-se de frutos fermentados, seiva de plantas e outros materiais em decomposição (DeVries 1987) e compreendem 50-75% das espécies da família Nymphalidae (Brown 2005). Sua taxonomia relativamente bem conhecida e diversidade de características ecológicas tornam as borboletas um modelo valioso para avaliar os impactos ecológicos das perturbações antrópicas (Freitas et al. 2003).

Dirzo e colaboradores (2014) em uma avaliação global encontrou fortes evidências de declínios de longo prazo em Lepidoptera (borboletas e mariposas), com uma redução de 35% na abundância nos últimos 40 anos e uma riqueza 7,6 vezes maior em habitats não perturbados do que em habitats perturbados, e sugerem que esses efeitos negativos podem ser menos graves em latitudes mais baixas. No entanto, estudos da América do Sul não foram incluídos na análise (Dirzo et al. 2014). Esse viés geográfico limita nossa capacidade de generalizar os padrões reportados, especialmente devido à alta riqueza de espécies e à complexidade ecológica das regiões neotropicais. Além disso, as respostas das borboletas às perturbações do habitat podem variar consideravelmente. Enquanto alguns estudos relataram aumento da riqueza e abundância em áreas perturbadas (Uehara-Prado et al. 2009), outros documentaram declínios significativos (Koh e Sodhi 2004). Em escala de paisagem, os poucos estudos disponíveis têm mostrado resultados distintos relativos à perda de floresta, incluindo efeitos negativos (Viljur et al. 2020), neutros (Brito et al. 2021) e positivos apenas para a abundância de espécies tolerantes à matriz (Brito et al. 2014). Essa variabilidade nas respostas foi parcialmente atribuída a mudanças na composição da comunidade, onde perturbações antrópicas muitas vezes levam a uma diminuição na riqueza de espécies e ao domínio de espécies generalistas (White e Kerr 2007; Thomas 2016). Esses resultados refletem a natureza dependente do contexto das respostas das borboletas às perturbações antrópicas. Dado que as borboletas apresentam uma ampla gama de requisitos ecológicos e características de história de vida, suas respostas às perturbações são provavelmente mediadas tanto por características biológicas intrínsecas quanto pelo contexto da paisagem (Bonebrake et al. 2010).

A diversidade de espécies em uma variedade de táxons está fortemente associada à manutenção da quantidade de habitat nativo em escala de paisagem (Püttker et al. 2020). No entanto, a resposta das espécies às mudanças na paisagem é complexa e os impactos da fragmentação *per se* (os efeitos da fragmentação independentes da quantidade de habitat) ainda são objeto de considerável debate (Fahrig 2017; Fletcher et al. 2018; Fahrig et al. 2019). Estudos que avaliam os efeitos da fragmentação *per se*, independentemente da perda de habitat, sobre as comunidades de borboletas ainda são escassos (por exemplo, Brito et al. 2021). Essa distinção é importante, pois a perda e a fragmentação de habitat podem ter consequências ecológicas contrastantes (Fahrig 2003, 2017), afetando tanto a dinâmica em nível de comunidade, quanto guildas e grupos funcionais específicos (Öckinger et al. 2010; Brito et al. 2014).

A variabilidade nas respostas das borboletas e a alta riqueza de espécies direcionam o foco deste estudo para a Mata Atlântica. A Mata Atlântica historicamente enfrenta altos níveis de desmatamento, com apenas cerca de 28% da cobertura original remanescente até o momento (Rezende et al. 2018), sendo que mais de 80% dos fragmentos restantes têm menos que 50 hectares (Ribeiro et al. 2009). No entanto, a Mata Atlântica é um dos cinco maiores *hotspots* de biodiversidade do mundo, abrigando mais de 20.000 espécies, com pelo menos 6.000 endêmicas (Marques e Grelle 2021) e, pelo menos, 2.000 espécies de borboletas (Brown e Freitas 2000; Iserhard et al. 2017), destas 52 espécies estão ameaçadas (ICMBio 2018).

Assim, a tese está dividida em três capítulos, cujo objetivo é avaliar os efeitos das perturbações antrópicas na diversidade de borboletas em florestas tropicais. No **capítulo 1**, sintetizamos as informações sobre os efeitos de diferentes tipos de perturbações antrópicas na riqueza e abundância de borboletas em florestas tropicais através de uma meta-análise que englobou estudos realizados em toda a região tropical. No **capítulo 2**, focamos na Mata Atlântica, realizamos coleta em campo e avaliamos como atributos locais e da paisagem influenciam a diversidade de borboletas em remanescentes de floresta. Especificamente, buscamos determinar como a riqueza, diversidade, equitatividade e abundância locais de borboletas (diversidade $\alpha$) e a sua dissimilaridade na composição desses fragmentos (diversidade $\beta$) variam ao longo de um gradiente de cobertura florestal e quais fatores explicam esses padrões. Por fim, no **capítulo 3**, ainda com o foco na Mata Atlântica, utilizamos a família Nymphalidae e classificamos cada espécie, de acordo com suas preferências tróficas e de habitat, em frugívoras, nectarívoras, espécies dependentes da floresta e espécies adaptadas a perturbações. Diferenciamos perda de floresta de fragmentação *per se*, e investigamos como esses fatores, juntamente com a estrutura local, afetam a diversidade taxonômica (riqueza, diversidade e abundância) dos diferentes grupos de borboletas Nymphalidae.

## Objetivo geral

Avaliar os efeitos das perturbações antrópicas na diversidade de borboletas em florestas tropicais.

## Objetivos específicos

**Capítulo 1**: Avaliar como diferentes tipos de perturbações antrópicas afetam a riqueza e a abundância de borboletas em florestas tropicais.

**Capítulo 2**: Avaliar como as características locais e da paisagem influenciam a diversidade α e β de espécies e tribos de borboletas em remanescentes de Mata Atlântica ao longo de um gradiente de cobertura florestal.

**Capítulo 3**: Avaliar como a perda de floresta e a fragmentação *per se*, juntamente com a estrutura do habitat local, influenciam a diversidade taxonômica das comunidades de borboletas Nymphalidae em remanescentes da Mata Atlântica.

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## Capítulo 1

# The effects of anthropogenic disturbances on butterfly richness and abundance in tropical forests: a meta-analysis

# The effects of anthropogenic disturbances on butterfly richness and abundance in tropical forests: a meta-analysis

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## Abstract

Approximately 90% of the world's butterfly species are found in tropical regions, which also experience the highest rates of deforestation and land-use change. These anthropogenic disturbances, driven by agriculture, pasture expansion, urbanization, and other anthropogenic activities, alter habitat spatial patterns with detrimental consequences for biodiversity. Here, we conducted a meta-analysis of 47 studies reporting 221 effect sizes to assess the impact of different types of anthropogenic disturbances on butterfly richness and abundance in tropical forests. The anthropogenic disturbances included land-use change (22 studies), declining patch size (13), forest degradation (8), multiple disturbances (6), edge effects (6), urbanization (6), forest loss (3), logging (3), isolation (3), and nut extraction (1). Overall, anthropogenic disturbances consistently reduced butterfly richness in response to declining patch size, forest degradation, urbanization, and multiple disturbances. Abundance, however, increased particularly in response to edge effects and land-use changes, likely due to the proliferation of generalist species adapted to disturbed habitats. Remarkably, urbanization has a negative impact on both richness and abundance. These results demonstrate that most anthropogenic disturbances in tropical forests result in the loss of butterfly species, even when abundance increases. This pattern may reflect a shift in community composition toward generalist species, potentially compromising key ecological functions performed by butterflies, such as pollination. Our findings highlight the importance of addressing the specific types of disturbances that most significantly threaten butterfly diversity, and ensuring that conservation strategies consider not only abundance but also the maintenance of species-rich communities and their ecological roles.

**Keywords**: Lepidoptera, landscape, patch size, forest degradation, land-use change, edge effect, urbanization.

## Introduction

Land-use changes, resulting from agriculture, pasture, urbanization, and other anthropogenic activities, alter habitat spatial patterns, with detrimental consequences for biodiversity. These impacts are particularly critical in tropical forests, as these ecosystems face high deforestation rates (Curtis et al. 2018) while simultaneously harboring the highest biodiversity, thereby concentrating most of the world's biodiversity hotspots (Mittermeier et al. 2004). Tropical forests are estimated to shelter at least half of the world's species (Myers 1988; Lewis et al. 2015), and approximately 82% of forest-dwelling species listed as threatened on the IUCN Red List (2025) are found in the tropics. In 2024 alone, 6.7 million hectares of primary tropical forest were lost (Global Forest Watch 2025). In tropical regions, deforestation typically results in highly fragmented landscapes, where forests are reduced to small and isolated remnants (Taubert et al. 2018). These remnants are exposed to a cascade of structural and ecological changes, including an increase in edge effects, isolation, reduced forest quality, and the loss of tall and large trees (Tabarelli et al. 2004; Oliveira et al. 2008). Together, these transformations severely compromise the integrity of tropical ecosystems and the persistence of their biodiversity.

Among the many taxa affected by human-induced habitat disturbances (Murphy and Romanuk 2012, 2014; Dirzo et al. 2014), insects are among the most affected group (Sánchez-Bayo and Wyckhuys 2019). Within this group, butterflies are widely recognized as important bioindicators due to their sensitivity to environmental changes, including alterations in microclimate, vegetation structure, and host plant availability (Brown Jr. 1997; Freitas et al. 2003; Uehara-Prado et al. 2009; Bonebrake et al. 2010; Ferrer-Paris et al. 2013; Beirão et al.

2020). Their well-known taxonomy and diversity of ecological traits make them a valuable model for assessing the ecological impacts of anthropogenic disturbances (Freitas et al. 2003). Indeed, a global assessment shows strong evidence of long-term declines in Lepidoptera (butterflies and moths), with a 35% reduction in abundance over the past 40 years and richness 7.6 times higher in undisturbed than in disturbed habitats (Dirzo et al. 2014). However, responses of butterfly diversity to habitat disturbance are not always consistent. While some studies have reported increased richness and abundance in disturbed habitats (Uehara-Prado et al. 2009), others have documented significant declines (Koh and Sodhi 2004), reflecting the context-dependent nature of these responses.

This variability in responses has been partially attributed to shifts in community composition, where anthropogenic disturbances often lead to a decrease in species richness and a dominance of generalist species (White and Kerr 2007; Thomas 2016). However, most of the evidence supporting these patterns comes from temperate regions, despite the fact that approximately 90% of the world's butterfly species occur in the tropics (Bonebrake et al. 2010), resulting in a knowledge gap regarding disturbance-driven biodiversity loss in tropical ecosystems (Murphy and Romanuk 2014). A global meta-analysis suggested that the negative effects of anthropogenic disturbance on butterfly richness may be less severe at lower latitudes (Dirzo et al. 2014). However, studies from South America were not included in the analysis (Dirzo et al. 2014). This geographic bias limits our ability to generalize global patterns, particularly given the high species richness and ecological complexity of tropical regions. Given that butterflies exhibit a wide range of ecological requirements and life-history traits, their responses to disturbance are likely mediated by both intrinsic biological characteristics and landscape context (Bonebrake et al. 2010). Improving our understanding of these context-dependent patterns is crucial for informing conservation strategies in increasingly human-modified tropical landscapes.

Here, we conducted a meta-analysis to synthesize existing evidence on the effects of human-induced habitat disturbances on butterfly richness and abundance in tropical forests. Specifically, our main objective was to evaluate how different types of anthropogenic disturbances (Table 1) affect butterfly richness and abundance. Based on previous findings, we hypothesize that anthropogenic disturbances will generally reduce butterfly richness and abundance in tropical forests. Among the anthropogenic disturbances evaluated, we predict that habitat loss will have the strongest negative effect, due to its direct impact on resource availability and habitat suitability. Furthermore, given the complexity of species-specific responses, we anticipate a higher sensitivity in richness than in abundance, as some generalist species may persist or even increase in disturbed areas, masking declines in specialist diversity.

## Methods

### *Literature survey and data inclusion criteria*

We conducted a systematic literature search in May 2025 to identify studies investigating the effects of human-induced habitat disturbance on butterfly richness and abundance in tropical environments. The search was performed using the Web of Science search engine, focusing on terms in the title, abstract, and/or keywords. We used the following English search terms: (butterfl*) AND ("fragmentation" OR "anthropic disturbance" OR "habitat loss" OR "environmental impact" OR "habitat destruction" OR “Land-use change” OR “Landscape” OR “Patch size” OR “Species-area relationship”) AND (Rainforest OR Forest OR Neotropic* OR Tropic* OR Atlantic). This search resulted in 886 studies. We screened titles and abstracts to include only studies published in English, conducted in tropical regions, and assessing the effects of any anthropogenic disturbance on adult butterflies (excluding studies focused on caterpillars and host plants). After this first screening, 230 articles remained for further analysis (Figure 1).

We performed a second screening, reading the full-text articles, to include only studies that (1) evaluated the effects of anthropogenic disturbances on butterfly richness and abundance in tropical forests; (2) included replication; (3) provided the sample size; and (4) provided quantitative measures of butterfly richness and/or abundance. We used the forest classification of Olson et al. (2001). We only included studies that evaluate anthropogenic disturbance, excluding those that compared biomes or habitats. We defined anthropogenic disturbances as human-induced changes to natural habitats, including landscape-scale disturbances such as deforestation and its consequences (e.g. reduced patch size, increased isolation, and edge effects), as well as land-use changes to agriculture and urbanization. We also consider local-scale disturbances such as selective logging, which alter forest structure and species composition (Barlow et al. 2016). Each study was classified according to the type of anthropogenic disturbance analysed (Table 1) and the feeding guilds analyzed (fruit-feeding or nectar-feeding butterflies). The studies examined either all butterfly families (combining fruit-and nectar-feeding species) or focused solely on fruit-feeding butterflies. Fruit-feeding butterflies include those of the family Nymphalidae that belong to the subfamilies Satyrinae, Biblidinae, Charaxinae, and the tribe Coeini of Nymphalinae (DeVries et al. 1997). No study evaluated nectar-feeding butterflies separately. Finally, for each study, we recorded an additional potential moderator variable, namely ecological response groups (forest-dependent species and disturbance-adapted species), when such classifications were provided in the original article.

In cases where the same dataset was reported in multiple publications, we selected the one that was either the oldest or had the most complete data. Review articles were excluded. We end up with 39 eligible studies. After full-text screening, another eight articles that were not identified in the initial search were found, read and considered eligible for inclusion, totaling 47 studies in the meta-analysis (Table S1). We used the PRISMA protocol to document the study selection process (Page et al. 2021) (Figure 1).

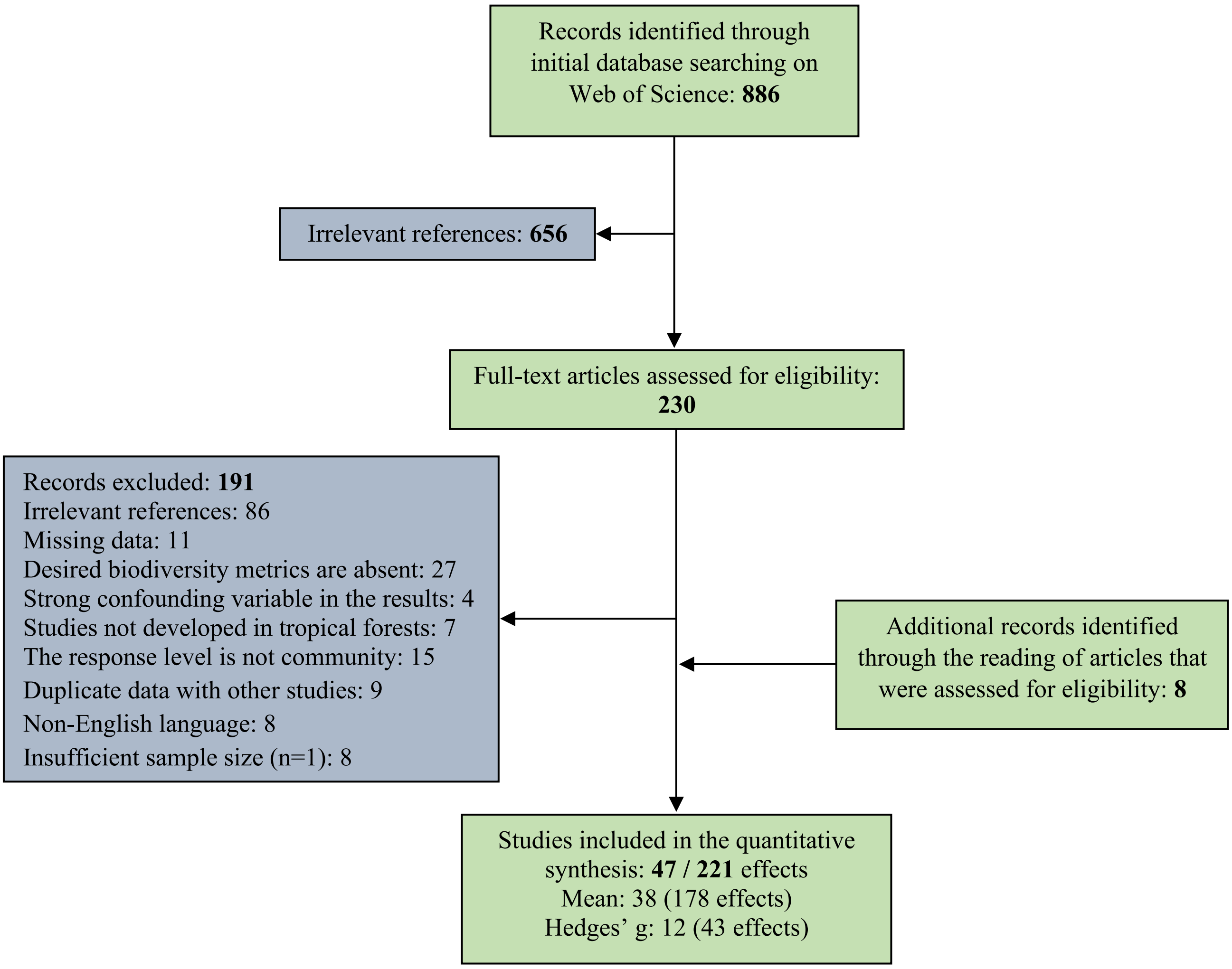

**Figure 1**: Prisma flow diagram showing the selection procedure to identify the studies to be included in the meta-analysis that evaluated the effects of anthropogenic disturbances on butterfly diversity and abundance.

**Table 1**: Anthropogenic disturbance variables used in the reviewed studies. The numbers in parentheses are the number of studies/effect sizes for each predictor variable.

| **Anthropogenic disturbances** | **Description** |
|---|---|
| Declining patch size (13/37) | Effect of forest fragment size on butterfly richness and abundance. |
| Edge Effect (6/25) | Influence of forest edges on butterfly richness and abundance, including comparisons between forest interior and edge or distance from the edge. |
| Forest degradation (8/18) | Comparison of butterfly richness and abundance between more preserved or less-degraded forests and more-degraded forests. |
| Forest loss (3/8) | Effects of the amount of forest cover in the landscape on butterfly richness and abundance. |
| Isolation (3/10) | Effect of the distance to the nearest fragment on butterfly richness and abundance, including Euclidean nearest neighbour distance and proximity index. |
| Land-use change (22/88) | Comparison of butterfly richness and abundance in forests versus surrounding agricultural matrices (e.g., pasture, crops, plantations). |
| Logging (3/6) | Effect of selective logging by comparing butterfly richness and abundance in unlogged forests versus logged forests. |
| Multiple (6/11) | Combined effect of two or more disturbance types on butterfly richness and abundance, when individual effects could not be disentangled (e.g., comparison between undisturbed forests and sites simultaneously affected by edge and fragmentation). |
| Nut extraction (1/2) | Influence of Brazil nut extraction on butterfly richness and abundance, comparing undisturbed forests and forests with nut extraction. |
| Urbanization (6/16) | Effect of urbanization on butterfly richness and abundance, including comparisons between undisturbed forests and urban parks or fragments, as well as the amount of open green and paved area around urban forest fragments. |

*Meta-analytical procedure*

We extracted information to calculate the effect sizes from each study. For studies comparing controls versus treatment (e.g., degraded vs. preserved forests), we extracted the sample size and the mean estimates and standard deviation of richness and/or abundance for both groups. For studies measuring a continuous gradient (e.g., patch size, forest loss), we extracted the sample size and the reported correlation coefficient. Among the 47 studies, 38 compared control versus treatment, and 12 studies evaluated disturbance gradients. Three of these studies provided both types of data, allowing us to assess the effects of disturbances using both control-treatment comparisons and correlation coefficients along a disturbance gradient. Most studies contain more than one effect (mean ± SD = 4.7 ± 4.04 effects per study). Therefore, we obtained 221effect sizes, of which 128 had richness and 93 had abundance as response variables (Table S2).

We used Hedges' g as the standardized effect size metric (Borenstein et al. 2009). For control-treatment studies, g was calculated using means, standard deviation, and sample sizes. For gradient studies, reported correlation coefficients (r) were converted into Hedges' g. Data were obtained from results, graphs, tables, and supplementary materials. When only graphical data were available, we used the WebPlotDigitizer program for data extraction (Drevon et al. 2017).

Negative Hedge's g values indicate a decrease in butterfly richness or abundance in response to anthropogenic disturbances, while positive values indicate an increase. For gradient studies, we adjusted the direction of the correlation coefficients so that negative values consistently represent negative effects of habitat disturbance on butterfly richness or abundance. Specifically, we reversed the sign of the correlations between butterfly richness or abundance and patch size, distance from the edge (edge effect), Euclidean nearest neighbour distance (isolation), proximity index (isolation), habitat amount (forest loss), open green area around urban forest fragments (urbanization), urban fragments area (urbanization), and one of the land-use intensity (in which the direction of the effect was opposite to the others); thus negative effects indicate adverse effects of anthropogenic disturbances on butterfly richness or abundance (Table S2).

We then performed a random-effect meta-analysis (Borenstein et al. 2009). Due to the expected differences in responses between richness and abundance, we performed two meta-analyses, one for richness and one for abundance. Because most studies (96%) reported multiple effects, either by evaluating more than one disturbance type, using multiple sample sites, we addressed potential non-independence among effect sizes within studies. To account for this, we used bootstrapped meta-analyses, which control for bias arising from lack of independence by randomly selecting one effect size per study in each iteration. We conducted 10,000 replications, calculated the mean effect size and the 95% confidence intervals across all simulations. A measure of between-study heterogeneity ($I^2$) was also calculated. $I^2$ reports the variance of the studies, reflecting the extent of overlap among their confidence intervals (Borenstein et al. 2009).

### *Moderators*

We used three moderators to understand how they contribute to the overall effect: anthropogenic disturbances (Table 1), ecological response group (forest-dependent and disturbance-adapted species), and feeding guilds (fruit-feeding or fruit- and nectar-feeding together). To ensure adequate statistical power, we only included subgroups within moderator variables that were represented by at least four studies. A bootstrapped mean effect size and 95% confidence interval were calculated for each category. We then compared the effect sizes among classes within the moderator variable to determine whether the moderator variable explained the heterogeneity among studies. The analyses were performed using the R software (R Development Core Team 2025) through the Metafor package (Viechtbauer 2010).

### *Publication bias*

We estimate the number of missing studies using the Trim-and-Fill Method (Duval and Tweedie, 2000) and the number of unpublished studies with no effect (Hedges' $g = 0$) using the Fail-Safe Number approach by Rosenthal to verify publication bias. Here we also took into account that most studies contained more than one effect, by performing a bootstrap meta-analysis, in which each of 10.000 resamples randomly selected only one effect per study.

## Results

We found 47 studies and 221 effects of anthropogenic disturbances on butterfly richness and abundance in tropical forests. Most studies are located in moist forests (45 studies). Only two studies were conducted in a dry forest (Mexico and Nicaragua; Figure 2), according to Olson et al. (2001). Most studies measured butterfly richness (45 studies, 128 effects), while 36 studies and 93 effects evaluated butterfly abundance. The main anthropogenic disturbances evaluated were: land-use change (22 studies and 88 effects), declining patch size (13/37), forest degradation (8/18), and multiple disturbances (6/11) (Table 1).

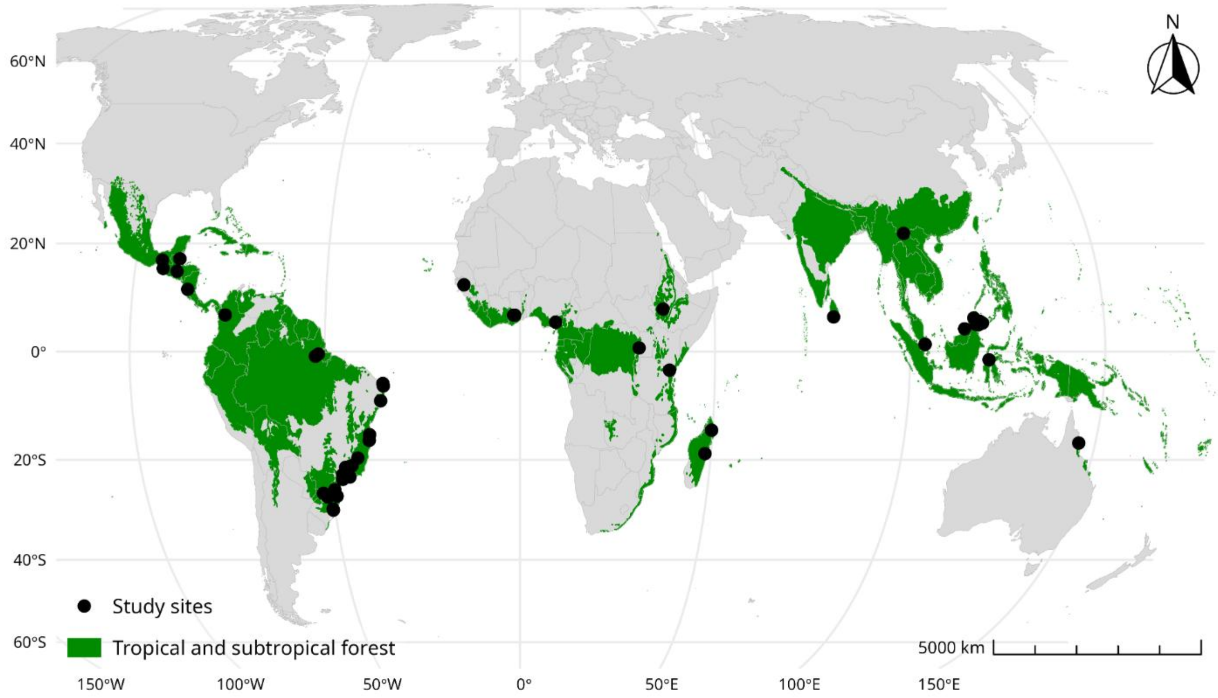

**Figure 2**: The geographic distribution of the study sites (black dot) in the reviewed papers'. The green area represents the Tropical and Subtropical Forests, as described by Olson et al. (2001).

There was an overall negative effect of anthropogenic disturbances on butterfly communities (Hedges' g: -0.31, CI: -0.53, -0.10; Figure 3). When analyzed separately, richness showed a consistent negative response (Hedges' g: -0.47, CI: -0.67, -0.28; Figure 3). In contrast, anthropogenic disturbances had a positive effect on butterfly abundance (Hedges' g: 0.22, CI: 0.03, 0.42; Figure 3).

Regarding richness, forest degradation (Hedges' g: -2.62, CI: -3.08, -2.16), urbanization (Hedges' g: -1.53, CI: -1.65, -1.45), multiple disturbances (Hedges' g: -0.48, CI: -0.56, -0.41), and declining patch size (Hedges' g: -0.42, CI: -0.71, -0.15) had negative effects (Figure 4a). In contrast, land-use change did not affect richness (Hedges' g: -0.17, CI: -0.49, 0.12), and edge effects increased butterfly richness (Hedges' g: 1.01, CI: 0.72, 1.37; Figure 4a). Our moderators explained a large portion of the heterogeneity among effect sizes (mean $I^2$ = 76.55%). Rosenthal's fail-safe number indicated that 183.29 studies with an average effect size of zero would be required to nullify the significance of this overall effect.

For abundance, land-use change (Hedges' g: 0.29, CI: 0.07, 0.51) and edge effects (Hedges' g: 1.21, CI: 0.79, 1.57) had a positive effect, while declining patch size had no effect (Hedges' g: 0.05, CI: -0.17, 0.22). However, urbanization had a negative effect on butterfly abundance (Hedges' g: -0.71, CI: -0.87, 0.55; Figure 4b). The heterogeneity among effect sizes was moderate (mean $I^2$ = 64.1 %). The Rosenthal's fail-safe number was 20.1.

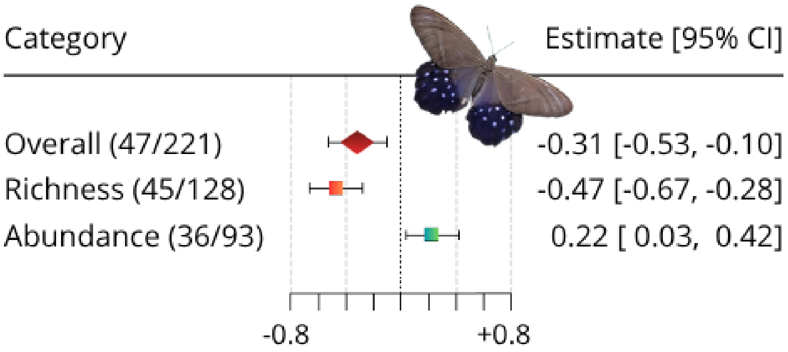

**Figure 3**: Effects of anthropogenic disturbances on butterfly richness and abundance. Mean and 95% confidence intervals are shown for global effects and response type. The number of studies and effects is shown in parentheses.

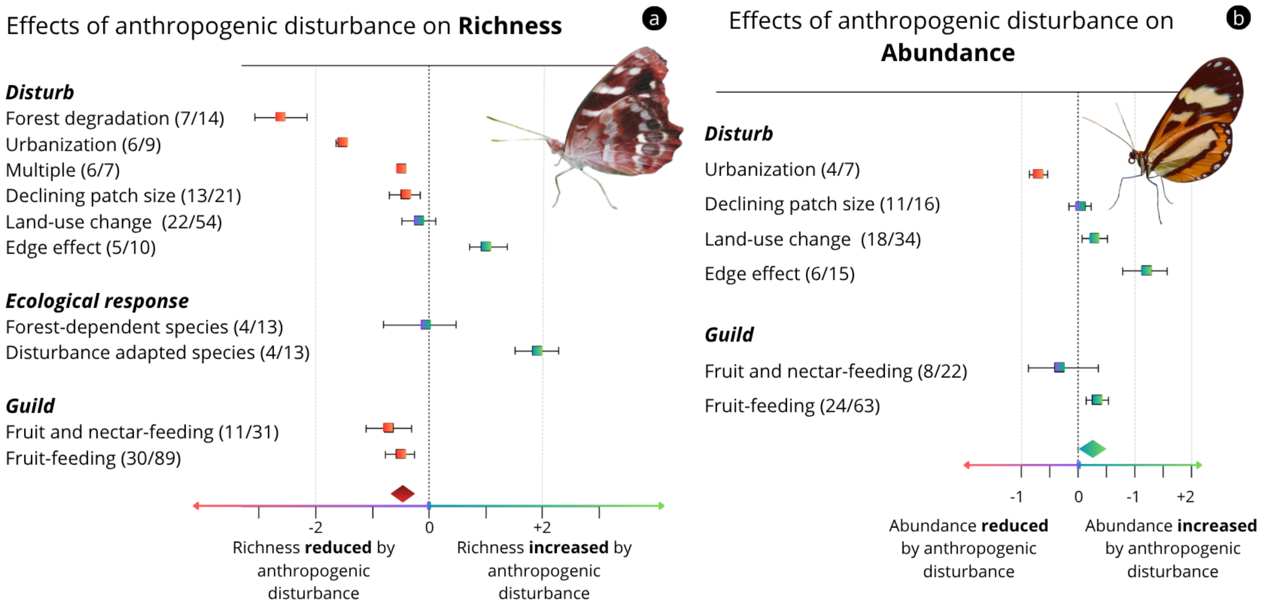

**Figure 4**: Effects of anthropogenic disturbances on butterfly richness (a) and abundance (b). Mean (squares) and 95% confidence intervals (whiskers) are shown for disturbance effects, response, functional group, and guild. The number of studies and effects are shown in parentheses. The diamond indicates the overall bootstrapped effect size, and the black dashed line indicates no effect of anthropogenic disturbance.

Four studies separately evaluated the richness and abundance of forest-dependent and disturbance-adapted species. Butterfly richness increased in disturbance-adapted species (Hedges' g: 1.9, CI: 1.52, 2.29), whereas forest-dependent species showed very small effects to anthropogenic disturbances, indicating a lack of effect (Hedges' g: -0.06, CI: -0.80, 0.48) of anthropogenic disturbances on their richness (Figure 4a). We lacked sufficient studies and data to evaluate the effects of different anthropogenic disturbances on each ecological response. There were no data to analyse abundance separately by ecological response.

For fruit-feeding butterflies, richness and abundance showed contrasting responses, in which anthropogenic disturbances decreased richness (Hedges' g: -0.50, CI: -0.77, -0.26) and increased abundance (Hedges' g: 0.34, CI: 0.14, 0.53) (Figure 4). When we excluded studies focusing exclusively on fruit-feeding species and analyzed mixed guilds, richness was negatively affected (Hedges' g: -0.70, CI: -1.12, -0.31), while butterflies' abundance was not significantly affected (Hedges' g: -0.32, CI: -0.89, 0.36) (Figure 4). We have no data to analyse nectar-feeding separately.

## Discussion

Our review of the effects of anthropogenic disturbances on butterfly richness and abundance in tropical forests highlights the overall negative effects of disturbances on butterfly communities. However, species richness and abundance respond in contrasting ways to disturbances. While overall butterfly richness declined in disturbed habitats, abundance tended to increase, particularly in response to edge effects and land-use change. This divergence suggests that anthropogenic pressures may favor certain species, potentially disturbance-adapted or generalist ones, while eroding overall diversity. Among the disturbance types, forest degradation, urbanization, declining patch size, and multiple concurrent disturbances consistently reduced butterfly richness, whereas urbanization had a negative effect on butterfly abundance. These findings highlight that disturbance can simplify butterfly communities by shifting composition toward more abundant but potentially less diverse assemblages, underscoring the importance of considering both abundance and richness when assessing biodiversity impacts.

### *Butterfly responses to disturbances*

We found that overall anthropogenic disturbances have a negative affect butterfly richness, corroborating the findings of a previous meta-analysis (Dirzo et al. 2014). However, unlike that study, we found a positive overall effect on butterfly abundance, which may reflect the geographic distribution of the studies included in our analysis, most of which were conducted in South America. While Dirzo et al. (2014) evaluated only 15 studies, most of which were conducted in temperate regions and only two in South America, our meta-analysis more than doubles that number, incorporating 47 studies exclusively from tropical ecosystems. The observed increase in abundance was mainly explained by edge effects that also positively affected butterfly richness. Edge effects increase light, temperature, and reduce humidity, which favors early successional vegetation and pioneer plant species (Magnago et al. 2015). Together, these changes promote the dominance of disturbance-adapted species and those originating from open areas, typically generalists with high reproductive rates, strong flight ability, and greater dispersal capacity (Lourenço et al. 2019, Öckinger et al. 2010; Koh 2007). Thus, while butterfly overall richness declines, abundance can increase due to the proliferation of disturbance-tolerant species in modified landscapes. It is important to note, however, that due to limited data, we were unable to assess whether the observed increase in abundance is concentrated in specific functional groups.

Different disturbances impacted butterfly richness in distinct ways, and most of them tend to reduce species richness. Among the disturbances we evaluated, forest degradation had a strong negative effect on butterfly richness. Habitat degradation often follows habitat loss and fragmentation, increasing edges and isolation, while reducing patch size (Barlow et al. 2016). It also facilitates human access for logging, hunting, and plant harvesting, further deteriorating habitat quality and altering microclimatic conditions and vegetation structure (Echeverría et al. 2007). These changes directly affect the availability of host plants and the survival of butterflies, especially rare and specialist species with narrow ecological requirements (Ramos 2000; Brito et al. 2014; Koh 2007). Urbanization also significantly reduces butterfly richness, reinforcing patterns found in a recent meta-analysis (Pignataro et al. 2025). A global synthesis identified Lepidoptera as the taxonomic group most negatively affected by urbanization (Liang et al. 2023), underscoring the group's vulnerability to anthropogenic pressures. Our results also detected a decline in species richness with declining patch size, consistent with the species-area relationship (Simberloff 1976). Smaller patches may offer fewer resources and reduced structural complexity, which can limit habitat suitability for many species (Malcolm 1994; Major et al. 2003; Veddeler et al. 2005; Laurance et al. 2006). Patch size is often correlated with the total amount of habitat in the landscape, a well-established predictor of biodiversity (Fahrig 2003). However, our database contains only three studies that assess forest loss at the landscape level, so we were unable to assess the effect of habitat loss on butterfly diversity. Surprisingly, land-use change, a category with the largest number of studies, did not show significant effects on richness, which may reflect the broad heterogeneity of this category or differences in spatial scale.

Both fruit-feeding and nectar-feeding butterfly richness were negatively affected by anthropogenic disturbances. However, the abundance of these two feeding guilds responded differently to such disturbances. We detected an increase in the abundance of fruit-feeding species in disturbed habitats, whereas no significant effect was found when both guilds were analysed together. This divergence may be explained by their reliance on different food resources. Fruit-feeding butterflies consumed fermented fruit, plant sap, and other decaying materials such as feces and animal carcasses. This guild is composed exclusively of the Nymphalidae family (Wahlberg et al. 2009; Freitas et al. 2014), representing 50-75% of the family diversity (Brown Jr. 2005). In contrast, the nectar-feeding butterflies feed on floral nectar and pollen and include members from all butterfly families (DeVries 1997). Because of their dependence on flowering plants, nectar-feeding species may be more vulnerable to anthropogenic disturbances that also reduce floral resource availability (Schulze et al. 2004).

### *Future Directions*

In addition to synthesizing the current knowledge on the effects of anthropogenic disturbances on butterfly communities in tropical regions, our meta-analysis highlights several important knowledge gaps and directions for future research. Firstly, although we compiled 47 studies, the vast majority (43) were conducted at local scales, for instance, evaluating forest degradation or declining patch size. Only three studies have evaluated the effects of habitat loss at the landscape level (Marín et al. 2009, Brito et al. 2014, Brito et al. 2021), representing a striking gap in our understanding of how broader spatial processes influence butterfly diversity and abundance in tropical systems. Interestingly, the limited number of studies available at the landscape scale reported neutral or even positive effects of habitat loss on richness and abundance. However, this evidence is still insufficient to draw robust generalizations, reinforcing the need for more studies that incorporate landscape-scale metrics across different tropical contexts.

Secondly, while our analysis suggests that disturbance-adapted species tend to increase in richness, and possibly abundance, following anthropogenic disturbances, we currently lack a consistent classification of tropical butterfly species based on forest dependence. Although binary classifications (e.g., forest-dependent vs. disturbance-adapted) are an important first step, they may oversimplify species responses to environmental change. The development of trait-based approaches to classify species sensitivity to disturbances, especially traits such as dispersal ability, host plant specialization, and microclimatic requirements, may provide a more mechanistic understanding of biodiversity responses and increase our capacity to predict changes in butterfly communities under future scenarios.

Thirdly, we observed a strong geographic bias in the current literature. The great majority of studies are concentrated in South America, with very few conducted in other tropical regions such as Africa and Southeast Asia. Moreover, the imbalance between tropical and temperate regions is even more pronounced. For instance, while our meta-analysis identified only six studies evaluating butterfly responses to urbanization, a recent meta-analysis focused on the effects of urbanization on butterfly communities compiled 27 studies, of which ~60% were conducted in temperate regions (Pignataro et al., 2025). This reinforces the urgent need for empirical research in tropical countries, especially in underrepresented biogeographic regions.

## Concluding remarks

Our study focused on the effects of anthropogenic disturbances only on butterflies' richness and abundance. While species richness is the most widely used metric to measure biodiversity loss it does not capture the full complexity of ecological communities (Murphy and Romanuk 2014). Among the 47 studies included in our analysis, 28 reported changes in butterfly species composition between treatments or along disturbance gradients, 16 did not analyse species composition, and only three found no differences. This suggests that even in the absence of significant effects on richness or abundance, anthropogenic disturbances still alter butterfly community structure (e.g., Uehara-Prado et al. 2007). Thus, we suggest that the impacts reported here would likely be stronger if species composition were systematically included.

Most anthropogenic disturbances result in a decline in butterfly species richness, revealing a consistent pattern of biodiversity loss across studies. Although some disturbances, such as edge effects or land-use changes, may result in increased butterfly abundance, this is typically due to the proliferation of generalist species that are tolerant to habitat disturbance. Such increases in abundance do not compensate for the loss of specialist species and may mask deeper shifts in community structure. Our meta-analysis identifies the types of disturbances, such as declining patch size, forest degradation, and urbanization, that most consistently reduce butterfly richness. These declines may also jeopardize important ecological functions performed by butterflies (Tylianakis et al. 2010; Valiente-Banuet et al. 2015), such as pollination.

Pollination is primarily carried out by insects, which are crucial for maintaining natural ecosystems and agricultural production (Lautenbach et al. 2012; Garibaldi et al. 2014). The order Lepidoptera, a group of insects that includes butterflies, has the highest species diversity of floral visitors (Wardhaugh 2015). Butterflies act as important secondary pollinators and are primary pollinators of several plant species in families such as Verbenaceae, Apocynaceae, Rubiaceae, and Fabaceae (Rech et al. 2014). The extinction of pollinators can trigger cascading effects, with the extinction of plants and secondary pollinators (Colwell et al. 2012). Future research should also explore butterfly-flower interactions more directly to improve our understanding of how different anthropogenic disturbances affect these mutualistic relationships and the broader ecosystem services they support.

## Acknowledgements

We thank PROPP/UESC (073.11010.2023.0028633-11) for financial support. GCNP thanks the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for her doctorate scholarship. We are also grateful for the research grant granted by CNPq to EC (PQ: 311545/2021–1).

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# Supplementary Information

# The effects of anthropogenic disturbances on butterfly richness and abundance in tropical forests: a meta-analysis

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**Table S2**: Summary of the 47 studies used in the meta-analysis, with the study number referring to those presented in Table S1.

| Study | Effect number | Reference | Region | Location | Cover type | Habitat disturbance | Study design | Guild | Response | yi | vi | Reversed sign |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 206 | 1 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | declining patch size | Old-growth forest X Forest fragment | fruit-feeding | richness | -0.53617212 | 0.208839204 | |
| 206 | 2 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Forest-derived vanilla agroforest | fruit-feeding | richness | 1.331229211 | 0.254489192 | |
| 206 | 3 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Fallow-derived vanilla agroforest | fruit-feeding | richness | 1.199115738 | 0.177380651 | |
| 206 | 4 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Woody fallow | fruit-feeding | richness | 0.908503171 | 0.225378011 | |
| 206 | 5 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Herbaceous fallow | fruit-feeding | richness | 1.091884922 | 0.236657127 | |
| 206 | 6 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Rice paddy | fruit-feeding | richness | 0.557659762 | 0.20956188 | |
| 206 | 7 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | declining patch size | Old-growth forest X Forest fragment | fruit-feeding | richness forest-dependent species | -0.97277606 | 0.229095809 | |
| 206 | 8 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Forest-derived vanilla agroforest | fruit-feeding | richness forest-dependent species | -0.09317981 | 0.200266961 | |
| 206 | 9 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Fallow-derived vanilla agroforest | fruit-feeding | richness forest-dependent species | -0.70659382 | 0.159507388 | |
| 206 | 10 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Woody fallow | fruit-feeding | richness forest-dependent species | -0.76231505 | 0.217867907 | |
| 206 | 11 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Herbaceous fallow | fruit-feeding | richness forest-dependent species | -2.40980678 | 0.378553816 | |

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| 206 | 12 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Rice paddy | fruit-feeding | richness forest-dependent species | -2.3890408 | 0.375489777 |
| 206 | 13 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | declining patch size | Old-growth forest X Forest fragment | fruit-feeding | richness disturbance-adapted species | 1.413227155 | 0.261408521 |
| 206 | 14 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Forest-derived vanilla agroforest | fruit-feeding | richness disturbance-adapted species | 1.789443696 | 0.298455678 |
| 206 | 15 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Fallow-derived vanilla agroforest | fruit-feeding | richness disturbance-adapted species | 2.660631061 | 0.284800306 |
| 206 | 16 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Woody fallow | fruit-feeding | richness disturbance-adapted species | 1.755680607 | 0.294775419 |
| 206 | 17 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Herbaceous fallow | fruit-feeding | richness disturbance-adapted species | 2.913407512 | 0.460979961 |
| 206 | 18 | Wurz et al. 2022 | Africa | Madagascar | Rainforest (lowland and mountainous) | land-use change | Old-growth forest X Rice paddy | fruit-feeding | richness disturbance-adapted species | 2.380467114 | 0.374232458 |
| 173 | 19 | Milheiras et al. 2020 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | nut extraction | Old-growth forest X Brazil nut extraction | fruit-feeding | richness | 1.306368547 | 0.436474647 |
| 173 | 20 | Milheiras et al. 2020 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | logging | Old-growth forest X reduced impact logging | fruit-feeding | richness | 0.135263932 | 0.334439104 |
| 173 | 21 | Milheiras et al. 2020 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | land-use change | Old-growth forest X Eucalyptus plantation | fruit-feeding | richness | -0.79942982 | 0.371957749 |
| 173 | 22 | Milheiras et al. 2020 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | nut extraction | Old-growth forest X Brazil nut extraction | fruit-feeding | abundance | 0.509026656 | 0.348992992 |
| 173 | 23 | Milheiras et al. 2020 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | logging | Old-growth forest X reduced impact logging | fruit-feeding | abundance | -0.09980171 | 0.333935307 |
| 173 | 24 | Milheiras et al. 2020 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | land-use change | Old-growth forest X Eucalyptus plantation | fruit-feeding | abundance | 2.439577991 | 0.693025219 |

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|---|---|---|---|---|---|---|---|---|---|---|
| 147 | 25 | Oliveira et al. 2018 | Neotropics | Brazil - Rio Grande do Norte | Atlantic Forest - vegetation growing as sandbank forests on sandy soils | urbanization | Park - Urban reserve X Plaza | fruit-feeding | richness | -2.38650345 | 0.553867763 |
| 34 | 26 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | declining patch size | Continuous forest X Forest fragment | fruit-feeding | richness | 0.631998229 | 0.487779392 |
| 34 | 27 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | declining patch size | Continuous forest X Forest fragment | fruit-feeding | abundance | 0.672812597 | 0.492816531 |
| 34 | 28 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | declining patch size | Non-disturbed (Floresta Contínua) X Disturbed habitats (forest fragments) | fruit-feeding | richness forest-dependent species | 0.372123599 | 0.463097779 |
| 34 | 29 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | declining patch size | Non-disturbed (Floresta Contínua) X Disturbed habitats (forest fragments) | fruit-feeding | abundance forest-dependent species | 0.477933864 | 0.471605228 |
| 34 | 30 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | declining patch size | Non-disturbed (Floresta Contínua) X Disturbed habitats (forest fragments) | fruit-feeding | richness disturbance-adapted species | 1.573045543 | 0.684048487 |
| 34 | 31 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | declining patch size | Non-disturbed (Floresta Contínua) X Disturbed habitats (forest fragments) | fruit-feeding | abundance disturbance-adapted species | 1.709516475 | 0.726420231 |
| 54 | 32 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of large mature forest | fruit-feeding | richness forest-dependent species | -0.18102516 | 0.335313853 |
| 54 | 33 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | declining patch size | Interiors of large mature forest (>1000 ha) X Interiors of small mature forest (<100 ha) | fruit-feeding | richness forest-dependent species | 0.44815599 | 0.345471683 |
| 54 | 34 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of small mature forest | fruit-feeding | richness forest-dependent species | 0.51318377 | 0.349249814 |
| 54 | 35 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | forest degradation | Interiors of large mature forest (>1000 ha) X Second-growth forests | fruit-feeding | richness forest-dependent species | -1.26110248 | 0.429450728 |
| 54 | 36 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | land-use change | Interiors of large mature forest (>1000 ha) X Shade cacao plantations | fruit-feeding | richness forest-dependent species | -2.46377443 | 0.700195659 |

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| 54 | 37 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of large mature forest | fruit-feeding | richness disturbance-adapted species | 0.72322073 | 0.364944677 |
| 54 | 38 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | declining patch size | Interiors of large mature forest (>1000 ha) X Interiors of small mature forest (<100 ha) | fruit-feeding | richness disturbance-adapted species | 0.54911764 | 0.351556843 |
| 54 | 39 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of small mature forest | fruit-feeding | richness disturbance-adapted species | 1.52318825 | 0.473552825 |
| 54 | 40 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | forest degradation | Interiors of large mature forest (>1000 ha) X Second-growth forests | fruit-feeding | richness disturbance-adapted species | 1.71440789 | 0.510968743 |
| 54 | 41 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | land-use change | Interiors of large mature forest (>1000 ha) X Shade cacao plantations | fruit-feeding | richness disturbance-adapted species | 1.123837949 | 0.40966568 |
| 54 | 42 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of large mature forest | fruit-feeding | abundance forest-dependent species | -0.71880883 | 0.364560173 |
| 54 | 43 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | declining patch size | Interiors of large mature forest (>1000 ha) X Interiors of small mature forest (<100 ha) | fruit-feeding | abundance forest-dependent species | 0.417722204 | 0.343879056 |
| 54 | 44 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of small mature forest | fruit-feeding | abundance forest-dependent species | 0.414432573 | 0.343713611 |
| 54 | 45 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | forest degradation | Interiors of large mature forest (>1000 ha) X Second-growth forests | fruit-feeding | abundance forest-dependent species | -1.09784142 | 0.406175097 |
| 54 | 46 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | land-use change | Interiors of large mature forest (>1000 ha) X Shade cacao plantations | fruit-feeding | abundance forest-dependent species | 0.118882217 | 0.334187485 |
| 54 | 47 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of large mature forest | fruit-feeding | abundance disturbance-adapted species | 1.218205048 | 0.423022919 |

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| 54 | 48 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | declining patch size | Interiors of large mature forest (>1000 ha) X Interiors of small mature forest (<100 ha) | fruit-feeding | abundance disturbance-adapted species | 1.898243855 | 0.551106934 |
| 54 | 49 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | edge effect | Interiors of large mature forest (>1000 ha) X Edges of small mature forest | fruit-feeding | abundance disturbance-adapted species | 2.132060707 | 0.608059711 |
| 54 | 50 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | forest degradation | Interiors of large mature forest (>1000 ha) X Second-growth forests | fruit-feeding | abundance disturbance-adapted species | 1.825413931 | 0.534716863 |
| 54 | 51 | Pardini et al. 2009 | Neotropics | Brazil - Bahia | Atlantic Forest - lowland rainforest | land-use change | Interiors of large mature forest (>1000 ha) X Shade cacao plantations | fruit-feeding | abundance disturbance-adapted species | 3.507915299 | 1.077036146 |
| 55 | 52 | Uehara-Prado et al. 2009 | Neotropics | Brazil - São Paulo | Atlantic Forest - montane rainforest | forest degradation | Undisturbed Forest X Disturbed Forest | fruit-feeding | abundance | 1.544165495 | 0.477441607 |
| 94 | 53 | da Rocha et al. 2013 | Neotropics | Brazil - Bahia | Atlantic Forest | land-use change | Continuous forest X Eucalyptus plantation | fruit-feeding | richness | 2.433538203 | 1.189493682 |
| 94 | 54 | da Rocha et al. 2013 | Neotropics | Brazil - Bahia | Atlantic Forest | declining patch size | Continuous forest X small Forest fragment | fruit-feeding | richness | 2.993150638 | 1.543064351 |
| 94 | 55 | da Rocha et al. 2013 | Neotropics | Brazil - Bahia | Atlantic Forest | land-use change | Continuous forest X Eucalyptus plantation | fruit-feeding | abundance | 4.861724152 | 3.251912252 |
| 94 | 56 | da Rocha et al. 2013 | Neotropics | Brazil - Bahia | Atlantic Forest | declining patch size | Continuous forest X small Forest fragment | fruit-feeding | abundance | 1.720336304 | 0.844572539 |
| 106 | 57 | Sant'Anna et al. 2014 | Neotropics | Brazil - São Paulo | Atlantic Forest - riparian forest | forest degradation | Native Forest X Restored forests of 11 years of age (Early) | fruit-feeding | richness | -3.33407862 | 3.052197902 |
| 106 | 58 | Sant'Anna et al. 2014 | Neotropics | Brazil - São Paulo | Atlantic Forest - riparian forest | forest degradation | Native Forest X Restored forests of 22 (Intermediate) | fruit-feeding | richness | -4.26954356 | 4.578644029 |
| 106 | 59 | Sant'Anna et al. 2014 | Neotropics | Brazil - São Paulo | Atlantic Forest - riparian forest | forest degradation | Native Forest X Restored forests of 54 years of age (Old) | fruit-feeding | richness | -7.39307766 | 12.39628742 |

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| 107 | 60 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | land-use change | Forest fragments X Agricultural matrices | fruit-feeding | richness | -0.43361705 | 0.228813381 |
| 107 | 61 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | land-use change | Forest fragments X Agricultural matrices | fruit-feeding | abundance | -0.1450119 | 0.222959373 |
| 150 | 62 | Bordin et al. 2019 | Neotropics | Brazil - Santa Catarina | Atlantic Forest - Mixed Ombrophilous Forest | declining patch size | Forest reserves X Forest fragment | fruit-feeding | richness | -0.80537621 | 0.805864036 |
| 150 | 63 | Bordin et al. 2019 | Neotropics | Brazil - Santa Catarina | Atlantic Forest - Mixed Ombrophilous Forest | declining patch size | Forest reserves X Forest fragment | fruit-feeding | abundance | 0.501000557 | 0.720532062 |
| 40 | 64 | Barlow et al. 2007 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | forest degradation | Primary forests X Secondary forests | fruit-feeding | richness | -3.1194613 | 1.174702861 |
| 40 | 65 | Barlow et al. 2007 | Neotropics | Brazil - Pará and Amapá | Amazon Forest | land-use change | Primary forests X Eucalyptus plantation | fruit-feeding | richness | -5.11574703 | 2.483502743 |
| 116 | 66 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | richness | 0.482730082 | 0.259499321 |
| 116 | 67 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | declining patch size | Forest Interior X small forest fragment | fruit-feeding | richness | 2.157420277 | 0.439737582 |
| 116 | 68 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | abundance | 0.600017967 | 0.264676157 |
| 116 | 69 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | declining patch size | Forest Interior X small forest fragment | fruit-feeding | abundance | 1.599281264 | 0.354263799 |
| 116 | 70 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | multiple | Non-disturbed (Forest Interior) X Disturbed habitats (forest edges and forest fragments) | fruit-feeding | richness forest-dependent species | 1.118540137 | 0.218377887 |
| 116 | 71 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | multiple | Non-disturbed (Forest Interior) X Disturbed habitats (forest edges and forest fragments) | fruit-feeding | abundance forest-dependent species | 1.178896121 | 0.221800109 |

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| 116 | 72 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | multiple | Non-disturbed (Forest Interior) X Disturbed habitats (forest edges and forest fragments) | fruit-feeding | richness disturbance-adapted species | 2.581307545 | 0.351946233 |
| 116 | 73 | Filgueiras et al. 2016 | Neotropics | Brazil - Alagoas | Atlantic Forest - lower montane rainforest | multiple | Non-disturbed (Forest Interior) X Disturbed habitats (forest edges and forest fragments) | fruit-feeding | abundance disturbance-adapted species | 1.270921168 | 0.227364072 |
| 32 | 74 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Riparian forest X Forest fallows | fruit-feeding | richness | 0.544688841 | 0.262094302 |
| 32 | 75 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Riparian forest X Live fence | fruit-feeding | richness | -0.06365112 | 0.250165157 |
| 32 | 76 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Riparian forest X Pastures with high tree cover | fruit-feeding | richness | -1.2231284 | 0.310985691 |
| 32 | 77 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Riparian forest X Forest fallows | fruit-feeding | abundance | 0.568229149 | 0.263162272 |
| 32 | 78 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Riparian forest X Live fence | fruit-feeding | abundance | -0.08487387 | 0.250293651 |
| 32 | 79 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Riparian forest X Pastures with high tree cover | fruit-feeding | abundance | -0.99957392 | 0.290729932 |
| 32 | 80 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Secondary forests X Forest fallows | fruit-feeding | richness | 0.267317859 | 0.252912995 |
| 32 | 81 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Secondary forests X Live fence | fruit-feeding | richness | -0.3916527 | 0.256252966 |
| 32 | 82 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Secondary forests X Pastures with high tree cover | fruit-feeding | richness | -1.61943159 | 0.356907718 |
| 32 | 83 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Secondary forests X Forest fallows | fruit-feeding | abundance | -0.20031444 | 0.251635718 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| 32 | 84 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Secondary forests X Live fence | fruit-feeding | abundance | -0.73139829 | 0.271806789 |
| 32 | 85 | Harvey et al. 2006 | Neotropics | Nicaragua | Dry Forest | land-use change | Secondary forests X Pastures with high tree cover | fruit-feeding | abundance | -1.42300112 | 0.332545677 |
| 63 | 86 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | forest degradation | Broadleaf forest X Successional vegetation | fruit-feeding and nectar-feeding | richness | 0.211890382 | 0.336046795 |
| 63 | 87 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | land-use change | Broadleaf forest X Pasture with high tree density | fruit-feeding and nectar-feeding | richness | 0.500715008 | 0.348485769 |
| 63 | 88 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | land-use change | Broadleaf forest X Pasture with low tree density | fruit-feeding and nectar-feeding | richness | -0.13677089 | 0.33446388 |
| 63 | 89 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | land-use change | Broadleaf forest X Live fence | fruit-feeding and nectar-feeding | richness | 1.000790445 | 0.393865682 |
| 63 | 90 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | forest degradation | Broadleaf forest X Successional vegetation | fruit-feeding and nectar-feeding | abundance | 0.605242287 | 0.355472423 |
| 63 | 91 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | land-use change | Broadleaf forest X Pasture with high tree density | fruit-feeding and nectar-feeding | abundance | 1.490170375 | 0.467539687 |
| 63 | 92 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | land-use change | Broadleaf forest X Pasture with low tree density | fruit-feeding and nectar-feeding | abundance | 2.339315308 | 0.664067264 |
| 63 | 93 | Milder et al. 2010 | Neotropics | Honduras | Humid broadleaf forest, pine/oak forest, and pre-montane moist forest | land-use change | Broadleaf forest X Live fence | fruit-feeding and nectar-feeding | abundance | 2.1987323 | 0.625510276 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| 82 | 94 | Lucey & Hill 2012 | Asia | Borneo | Rainforest | land-use change | Forest X Oil palm plantation | fruit-feeding | richness | -1.25182429 | 2.567064055 |
| 82 | 95 | Lucey & Hill 2012 | Asia | Borneo | Rainforest | land-use change | Forest X Oil palm plantation | fruit-feeding | abundance | 2.376697311 | 6.64869011 |
| 109 | 96 | Itioka et al. 2015 | Asia | Borneo | Lowland dipterocarp forest | multiple | Primary forest (Reserve) X Isolated primary forest | fruit-feeding and nectar-feeding | richness | -3.86711446 | 1.914481585 |
| 109 | 97 | Itioka et al. 2015 | Asia | Borneo | Lowland dipterocarp forest | forest degradation | Primary forest (Reserve) X Old fallows (20–60 years) | fruit-feeding and nectar-feeding | richness | -7.47244021 | 5.781388822 |
| 109 | 98 | Itioka et al. 2015 | Asia | Borneo | Lowland dipterocarp forest | forest degradation | Primary forest (Reserve) X Young fallows (5–13 years) | fruit-feeding and nectar-feeding | richness | -6.31086815 | 9.213626196 |
| 109 | 99 | Itioka et al. 2015 | Asia | Borneo | Lowland dipterocarp forest | forest degradation | Primary forest (Reserve) X New fallows where 1 year had elapsed since cessation | fruit-feeding and nectar-feeding | richness | -8.10593713 | 14.76734146 |
| 125 | 100 | Scriven et al. 2017 | Asia | Borneo | Rainforest | land-use change | Forest X Oil palm plantation | fruit-feeding | richness | 0.670604097 | 0.552358399 |
| 125 | 101 | Scriven et al. 2017 | Asia | Borneo | Rainforest | land-use change | Forest X Oil palm plantation | fruit-feeding | abundance | 1.007968308 | 0.618289912 |
| 25 | 102 | Veddeler et al. 2005 | Asia | Indonesia | Rainforest | forest degradation | Mature forests X Old secondary forests | fruit-feeding | richness | -6.18331013 | 2.685698523 |
| 25 | 103 | Veddeler et al. 2005 | Asia | Indonesia | Rainforest | forest degradation | Mature forests X Intermediate secondary forests | fruit-feeding | richness | -5.46020115 | 2.176849492 |
| 25 | 104 | Veddeler et al. 2005 | Asia | Indonesia | Rainforest | forest degradation | Mature forests X Young secondary forests | fruit-feeding | richness | -9.37406837 | 5.6857696 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| 18 | 105 | Koh & Sodhi 2004 | Asia | Singapore | Rainforest | urbanization | Forest reserves X Urban parks adjoining forests | fruit-feeding and nectar-feeding | richness | -2.3012237 | 0.507066518 |
| 18 | 106 | Koh & Sodhi 2004 | Asia | Singapore | Rainforest | urbanization | Forest reserves X Isolated urban parks | fruit-feeding and nectar-feeding | richness | -2.10544533 | 0.697469272 |
| 18 | 107 | Koh & Sodhi 2004 | Asia | Singapore | Rainforest | declining patch size | Forest reserves X Forest fragment | fruit-feeding and nectar-feeding | richness | -3.53382901 | 0.759192671 |
| 18 | 108 | Koh & Sodhi 2004 | Asia | Singapore | Rainforest | urbanization | Forest reserves X Urban parks adjoining forests | fruit-feeding and nectar-feeding | abundance | -2.88713554 | 0.613630734 |
| 18 | 109 | Koh & Sodhi 2004 | Asia | Singapore | Rainforest | urbanization | Forest reserves X Isolated urban parks | fruit-feeding and nectar-feeding | abundance | -2.11658018 | 0.700699731 |
| 18 | 110 | Koh & Sodhi 2004 | Asia | Singapore | Rainforest | declining patch size | Forest reserves X Forest fragment | fruit-feeding and nectar-feeding | abundance | -3.4195001 | 0.731325178 |
| 145 | 111 | Sambhu et al. 2018 | Oceania | Australia | Rainforest | land-use change | Forest X Sugarcane plantation | fruit-feeding | richness | 1.081846298 | 0.263250209 |
| 145 | 112 | Sambhu et al. 2018 | Oceania | Australia | Rainforest | urbanization | Forest X Urban | fruit-feeding | richness | 0.586506885 | 0.234280778 |
| 145 | 113 | Sambhu et al. 2018 | Oceania | Australia | Rainforest | land-use change | Forest X Sugarcane plantation | fruit-feeding | abundance | 0.02830382 | 0.222250305 |
| 145 | 114 | Sambhu et al. 2018 | Oceania | Australia | Rainforest | urbanization | Forest X Urban | fruit-feeding | abundance | -0.06948316 | 0.222391464 |

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|---|---|---|---|---|---|---|---|---|---|---|
| 83 | 115 | Kudavidanage et al. 2012 | Asia | Sri Lanka | Rainforest | multiple | Habitat florestal (Primary forest and Logged forest) X Anthropogenic habitats (Home gardens e Pinus plantations) | fruit-feeding and nectar-feeding | richness | 0.772404819 | 1.596609204 |
| 83 | 116 | Kudavidanage et al. 2012 | Asia | Sri Lanka | Rainforest | multiple | Habitat florestal (Primary forest and Logged forest) X Anthropogenic habitats (Home gardens e Pinus plantations) | fruit-feeding and nectar-feeding | abundance | 1.02183304 | 2.044142761 |
| 110 | 117 | Vasconcelos et al. 2015 | Africa | Guinea-Bissau | Open forest | land-use change | Native woodlands X Cashew orchards | fruit-feeding and nectar-feeding | richness | -0.9181007 | 0.106255092 |
| 110 | 118 | Vasconcelos et al. 2015 | Africa | Guinea-Bissau | Open forest | land-use change | Native woodlands X Cashew orchards | fruit-feeding and nectar-feeding | abundance | -0.42186603 | 0.097564213 |
| 126 | 119 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Timber plantation | fruit-feeding and nectar-feeding | richness | 0.657048904 | 0.648596997 |
| 126 | 120 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Semi-managed coffee forest | fruit-feeding and nectar-feeding | richness | 0.370206859 | 0.402274915 |
| 126 | 121 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Open woodland | fruit-feeding and nectar-feeding | richness | -1.46498068 | 0.749872089 |
| 126 | 122 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Pasture | fruit-feeding and nectar-feeding | richness | -0.55887438 | 0.479542799 |
| 126 | 123 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Cropland | fruit-feeding and nectar-feeding | richness | -0.62641422 | 0.447905814 |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| 126 | 124 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Timber plantation | fruit-feeding and nectar-feeding | abundance | -0.15585465 | 0.587005442 |
| 126 | 125 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Semi-managed coffee forest | fruit-feeding and nectar-feeding | abundance | 0.284868094 | 0.398433452 |
| 126 | 126 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Open woodland | fruit-feeding and nectar-feeding | abundance | -1.0133978 | 0.619567699 |
| 126 | 127 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Pasture | fruit-feeding and nectar-feeding | abundance | -2.56477539 | 1.072188417 |
| 126 | 128 | Norfolk et al. 2017 | Africa | Ethiopia | Forest | land-use change | Natural forest X Cropland | fruit-feeding and nectar-feeding | abundance | -3.68239814 | 1.496203441 |
| 183 | 129 | Schmitt et al. 2020 | Africa | Kenya | Dense cloud forest | land-use change | Forest interior X Agricultural land | fruit-feeding and nectar-feeding | richness | 4.20473012 | 0.970709257 |
| 183 | 130 | Schmitt et al. 2020 | Africa | Kenya | Dense cloud forest | land-use change | Forest interior X Plantation | fruit-feeding and nectar-feeding | richness | 1.790113323 | 0.380630593 |
| 183 | 131 | Schmitt et al. 2020 | Africa | Kenya | Dense cloud forest | edge effect | Forest interior X Forest edge | fruit-feeding and nectar-feeding | richness | 6.481457686 | 1.96249467 |
| 183 | 132 | Schmitt et al. 2020 | Africa | Kenya | Dense cloud forest | land-use change | Forest interior X Agricultural land | fruit-feeding and nectar-feeding | abundance | -0.64336503 | 0.26687325 |

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| 183 | 133 | Schmitt et al. 2020 | Africa | Kenya | Dense cloud forest | land-use change | Forest interior X Plantation | fruit-feeding and nectar-feeding | abundance | -1.17005612 | 0.305808099 |
| 183 | 134 | Schmitt et al. 2020 | Africa | Kenya | Dense cloud forest | edge effect | Forest interior X Forest edge | fruit-feeding and nectar-feeding | abundance | 3.5962336 | 0.777205142 |
| 26 | 135 | Bossart et al. 2006 | Africa | Ghana | Moist semi-deciduous forest | declining patch size | Large forest reserves X remnant, sacred forest groves | fruit-feeding | richness | -2.70909614 | 2.325006202 |
| 26 | 136 | Bossart et al. 2006 | Africa | Ghana | Moist semi-deciduous forest | declining patch size | Large forest reserves X remnant, sacred forest groves | fruit-feeding | abundance | -1.89365421 | 1.519546361 |
| 114 | 137 | Bossart & Antwi 2016 | Africa | Ghana | Moist semi-deciduous forest | declining patch size | Large forest reserves X Sacred forest groves | fruit-feeding | richness | -2.25015793 | 1.465423979 |
| 114 | 138 | Bossart & Antwi 2016 | Africa | Ghana | Moist semi-deciduous forest | declining patch size | Large forest reserves X Sacred forest groves | fruit-feeding | abundance | -2.34825014 | 1.533613571 |
| 127 | 139 | Jain et al. 2017 | Asia | Singapore | Dipterocarp rainforest | forest degradation | Mature forests X Degraded Forest | fruit-feeding and nectar-feeding | richness | -2.39454819 | 1.042338467 |
| 127 | 140 | Jain et al. 2017 | Asia | Singapore | Dipterocarp rainforest | declining patch size | Mature forests X Forest fragment | fruit-feeding and nectar-feeding | richness | -3.52313773 | 1.31127336 |
| 127 | 141 | Jain et al. 2017 | Asia | Singapore | Dipterocarp rainforest | urbanization | Mature forests X Urban | fruit-feeding and nectar-feeding | richness | -7.30654025 | 6.748854014 |
| 127 | 142 | Jain et al. 2017 | Asia | Singapore | Dipterocarp rainforest | declining patch size | Large Forest X Small Forest | fruit-feeding and nectar-feeding | richness | -3.16466542 | 0.660195337 |
| 33 | 143 | Benedick et al. 2006 | Asia | Borneo | Lowland rainforest | declining patch size | Continuous forest X Forest fragment | fruit-feeding | richness | 0.473075979 | 0.64281713 |

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| 33 | 144 | Benedick et al. 2006 | Asia | Borneo | Lowland rainforest | declining patch size | Continuous forest X Forest fragment | fruit-feeding | abundance | 0.852854047 | 0.682906242 |
| 207 | 145 | Lourenço et al. 2019 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | abundance Biblidinae | 0.856862752 | 0.824230291 |
| 207 | 146 | Lourenço et al. 2019 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | abundance Charaxinae | -0.10232529 | 0.668913648 |
| 207 | 147 | Lourenço et al. 2019 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | abundance Morphini and Brassolini | 0.138381879 | 0.670776194 |
| 207 | 148 | Lourenço et al. 2019 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | abundance Nymphalinae | 0.792400753 | 0.801414935 |
| 207 | 149 | Lourenço et al. 2019 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - rainforest | edge effect | Forest Interior X Forest edge | fruit-feeding | abundance Satyrini | 0.437465065 | 0.70773624 |
| 208 | 150 | Lewis 2001 | Neotropics | Belize | Moist tropical forest - deciduous seasonal forest and deciduous/semi-evergreen seasonal forest | logging | Unlogged forest X Logged forest | fruit-feeding | richness | 0.504626504 | 1.254647909 |
| 208 | 151 | Lewis 2001 | Neotropics | Belize | Moist tropical forest - deciduous seasonal forest and deciduous/semi-evergreen seasonal forest | logging | Unlogged forest X Logged forest | fruit-feeding | abundance | 0.649660923 | 1.422059314 |
| 209 | 152 | Willott et al. 2000 | Asia | Borneo | Lowland dipterocarp rainforest | logging | Primary forests X Logged forest | fruit-feeding and nectar-feeding | richness | 0.833432871 | 0.580871445 |

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| 209 | 153 | Willott et al. 2000 | Asia | Borneo | Lowland dipterocarp rainforest | land-use change | Primary forests X Open areas | fruit-feeding and nectar-feeding | richness | -3.81936226 | 3.88051032 | |
| 209 | 154 | Willott et al. 2000 | Asia | Borneo | Lowland dipterocarp rainforest | logging | Primary forests X Logged forest | fruit-feeding and nectar-feeding | abundance | 0.33664607 | 0.513194747 | |
| 209 | 155 | Willott et al. 2000 | Asia | Borneo | Lowland dipterocarp rainforest | land-use change | Primary forests X Open areas | fruit-feeding and nectar-feeding | abundance | -3.14694127 | 2.875253349 | |
| 81 | 156 | Ribeiro et al. 2012 | Neotropics | Brazil - São Paulo | Atlantic Forest - dense humid forest | declining patch size | Fragment area | fruit-feeding | richness | -0.20050897 | 0.375986368 | * |
| 81 | 157 | Ribeiro et al. 2012 | Neotropics | Brazil - São Paulo | Atlantic Forest - dense humid forest | declining patch size | Fragment area | fruit-feeding | abundance | 0.222894861 | 0.37703951 | * |
| 34 | 158 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic forest - montane rainforest | declining patch size | Fragment area | fruit-feeding | richness | -3.30358657 | 3.368421053 | * |
| 34 | 159 | Uehara-Prado et al. 2007 | Neotropics | Brazil - São Paulo | Atlantic forest - montane rainforest | declining patch size | Fragment area | fruit-feeding | abundance | -1.44725445 | 1.163636364 | * |
| 52 | 160 | Marin et al. 2009 | Neotropics | México | Dry Forest | forest loss | Forest cover (secondary forest - %) | fruit-feeding | richness | 0.256205074 | 0.65641026 | * |
| 52 | 161 | Marin et al. 2009 | Neotropics | México | Dry Forest | forest loss | Forest cover (secondary forest - %) | fruit-feeding | abundance | 0.134558681 | 0.64452651 | * |
| 189 | 162 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | declining patch size | Fragment area | fruit-feeding | richness | 0.340793441 | 0.26369124 | * |
| 189 | 163 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | isolation | Euclidean nearest neighbour distance | fruit-feeding | richness | 0.464416287 | 0.270801406 | * |
| 189 | 164 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | forest loss | Habitat amount | fruit-feeding | richness | -0.63971574 | 0.284626673 | * |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 189 | 165 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | isolation | Proximity index | fruit-feeding | richness | 0.467696574 | 0.271019805 | * |
| 189 | 166 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | declining patch size | Fragment area | fruit-feeding | abundance | 0.135734818 | 0.256711509 | * |
| 189 | 167 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | isolation | Euclidean nearest neighbour distance | fruit-feeding | abundance | -0.14747329 | 0.256948969 | * |
| 189 | 168 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | forest loss | Habitat amount | fruit-feeding | abundance | -0.21874307 | 0.258813266 | * |
| 189 | 169 | Brito et al. 2021 | Neotropics | Brazil - Rio Grande do Norte | Atlantic forest | isolation | Proximity index | fruit-feeding | abundance | 0.28993893 | 0.261400127 | * |
| 184 | 170 | Miao et al. 2021 | Asia | China | Rainforest | multiple | Land-use intensity | fruit-feeding and nectar-feeding | richness | -1.11782101 | 0.952380952 | * |
| 33 | 171 | Benedick et al. 2006 | Asia | Borneo | Lowland rainforest | declining patch size | Fragment area | fruit-feeding | richness | -0.62498447 | 0.414919895 | * |
| 33 | 172 | Benedick et al. 2006 | Asia | Borneo | Lowland rainforest | isolation | Isolation | fruit-feeding | richness | -0.2774245 | 0.380070869 | |
| 33 | 173 | Benedick et al. 2006 | Asia | Borneo | Lowland rainforest | declining patch size | Fragment area | fruit-feeding | abundance | 0.818632885 | 0.445981474 | * |
| 33 | 174 | Benedick et al. 2006 | Asia | Borneo | Lowland rainforest | isolation | Isolation | fruit-feeding | abundance | -0.57983578 | 0.408875889 | |
| 49 | 175 | Bossart & Opuni-Frimpong 2009 | Africa | Ghana | Moist semi-deciduous forest | edge effect | Distance from Edge | fruit-feeding | richness | 0.404232922 | 0.680851064 | * |
| 49 | 176 | Bossart & Opuni-Frimpong 2009 | Africa | Ghana | Moist semi-deciduous forest | edge effect | Distance from Edge | fruit-feeding | richness | -1.95959179 | 1.6 | * |
| 49 | 177 | Bossart & Opuni-Frimpong 2009 | Africa | Ghana | Moist semi-deciduous forest | edge effect | Distance from Edge | fruit-feeding | richness | -0.82492808 | 0.810126582 | * |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 49 | 178 | Bossart & Opuni-Frimpong 2009 | Africa | Ghana | Moist semi-deciduous forest | edge effect | Distance from Edge | fruit-feeding | abundance | 0.228571429 | 0.653061224 | * |
| 49 | 179 | Bossart & Opuni-Frimpong 2009 | Africa | Ghana | Moist semi-deciduous forest | edge effect | Distance from Edge | fruit-feeding | abundance | 1.6653328 | 1.333333333 | * |
| 49 | 180 | Bossart & Opuni-Frimpong 2009 | Africa | Ghana | Moist semi-deciduous forest | edge effect | Distance from Edge | fruit-feeding | abundance | 1.880222884 | 1.523809524 | * |
| 187 | 182 | Orlandin & Carneiro 2021 | Neotropics | Brazil - Paraná | Atlantic Forest - Araucaria forest (a component of mixed ombrophilous forest) | urbanization | Urban fragments area - 600 m | fruit-feeding and nectar-feeding | richness | -0.91775621 | 0.250632763 | * |
| 187 | 184 | Orlandin & Carneiro 2021 | Neotropics | Brazil - Paraná | Atlantic Forest - Araucaria forest (a component of mixed ombrophilous forest) | urbanization | Urban fragments area - 600 m | fruit-feeding and nectar-feeding | abundance | -0.20182697 | 0.206102633 | * |
| 187 | 187 | Orlandin & Carneiro 2021 | Neotropics | Brazil - Paraná | Atlantic Forest - Araucaria forest (a component of mixed ombrophilous forest) | urbanization | Open green area (ha) around urban forest fragments - 1 km | fruit-feeding and nectar-feeding | richness | -0.83225455 | 0.24232005 | * |
| 187 | 190 | Orlandin & Carneiro 2021 | Neotropics | Brazil - Paraná | Atlantic Forest - Araucaria forest (a component of mixed ombrophilous forest) | urbanization | Open green area (ha) around urban forest fragments - 1 km | fruit-feeding and nectar-feeding | abundance | -0.09196964 | 0.204309538 | * |
| 187 | 191 | Orlandin & Carneiro 2021 | Neotropics | Brazil - Paraná | Atlantic Forest - Araucaria forest (a component of mixed ombrophilous forest) | urbanization | Paved area (ha) around urban forest fragments-100 m | fruit-feeding and nectar-feeding | richness | -1.49257171 | 0.327604644 | |
| 187 | 193 | Orlandin & Carneiro 2021 | Neotropics | Brazil - Paraná | Atlantic Forest - Araucaria forest (a component of mixed ombrophilous forest) | urbanization | Paved area (ha) around urban forest fragments - 100 m | fruit-feeding and nectar-feeding | abundance | -0.41859878 | 0.213574345 | |

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| 107 | 195 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | forest loss | Forest cover (%) 200 m | fruit-feeding | richness | -0.36454315 | 0.424519892 | * |
| 107 | 198 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | forest loss | Forest cover (%) 400 m | fruit-feeding | abundance | -0.51520029 | 0.441087346 | * |
| 107 | 199 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | forest loss | Fragment area - 200 m | fruit-feeding | richness | -0.3428572 | 0.422602311 | * |
| 107 | 201 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | isolation | Nearest neighbor distance - 200 m | fruit-feeding | richness | 0.153568073 | 0.410856323 |  |
| 107 | 203 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | isolation | Proximity index mean of landscape - 400 m | fruit-feeding | richness | -3.12886598 | 1.631633715 | * |
| 107 | 205 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | forest loss | Fragment area - 400m | fruit-feeding | abundance | -0.51520029 | 0.441087346 | * |
| 107 | 206 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | isolation | Nearest neighbor distance - 200 m | fruit-feeding | abundance | 0.252933272 | 0.415905334 |  |
| 107 | 208 | Brito et al. 2014 | Neotropics | Brazil - Minas Gerais | Atlantic Forest - semi-deciduous seasonal rainforest | isolation | Proximity index mean of landscape - 400 m | fruit-feeding | abundance | -0.83053317 | 0.494131597 | * |
| 100 | 209 | Nyafwono et al. 2014 | Africa | Uganda | Moist, evergreen medium altitude tropical forest | multiple | Land-use intensity | fruit-feeding | richness | 0.362887369 | 0.470311581 |  |
| 100 | 210 | Nyafwono et al. 2014 | Africa | Uganda | Moist, evergreen medium altitude tropical forest | multiple | Land-use intensity | fruit-feeding | abundance | 0.325313472 | 0.466617526 |  |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| 210 | 211 | Perfecto et al. 2003 | Neotropics | México | Evergreen montane moist forests | land-use change | Land-use intensity | fruit-feeding | richness | -2.79783203 | 1.808739785 |
| 211 | 212 | Beck & Schulze 2000 | Asia | Malaysia | Dipterocarp rainforest | multiple | Land-use intensity | fruit-feeding | richness | -2.46338061 | 2.157061004 |
| 214 | 213 | Rossato et. al 2025 | Neotropical | Brazil - Rio Grande do Sul | Atlantic Forest | land-use change | Native forest X Agroforestry banana plantations | fruit-feeding and nectar-feeding | richness | 2.158960096 | 0.351697464 |
| 214 | 214 | Rossato et. al 2025 | Neotropical | Brazil - Rio Grande do Sul | Atlantic Forest | land-use change | Native forest X Conventional banana plantations | fruit-feeding and nectar-feeding | richness | 1.157601935 | 0.259445618 |
| 214 | 215 | Rossato et. al 2025 | Neotropical | Brazil - Rio Grande do Sul | Atlantic Forest | land-use change | Native forest X Agroforestry banana plantations | fruit-feeding and nectar-feeding | abundance | 1.693610942 | 0.301897723 |
| 214 | 216 | Rossato et. al 2025 | Neotropical | Brazil - Rio Grande do Sul | Atlantic Forest | land-use change | Native forest X Conventional banana plantations | fruit-feeding and nectar-feeding | abundance | 0.870445034 | 0.243268738 |
| 216 | 217 | Hannoteau et. al 2025 | Africa | Madagascar | Humid evergreen forests | land-use change | Protected areas X Anthropized areas | fruit-feeding and nectar-feeding | richness | -0.74984666 | 1.070283752 |
| 216 | 218 | Hannoteau et. al 2025 | Africa | Madagascar | Humid evergreen forests | land-use change | Protected areas X Anthropized areas | fruit-feeding and nectar-feeding | abundance | 0.578681138 | 1.041858982 |
| 218 | 219 | Bellaver et. al 2023 | Neotropical | Brazil - Rio Grande do Sul | Atlantic Forest | edge effect | Forest interior X Forest edge | fruit-feeding | richness | 0.182268373 | 0.200830544 |
| 218 | 220 | Bellaver et. al 2023 | Neotropical | Brazil - Rio Grande do Sul | Atlantic Forest | edge effect | Forest interior X Forest edge | fruit-feeding | abundance | 1.28072572 | 0.241006459 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 219 | 221 | Orlandin et. al 2019 | Neotropical | Brazil - Santa Catarina | Atlantic Forest | land-use change | Forest interior X Farm | fruit-feeding and nectar-feeding | richness | 1.699198357 | 0.907272921 |
| 219 | 222 | Orlandin et. al 2019 | Neotropical | Brazil - Santa Catarina | Atlantic Forest | land-use change | Forest interior X Road | fruit-feeding and nectar-feeding | richness | 2.30770485 | 1.110458473 |
| 219 | 223 | Orlandin et. al 2019 | Neotropical | Brazil - Santa Catarina | Atlantic Forest | land-use change | Forest interior X Abandoned | fruit-feeding and nectar-feeding | richness | 3.253401671 | 1.548718536 |
| 219 | 224 | Orlandin et. al 2019 | Neotropical | Brazil - Santa Catarina | Atlantic Forest | land-use change | Forest interior X Farm | fruit-feeding and nectar-feeding | abundance | 1.684275839 | 0.903065425 |
| 219 | 225 | Orlandin et. al 2019 | Neotropical | Brazil - Santa Catarina | Atlantic Forest | land-use change | Forest interior X Road | fruit-feeding and nectar-feeding | abundance | 2.137989193 | 1.047583149 |
| 219 | 226 | Orlandin et. al 2019 | Neotropical | Brazil - Santa Catarina | Atlantic Forest | land-use change | Forest interior X Abandoned | fruit-feeding and nectar-feeding | abundance | 1.752990973 | 0.922748113 |
| 220 | 227 | Bobo et. al 2006 | Africa | Cameroon | Evergreen Rainforest | land-use change | Forest X Secondary forest | fruit-feeding | richness | 1.337116361 | 0.40782834 |
| 220 | 228 | Bobo et. al 2006 | Africa | Cameroon | Evergreen Rainforest | land-use change | Forest X Cocoa forest | fruit-feeding | richness | 0.157607056 | 0.334368333 |
| 220 | 229 | Bobo et. al 2006 | Africa | Cameroon | Evergreen Rainforest | land-use change | Forest X Annual crops | fruit-feeding | richness | -1.64100644 | 0.445537589 |
| 221 | 230 | Pignataro et. al 2020 | Neotropical | Brazil - Minas Gerais | Atlantic Forest - Semideciduous Montane Stationary Forest | land-use change | Forest X Rural | fruit-feeding and nectar-feeding | richness | -0.9929265 | 0.249608418 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 221 | 231 | Pignataro et. al 2020 | Neotropical | Brazil - Minas Gerais | Atlantic Forest - Semideciduous Montane Stationary Forest | urbanization | Forest X Urban | fruit-feeding and nectar-feeding | richness | -1.53546317 | 0.287712421 |
| 221 | 232 | Pignataro et. al 2020 | Neotropical | Brazil - Minas Gerais | Atlantic Forest - Semideciduous Montane Stationary Forest | land-use change | Forest X Rural | fruit-feeding and nectar-feeding | abundance | -0.50188184 | 0.229219038 |
| 221 | 233 | Pignataro et. al 2020 | Neotropical | Brazil - Minas Gerais | Atlantic Forest - Semideciduous Montane Stationary Forest | urbanization | Forest X Urban | fruit-feeding and nectar-feeding | abundance | -0.73555149 | 0.237251 |
| 213 | 234 | Alvarez et. al 2024 | Neotropical | Colombia | Cloud forest | land-use change | Cloud forest X Cattle pastures | fruit-feeding | richness | -10.0357329 | 7.77732865 |
| 213 | 235 | Alvarez et. al 2024 | Neotropical | Colombia | Cloud forest | land-use change | Cloud forest X Cattle pastures | fruit-feeding | abundance | -4.30873795 | 1.909420674 |

## Capítulo 2

# Alpha and Beta diversity of Butterflies in Atlantic Forest remnants

# Alpha and Beta diversity of Butterflies in Atlantic Forest remnants

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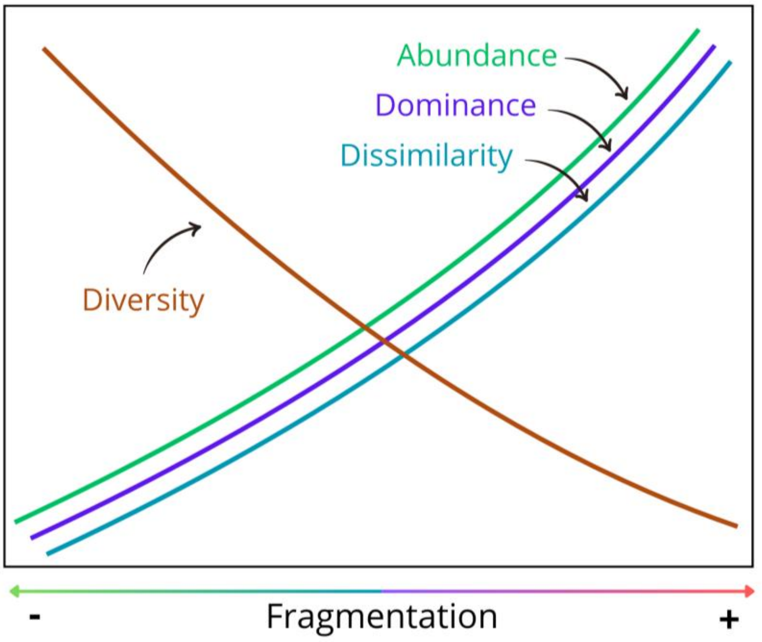
## Abstract

Landscape and local-scale changes alter alpha and beta diversity, often leading to a scenario where many species decline and few thrive. In this study, we evaluate the effect of changes in the landscape and local features of Atlantic Forest remnants on alpha and beta diversity of butterflies across a forest cover gradient. We sampled butterflies in forest fragments in 17 landscapes to assess how landscape forest loss and fragmentation, along with local habitat structure affect richness ($^0D$), diversity ($^1D$), and effective number of dominant species and tribes ($^2D$), as well as abundance, and also beta diversity (total, turnover, and richness) based on abundance. We recorded a total of 2,515 butterfly individuals, representing 281 species, 195 genera, 45 tribes, and six families. We found that fragmentation, measured by the number of forest fragments in the landscape, positively influenced butterfly abundance. However, this increase was accompanied by greater species and tribe dominance and reduced tribe diversity. These shifts were preceded by changes in both species and tribe composition. Beta diversity was primarily driven by turnover, including changes in species relative abundance among landscapes. For species, beta diversity was best explained by forest cover. Whereas tribe beta diversity was best explained by the number of forest fragments in the landscape. Our results indicate that forest fragmentation has affected butterfly communities by increasing the abundance of a few species and leading to less diverse and equitable communities. Forest loss has resulted in changes to the species composition of Atlantic Forest fragments. Meanwhile, fragmentation influences the composition of butterfly tribes. In addition, in the Brazilian Atlantic Forest, the legally required 20% forest cover is insufficient to sustain butterfly assemblages comparable to those in more forested areas.

**Keywords**: Beta diversity, alpha diversity, landscape ecology, fragmentation, forest loss, butterfly, Lepidoptera.



**Graphical summary of results**: The number of fragments in the landscape had a positive effect on butterfly abundance and a negative effect on the number of dominant species. This indicates that fragmentation increased abundance by promoting species dominance. The number of fragments in the landscape had a negative effect on butterfly tribe diversity and the number of dominant tribes. It was also the predictor that best explained the differences in tribe composition among the forest fragments. These indicate that fragmentation decreased diversity, increased butterfly tribe dominance, and increased tribe dissimilarity.

## Introduction

Landscape and local-scale changes alter species composition, often leading to a scenario where many species decline and few thrive. Habitat loss, in particular, can promote biotic homogenization (McKinney and Lockwood 1999; Maurenza et al. 2025), where generalist species proliferate and specialists disappear or persist at dangerously low densities, threatening their long-term viability (Filgueiras et al. 2019; 2021). These shifts can negatively impact distinct ecosystem functions, including vital services such as pollination and pest control (Millennium Ecosystem Assessment 2005; Díaz et al. 2006).

At the landscape scale, forest loss causes changes in local vegetation structure, leading to the degradation of remaining forest fragments (Tabarelli et al. 2004). These fragments begin to exhibit reduced tree diversity, smaller and fewer trees, and more open canopies, resulting in a drier and warmer microclimate (Oliveira et al. 2008; Magnago et al. 2015; Rocha-Santos et al. 2016). Such landscape and local-scale changes frequently impact species richness, diversity, evenness, and abundance, commonly referred to as alpha diversity. Changes in alpha diversity are often accompanied by changes in beta diversity, which captures the variation or dissimilarity in species composition across space or time (Whittaker 1972; Calderón-Patrón and Moreno 2019). Although fragmented landscapes may exhibit higher beta diversity than continuous habitats due to increased spatial heterogeneity, they often show reduced alpha and gamma (regional diversity) diversities. This suggests that compositional variation does not necessarily translate into greater overall biodiversity (Gonçalves-Souza et al. 2025).

Given their rapid response to habitat changes and their large representation, butterflies are widely used as environmental indicators in biodiversity monitoring studies. Butterflies exhibit sensitivity to changes in the habitat, microclimate, vegetation structure, and availability of host plants (Brown Jr and Hutchings 1997; Uehara-Prado et al. 2009; Bonebrake et al. 2010; Ferrer-Paris et al. 2013). Although species-level identification can be challenging, especially in hyperdiverse tropical regions, tribe level identification offers valuable insights into environmental quality (Santos et al. 2016). In fact, tribe-level approaches have been shown to be effective for detecting patterns of community response to environmental gradients and identifying groups particularly sensitive to disturbance (Santos et al. 2016). Therefore, the use of tribes as surrogate units may provide a robust and complementary perspective to species-level analyses in landscape-scale conservation studies.

Studies on butterflies in fragmented environments of the Atlantic Forest have shown that butterflies exhibit a certain degree of resistance to landscape modification (Uehara-Prado et al. 2007). Although some studies have assessed the effect of landscape heterogeneity on butterflies at the landscape scale (Öckinger and Smith 2006; Oliver et al. 2010; Brito et al. 2014), the results regarding forest loss have been inconsistent, showing both negative (Viljur et al. 2020) and neutral effects (Brito et al. 2021). Furthermore, Brito et al. (2014) found that the abundance of matrix-tolerant species increased with the reduction of forest cover. However, species composition is strongly affected by habitat loss, such that species that are more abundant in deforested landscapes rarely occur in well-preserved areas with continuous forest cover (Uehara-Prado et al. 2007). In butterfly communities, shifts in compositions often correspond to differences in the presence and abundance of functional groups, suggesting that species turnover may have ecological consequences beyond taxonomic replacement (Lazarina et al. 2023).

In this study, we evaluated how local and landscape attributes influence butterfly alpha and beta diversity in Atlantic Forest remnants. Specifically, we aimed to determine how species and tribes' richness, diversity, evenness, abundance (α-diversity), and composition (β-diversity) vary across a forest cover gradient, and which factors best explain these patterns. We hypothesize that: (i) forest cover will not be related to butterfly α-diversity, as species replacement in more deforested landscapes could maintain richness and diversity despite increased dominance; (ii) fragmentation would have a positive effect on butterfly abundance and dominance at both species and tribe levels. Regarding β-diversity, we expected that: (iii) differences in forest cover among fragments would be the main driver of compositional turnover, with higher cover differences leading to greater species and tribe dissimilarity; and (iv) broader differences in landscape configuration would further increase β-diversity by enhancing dissimilarity in community composition across sites.

## Methods

### *Study area*

The study was conducted in forest remnants of the Atlantic Forest in southern Bahia, Brazil, specifically within the municipalities of Belmonte, Canavieiras, Mascote, and Una (15°0'–16°0' S and 39°0'–39°30' W) (Figure 1). As one of three key endemic centers for this biodiversity *hotspot*, the region has experienced particularly severe deforestation pressures, with recent data indicating a loss of 4,717 hectares of native forest cover in 2024 (SOS Mata Atlântica and INPE 2025), predominantly converted to agricultural and pastoral land uses. Currently, the region is heterogeneous, comprising a mosaic of different land cover types, including cattle pastures, cacao plantations (*Theobroma cacao*), and rubber tree plantations (*Hevea brasiliensis*) (Pardini 2004). The climate is tropical and humid, with no distinct dry season (Alvares et al. 2013), a mean annual temperature of 24°C, and an average annual precipitation of 1,800 mm (Thomas et al. 1998).

We sampled 17 forest fragments previously surveyed by REDE SISBIOTA, a project assessing deforestation impacts on biodiversity in southern Bahia (see Faria et al. 2023). Fragments share similar floristic traits but are embedded in distinct landscapes.

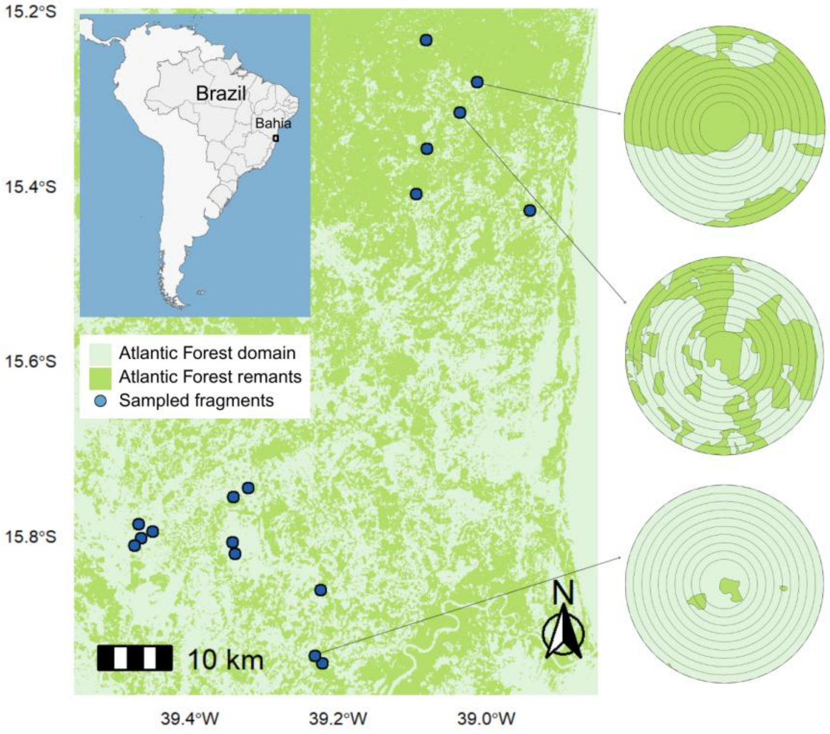


**Figure 1**: Location of the 17 surveyed forest fragments in southern Bahia, Brazil. Sampled fragments are shown in blue. On the right, detailed views of some selected landscapes illustrate the circular buffers surrounding forest fragments, ranging from 300 to 1,200 m. Forest cover within these buffers is highlighted in dark green. Forest data sourced from MapBiomas (2023). Map projection: Albers Equal Area Conic.

### *Butterfly Survey*

Four fieldwork campaigns were conducted in 2023 (January-February, April-May, July-August, October-November) to account for seasonal variation. In each campaign, each forest fragment was sampled on alternate days for two hours in two time slots (09:00-12:00 and 12:00-15:00), covering peak butterfly activity. Two researchers walked pre-existing trails per sampling event, capturing butterflies with entomological nets. Specimens were immediately sacrificed, stored in labeled glassine envelopes (date, time, sampling fragment, and collector), and later identified. All individuals were identified to the lowest possible taxonomic level using identification guides (Uehara-Prado et al. 2004; Warren et al. 2017) and specialist verification when needed. Part of the material was deposited at LABBOR (Unicamp - Campinas, Brazil) and LABINT (UESC – Ilhéus, Brazil).

### *Landscape variables*

We adopted a patch-landscape approach (Fahrig 2013) to evaluate butterfly community responses while accounting for multi-scale environmental drivers. Butterfly data were assessed at the fragment level, while landscape predictors were quantified across six spatial scales (300-1200 m radii in 100 m increments) from the centroid of the sampled area of each forest fragment. Using high-resolution satellite imagery, we extracted three landscape metrics to characterize the surroundings of each sampling fragment: percentage of native forest cover, edge density, and the number of forest fragments (see Faria et al. 2023). Forest cover, used here as a proxy for habitat amount, represents the main metric of landscape composition. In contrast, edge density and the number of forest fragments describe landscape configuration and are commonly associated with habitat fragmentation (Fahrig 2003). The minimum buffer size (300 m) was selected to exceed the spatial extent of sampling transects, while the upper limit (1200 m) prevented spatial overlap between adjacent study landscapes. To ensure analytical rigor, fragments appearing in multiple nested buffers were counted only once during quantification. All spatial analyses were performed using the R packages *terra* and *tidyterra* (R Core Team 2025; Hijmans et al. 2025; Hernangómez et al. 2025), using the UTM Zone 24 projection to ensure accurate area calculations.

### *Local variables*

To characterize vegetation structure within each sampling fragment, we used mean and maximum tree height and mean diameter at breast height (DBH), based on data from Rocha-Santos et al. (2017). Additionally, we assessed canopy openness and vegetation structure. During initial fragment visits, digital images were captured at 1.5 m height at 20 m intervals along all sampling trials using a fisheye lens-equipped camera. These images were subsequently processed through computational analysis of pixel luminosity distributions, where canopy openness was quantified as the proportional area of unobstructed sky (white pixels) relative to vegetation coverage (black pixels). Fragment-level canopy openness indices were calculated as the mean value across all photographic samples per fragment, with repeated measurements across all seasonal sampling campaigns to account for potential temporal variation in canopy structure. Image processing was conducted in the R environment (R Core Team 2025).

We simplified the explanation of the effects of local variables (mean and maximum height of tree, DBH, and canopy openness) on butterfly diversity, performing dimensionality reduction using Principal Component Analysis (PCA). We retained only the first component, which explained 55.3% of the variance. The first axis of the PCA is negatively related to canopy openness and positively related to mean and maximum tree height and mean diameter at breast height (DBH) (Figure S1 - Table S1).

## *Data analysis*

### Alpha diversity

Butterfly alpha diversity was estimated using the Hill numbers approach (Hill 1973; Jost 2006; Chao et al. 2021), which partition diversity into three orders: ${}^0D$ (equal to species richness); ${}^1D$ (effective number of equal abundant species, equal to Shannon exponential; hereafter "diversity"); and ${}^2D$ (effective number of dominant species, equal to inverse Simpson index and equivalent to classical evenness measure). Alpha diversity estimates were performed for species and tribes. To reduce bias in comparing diversity, due to sampling coverage differences, we applied the interpolation-extrapolation protocol of Chao and Jost (2012) to estimate diversity orders for each sampling fragment–species/tribe. Taxonomic diversity for species was standardized to a common level of sample coverage, calculated as twice the observed abundance for each sampling fragment, using the lowest value serving as reference (Chao et al. 2014; Hsieh et al. 2016)

(Figure S2). For the analysis of diversity at the tribe level, the 95% confidence intervals of the sampling coverage overlapped, so we used the observed diversity values without extrapolating or interpolating. All taxonomic diversity estimates were performed using the R package iNEXT (Hsieh et al. 2016; R Core Team 2025).

To assess potential collinearity among the landscape variables, including forest cover, edge density, and number of forest fragments, we computed Pearson correlation coefficients (Quinn and Keough 2002). As no strong correlations were found ($r < 0.7$), all variables were retained for analysis. Then, we evaluated the scale of effect the landscape variables exhibit the greatest influence on the richness (${}^0D$), abundance, diversity (${}^1D$), and number of dominant species (${}^2D$) of species and tribes. This approach was adopted because the scale at which these variables are measured can significantly affect the observed relationships between landscape structure and ecological responses (Jackson and Fahrig 2015). To account for this, we fitted generalized linear models (GLMs) for each landscape variable, using Gaussian distributions for ${}^0D$, ${}^1D$, and ${}^2D$ and Poisson distribution for abundance and ${}^0D$ of tribes. The response variable was modeled as a function of landscape variables individually, across a range of buffer sizes ranging from 300 to 1200 meters, in 100-meter intervals. Subsequently, we evaluated the effect of each potential model, with a single explanatory variable, on the response variable and ranked them based on their Akaike Information Criterion corrected by sample size (AICc) using the "dredge" function from the MuMin package (Bartoń 2025).

To evaluate the effect of landscape variables and habitat structure on butterflies' alpha diversity, we fitted generalized linear models (GLMs) using Gaussian distributions for ${}^0D$, ${}^1D$, and ${}^2D$, Poisson for ${}^0D$ of tribes, and Binomial negative for abundance. Models were inspected by ensuring that residuals did not exhibit overdispersion, showed no clear patterns of heteroscedasticity, and its simulated residuals followed a uniform distribution (Hartig 2016). Additionally, variables with high variance inflation factors ($VIF > 10$) were removed (Hartig 2016; Zuur et al. 2009). When the confidence intervals of the VIF values for two or more high-VIF variables overlapped, we tested alternative global models by sequentially removing one variable at a time. We selected the most parsimonious models using AICc, among the models with $\Delta AICc \leq 2$, we selected the simplest one, based on the principle that, generally, simpler models are more plausible. When the null model was present among the models with $\Delta AICc \leq 2$, we selected it (Burnham and Anderson 2002; Richards 2015; Zuur 2009).

*Beta diversity*

To assess dissimilarity in the composition of butterfly species and tribes across forest fragments, we followed the approach proposed by Carvalho et al. (2013), which partitions total beta diversity ($\beta_{total}$) into two components: turnover of species or tribes ($\beta_{repl}$) and richness difference ($\beta_{rich}$) (Legendre 2014; Podani and Schmera 2011). We used the abundance-based Jaccard dissimilarity (also known as Ružička dissimilarity), as we aimed to account for changes in the abundance of species and tribes across sampling fragments. All calculations were conducted in R using the BAT package (Cardoso et al. 2015; R Core Team 2025).

To evaluate how dissimilarities in butterfly species and tribe composition grouped sampling fragments, we performed hierarchical clustering using the UPGMA method (Legendre and Legendre 2012; Suzuki et al. 2019). The number of groups in each dendrogram was determined using the gap statistic method (Tibshirani et al., 2001), which compares the observed within-cluster dispersion to that of a random reference distribution and identifies the optimal number of clusters. Cluster support was evaluated using bootstrap (1,000 iterations). To assess how well the dendrograms reflected the original dissimilarity matrices, we calculated cophenetic correlations between each dendrogram and its corresponding distance matrix (Legendre and Legendre, 2012). To explore how fragment groupings relate to the relative abundance of butterflies, we used heatmaps and rank-abundance curves. All clustering analyses, including group estimation and bootstrap support, were performed in R using the pvclust, NbClust, and fpc packages (Charrad et al. 2014; Hennig 2024; R Core Team 2025; Suzuki et al. 2019). Heatmaps and rank-abundance curves were generated using ggplot2 and ComplexHeatmap (Gu et al. 2016; Wickham 2016).

To evaluate the influence of environmental variables on compositional dissimilarity among fragments, we fitted Generalized Dissimilarity Models (GDMs) (Ferrier et al. 2007). GDMs are nonlinear statistical models that relate ecological dissimilarity (species or tribe dissimilarity) with environmental gradients (changes in environmental variables and geographic distance) among site pairs (Mokany et al. 2022). GDMs allow for the identification and quantification of how compositional dissimilarity rates vary along environmental gradients, facilitating interpretation of the relative influence of each variable on biological gradients. First, we fitted GDMs using all spatial scales of each landscape variable to define the scale of effect that maximizes the ecological responses, using the importance of the variable as criteria (Mokany et al., 2022). Variable importance in GDMs was assessed by sequentially removing each predictor and refitting the model (10,000 iterations). Model performance was evaluated based on p-values, the percentage of deviance explained, and predictive power in cross-validation tests (10,000 iterations) (Mokany et al. 2022). Model fitting and validation were carried out in R using the gdm package (Fitzpatrick et al. 2015; R Core Team 2025).

## Results

We recorded a total of 2,515 butterflies, representing 281 species, 195 genera, 45 tribes, and six families (Table S2). The family with the highest abundance was Nymphalidae, with 1,609 individuals across 18 tribes and 91 species, while Hesperiidae was the most species-rich family, comprising 110 species and 482 individuals across 12 tribes. The remaining families included Riodinidae (253 individuals, 43 species, and 9 tribes), Lycaenidae (139, 29 species, and 2 tribes), Pieridae (30, 7 species, and 3 tribes), and Papilionidae (2 individuals, 1 species, and 1 tribe). The three most abundant species were all from the Nymphalidae family: *Hypothyris euclea* (385 individuals), *Hermeuptychia* sp. (165), and *Amiga arnaca* (89), followed by *Cecropterus (Thorybes) dorantes* (82) from the Hesperiidae family. We recorded 91 singletons (species represented by a single individual) and 54 doubletons (species represented by two individuals). No species was recorded across all 17 sampling fragments.

Butterfly species richness ($^0D$) and species diversity ($^1D$) were not explained by either local or landscape predictors, as the null model ranked among the best models ($\Delta AICc < 2$). However, the number of forest fragments positively affected butterfly abundance ($p < 0.05$), while negatively affecting the number of dominant species ($^2D$) ($p < 0.05$) (Figure 2A-B, Table S3). Regarding tribes, butterfly richness ($^0D$) was also not explained by either local or landscape predictors. While diversity ($^1D$) and the number of dominant species ($^2D$) were positively related to the number of forest fragments (Figure 2C-D, Table S3).

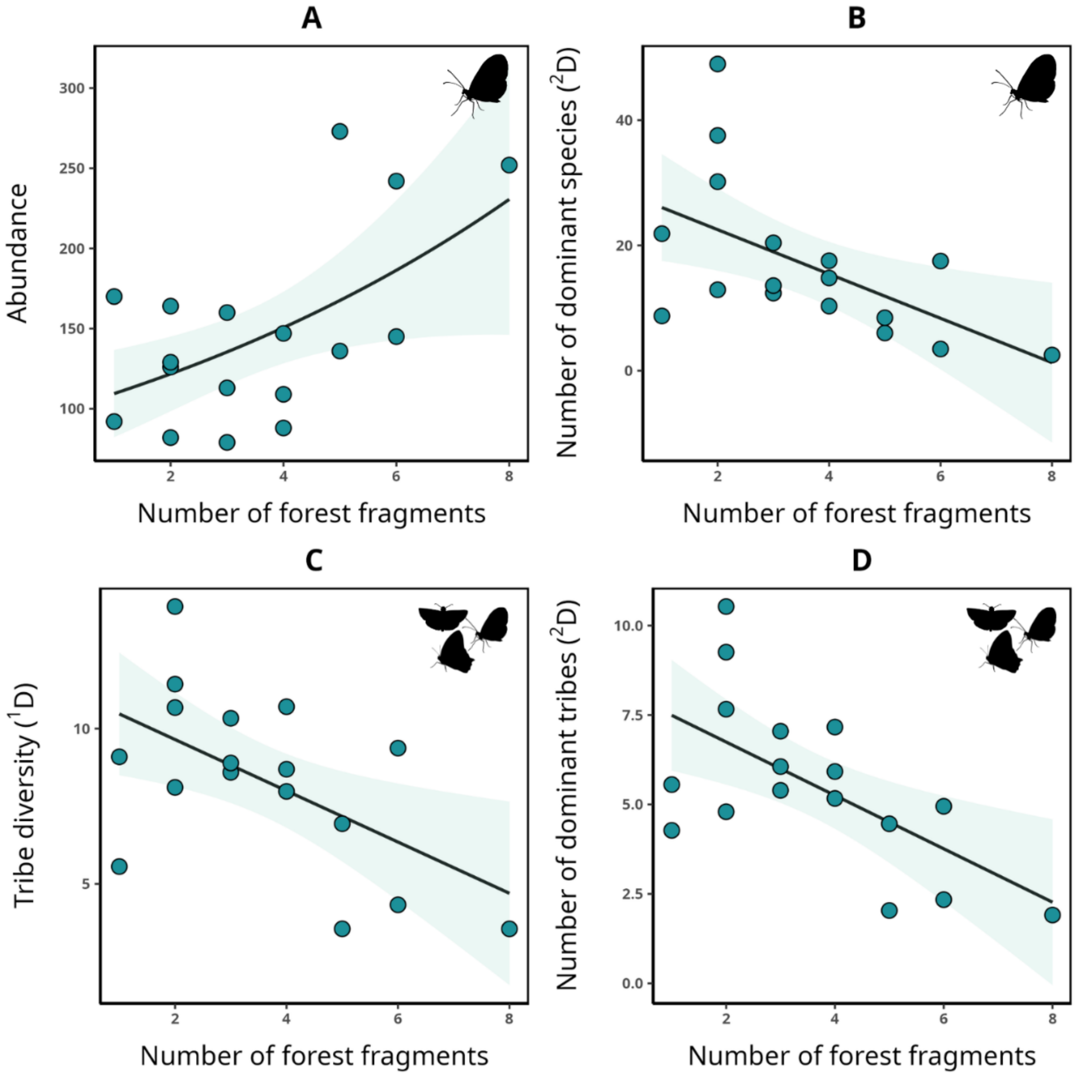


**Figure 2**: Relationships between the number of forest fragments and butterfly metrics in 17 Atlantic Forest fragments in southern Bahia, Brazil. Panels show the effects on abundance (A), number of dominant species ($^2$D) (B), tribe diversity ($^1$D) (C), and number of dominant tribes ($^2$D) (D). Shaded areas around the lines represent the 95% confidence intervals of the fitted models.

Regarding species, the sampling fragments exhibited a mean $\beta_{total}$ of 0.88 (±0.03 SD), with an average contribution of species turnover ($\beta_{repl}$) of 0.65 (±0.02), and differences in richness ($\beta_{rich}$) of 0.24 (±0.03). For tribes, sampling fragments had a mean total compositional dissimilarity ($\beta_{total}$) of 0.69 (±0.22 SD), explained mainly by tribe turnover ($\beta_{repl} = 0.41 \pm 0.17$), and with less importance by differences in richness ($\beta_{rich} = 0.27 \pm 0.14$).

In the cluster analyses based on species, the sampling fragments were grouped into two main clusters for all three dissimilarity components: $\beta_{total}$, $\beta_{repl}$, and $\beta_{rich}$ (Figure 3 A-C). In contrast, analyses based on tribes revealed three consistent clusters across all components of dissimilarity (Figure 3 D-F). The cophenetic correlation between the dendrograms and the dissimilarity matrices was above 0.80 for most cases, except for $\beta_{repl}$, which showed lower values: 0.51 for species and 0.54 for tribes.

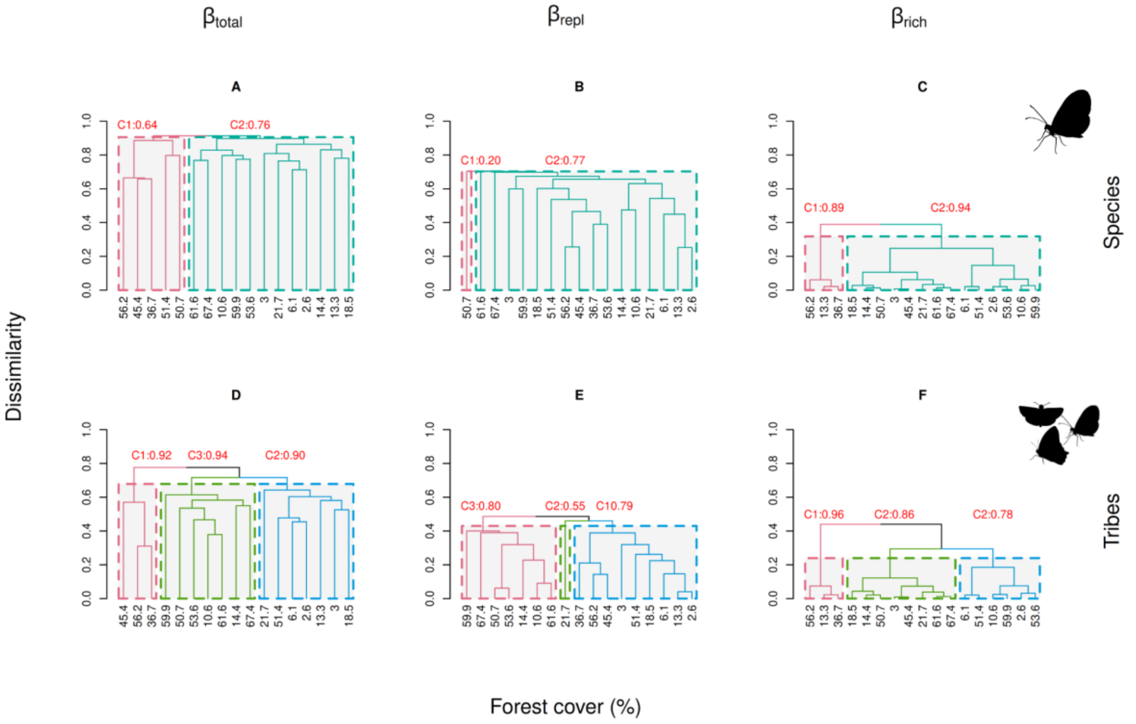


**Figure 3:** Clustering of fragments (represented by the percentage of landscape-scale forest cover) based on butterfly composition in 17 forest fragments in southern Bahia, Brazil. Top panels refer to species-level data; bottom panels to tribe-level data. Panels A and D show total dissimilarity ($\beta_{total}$); B and E show species turnover ($\beta_{repl}$); and C and F show richness differences ($\beta_{rich}$). Colors indicate clusters identified by the gap statistic method. Bootstrap support values (based on 1,000 replicates) are shown above each node.

The observed clustering was reflected in differences in the relative abundance of species and tribes among local communities (as seen in the heat map, Figure S3-S4). Furthermore, community structure and the identity of the dominant species and tribes within them also varied among groups, as evidenced by the range-abundance curves (Figure 4).

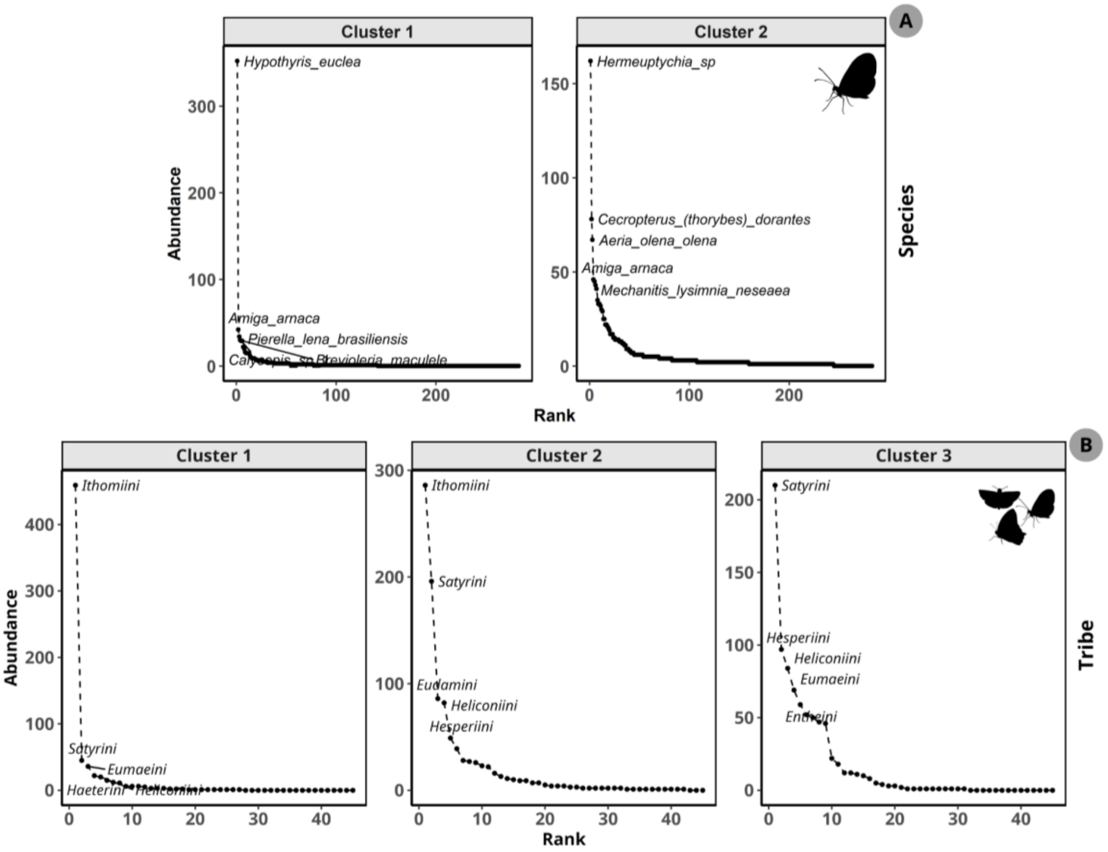


**Figure 4**: Rank-abundance curves for the clusters identified based on $\beta_{total}$ for butterfly species (A) and tribes (B) in 17 Atlantic Forest fragments in southern Bahia, Brazil. The identity of the five most abundant species and tribes in each group are shown.

Differentiation in species composition between sampling fragments was marginally significantly explained by forest cover (p-value = 0.08, Figure 5 A, model p-value < 0.01, explained deviation = 21.50%). While for the composition of tribes, the differentiation between them was marginally significantly explained by the number of forest fragments (p-value = 0.05, Figure 5 B, model p-value = 0.01, explained deviance = 23.46%) (Table S4).

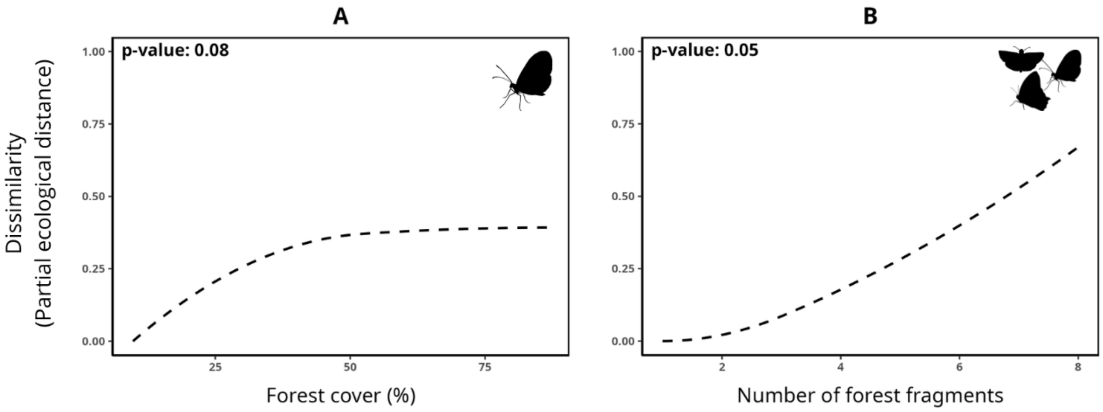


**Figure 5**: Splines of variables that most contributed to differences in butterfly composition among forest fragments in southern Bahia, Brazil, based on the Generalized Dissimilarity Model (GDM). Panel (A) shows species-level data and panel (B) shows tribe-level data. Dotted lines represent marginally significant relationships ($0.05 < p\text{-value} \leq 0.1$).

## Discussion

Here, we assessed the effects of habitat loss, fragmentation, and local habitat changes on butterfly communities in human-modified landscapes. We found that fragmentation, measured by the number of forest fragments in the landscapes, positively influenced butterfly abundance. However, this increase was accompanied by greater species and tribe dominance and reduced tribe diversity. These shifts were preceded by changes in both species and tribe composition. Although species and tribe richness varied little among sampling fragments, compositional differences were primarily driven by turnover, including changes in species relative abundance among localities. Forest cover best explained variation in species composition across sampling fragments, whereas the number of forest fragments was the most important predictor of differences in tribe composition.

### *Alfa diversity*

Fragmentation, measured by the number of forest fragments, increased abundance while decreasing diversity and increasing dominance of species and tribes. Moderate habitat disturbances, including fragmentation, however, can enhance butterfly diversity by creating new niches, edge effects, and altered energy flows, as well as releasing resources. The negative effects of even large-scale disturbances may be mitigated by genetic variation and metapopulation dynamics, which allow for cycles of expansion and contraction, species migration, and the colonization of new microsites (Brown 2005). In contrast, intense anthropogenic disturbance consistently results in a reduction of diversity (Brown 2005). Furthermore, disturbances, even when increasing richness and abundance, are known to drive compositional shifts (Rocha et al. 2013). These results may indicate that fragmentation simplifies butterfly communities by promoting the success of a few species that are particularly well adapted to disturbance.

Species and tribe richness were not affected by landscape and local variables (forest cover, number of forest fragments, edge density, and vegetation structure), suggesting that even highly fragmented, low-forest areas can still support species-rich butterfly communities. This finding aligns with the observation that butterflies track their host plants, meaning habitat amount does not directly determine butterfly richness (MacDonald et al. 2018). Additionally, the region has experienced a long history of anthropogenic disturbance, with increased deforestation since the mid-1980s (Rocha-Santos et al. 2017), which may have already led to the local extinction of species sensitive to forest loss and fragmentation. As a result, a process of community homogenization may be underway, in which only those species and tribes that exhibit some level of resistance to disturbances persist. The communities persisting in studied landscapes differ mainly in their relative abundances and composition rather than in species richness. This could explain the lack of significant effects of the predictor variables on species richness and the significant effects on abundance and dominance, as changes in relative abundance may be more strongly influenced by landscape features such as fragmentation and potentially by the availability of host plants. Abundance is particularly relevant because fragments with many rare species are more prone to local extinctions.

### *Beta diversity*

Our cluster analyses showed two species groups. The first group was dominated by a single species, *Hipothyris euclea*, while the second was more equitable, dominated by *Hermeupthychia* sp., *Cecropterus dorantes, Amiga anarca, Aeria olena olena,* and

*Mechanitis lysimnia naseae*. Regarding tribes, three groups were formed: the first dominated by Ithomiini, the second by Ithomiini and Satyrini, and the third by Satyrini. The Ithomiini tribe is a Neotropical group of butterflies with a wide distribution. These butterflies are often abundant, conspicuous, and easily sampled. Mainly species use plants of the Solanaceae family as larval hosts. All Ithomiini are unpalatable and exhibit aposematic coloration. Their unpalatability stems from pyrrolizidine alkaloids acquired primarily by adult males feeding on withered Boraginaceae and Asteraceae (Willmott and Freitas 2006). Although Ithomiinis are persistent in disturbed environments, they need nearby forests and high humidity to thrive (Brown and Freitas 2002). Satyrini caterpillars primarily feed on grasses of the family Poaceae (Peña et al. 2006) while adults consume fermented fruits, plant sap, and other decaying materials (DeVries 1987). The high abundance of Ithomiini indicates a prevalence of alkaloid-rich plant species such as Solanum, Eupatorium, and various Boraginaceae flowers, in addition to rich forest edges. Conversely, the abundance of *Hermeupthychia* and Satyrini suggests a significant level of habitat disturbance and the proximity of grasses (Brown and Hutchings 1997). These patterns of separation, observed both at the species and tribe levels, suggest a clear turnover in the butterfly groups present across the evaluated landscapes. In some fragments, communities are clearly dominated by disturbance-tolerant species that nonetheless require forest remnants for reproduction (i.e., Ithomiini). In contrast, other areas are dominated by species typically associated with open habitats (i.e., Satyrinae), which reproduce primarily on grasses and herbaceous plants. Interestingly, the separation based on tribes reveals intermediate conditions, where both Ithomiini and Satyrinae occur in relatively similar proportions, likely reflecting landscapes with a more balanced mixture of open areas and forest remnants.

Our beta diversity analysis for species revealed a high value (0.88) among the sampled forest fragments. This difference is primarily attributed to species turnover (0.65). This high beta diversity suggests significant habitat heterogeneity across the sampled forest fragments. Since our analysis also considered abundance, the turnover further indicates differences in the relative abundances of species. Conversely, beta diversity for richness was low (0.24), indicating that our sampling fragments harbored similar numbers of species. Our final GDM partially explained these differences in species composition among the sampled forest fragments (21.5%). This pattern is consistent with the results from the alpha diversity analysis, where we found no relationship between species richness and the explanatory variables. Additionally, most of the beta diversity was explained by species turnover between forest fragments, as found by Pereira et al. (2017). Together, these findings suggest that the number of species across the landscapes remains relatively constant, while it is the identity of species and their relative abundances that respond to environmental variables within each landscape. One possible explanation is that specialist species may persist in disturbed fragments at very low abundances, which could compromise their long-term viability even though their presence still contributes to species richness.

Dissimilarity in species composition did not follow a linear trend along the forest cover gradient. Although the best model for species incorporated all explanatory variables (i.e., forest cover, number of forest fragments, edge density, vegetation structure, and geographic distance), forest cover emerged as the most influential variable within the model, and the only one with a marginally significant effect. Dissimilarity increased linearly with forest cover up to approximately 45% coverage, after which it exhibits little variation (asymptotic pattern). This suggests that species composition differs markedly between fragments with low (< 45%) and high (> 45%) forest cover. However, among fragments with similarly high forest cover (> 45%), differences in species composition are minimal. Thus, landscapes with more than 45% of forest cover can support similar butterfly communities without substantial species loss or alterations in relative abundances. Conversely, communities in landscapes with less than 45% of forest cover already exhibit considerable differentiation due to the replacement of species, likely forest specialists by generalist or open-area species, alongside an increase in the abundance of a few dominant species. This finding suggests that landscapes with less than 45% of forest cover may be insufficient to sustain butterfly forest-dependent communities. Although these landscapes can support a species richness comparable to that of more forested habitats, they primarily function as habitats for butterflies associated with open areas, as well as generalist species that are more tolerant of disturbance.

Fragmentation significantly influenced tribe composition. Beta diversity for tribes was relatively high (0.69 ± 0.22 SD), with turnover (0.41) contributing more than richness differences (0.27). The best model for tribes included the same variables as for species, but the number of forest fragments was the strongest and the only marginally significant predictor of compositional dissimilarity. Dissimilarity increased nearly linearly with the number of forest fragments. These findings suggest that fragmentation promotes compositional differentiation among butterfly communities. In light of the alpha diversity analyses, which show a negative effect of fragmentation on diversity and the effective number of dominant tribes, we suggest that fragmentation simplifies butterfly communities. As fragmentation increases, communities tend to be dominated by a smaller number of tribes, resulting in highly uneven assemblages that differ markedly in composition from those in more forested landscapes. In such fragmented environments, only a few taxonomic groups are able to persist at high abundances.

## Conservation implications

Particularly in the Brazilian Atlantic Forest, one of the most threatened biomes on the planet, there is a specific law (Brazilian Forest Code) requiring rural properties to maintain at least 20% forest cover to ensure the preservation of biodiversity and the provision of vital ecosystem services for human well-being, such as water quality and pollination (Soares-filho et al. 2014). Our findings demonstrate that although landscapes with minimal forest cover can sustain rich and abundant butterfly communities, 20% forest coverage is insufficient to maintain butterfly assemblages as found in areas with extensive forest cover. Our results indicate that the composition of butterfly communities remains stable, or exhibits minimal change, in areas with more than 45% forest cover. Therefore, we suggest that a minimum forest cover of 45% is required to maintain diverse forest communities. Other studies have shown that the value of 20% is insufficient for maintaining the biodiversity of distinct groups, such as birds (Morante-Filho et al. 2021) and woody plants (Rocha-Santos et al. 2016), and consequently their ecological functions. Therefore, future research that integrates all these lines of evidence regarding the need for higher percentages of conserved forest in regional landscapes is crucial. Such efforts are essential to building a solid scientific foundation upon which effective public policies can be developed to safeguard and restore the remaining forested landscapes in the region.

Regarding environmental monitoring, the use of butterfly tribes to identify ecological patterns proved effective. While species and tribe-level metrics responded similarly to fragmentation in terms of alpha diversity, tribe diversity exhibited an additional response: it declined significantly with increasing fragmentation. In tropical rainforests, butterfly populations tend to occur at low densities, species pools are large, and cryptic species are frequently common (Basset et al. 2012). The use of butterfly tribes in environmental monitoring efforts may reduce misidentification errors (Uehara-Prado et al. 2009) and enable field-based identification followed by specimen release.

Our study highlights the role of fragmentation, and to a lesser extent, forest cover, as key forces shaping the composition of species that persist in human-modified landscapes. While fragmentation is often associated with habitat loss, the increase in the number of fragments exacerbates conditions for many species (e.g., by intensifying edge effects or hindering connectivity between distant patches), acting as a strong environmental filter that leads to the simplification of butterfly communities. Similarly, forest cover also operates as an environmental filter, likely through its influence on the availability of host plants.

In addition to these findings, our study raises further questions about how other dimensions of biodiversity may be affected by landscape change. For example, while we observed that the most abundant species and tribes belonged to the family Nymphalidae, it remains unclear whether fragmentation increases phylogenetic or lineage-level dominance within butterfly communities. If closely related lineages are disproportionately favored in fragmented landscapes, this could indicate a loss of evolutionary diversity and functional redundancy. Future studies should explore whether phylogenetic diversity declines as a result of fragmentation in Atlantic forest and whether such losses are associated with the disappearance of specific ecological functions. Identifying which functional traits are retained or lost in fragmented landscapes will be critical for understanding the long-term implications of community simplification on ecosystem functioning and resilience.

## Acknowledgements

We want to thank everyone who assisted us with the fieldwork. We also thank André Victor Lucci Freitas, Augusto Rosa, Eduardo Barbosa, Diego Dolibaina, Luísa Mota, and Ricardo Siewert for butterfly identification. We also thank Larissa Rocha-Santos for the data of vegetation structure. GCNP thanks the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for her doctorate scholarship. We also want to thank the Fundo Brasileiro para a Biodiversidade (FunBio nº 025/2023), The Rufford Foundation (nº 36969-1), and the Pró-Reitoria de Pesquisa e Pós-Graduação da Universidade Estadual de Santa Cruz (073.11010.2023.0028633-11) for the grants. Authorization (ICMBio 80610-3) conceived by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/SISBIO).

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## Supplementary Information

## Alpha and Beta diversity of Butterflies in Atlantic Forest remnants

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**Table S1**: Environmental variables and their correlation with the first axis derived from the PCA ordination.

| **Variable** | **PC1** |
|---|---|
| Mean tree height | 0.601365 |
| Maximum tree height | 0.580513 |
| Mean DAP | 0.473937 |
| Canopy openness | -0.277036 |

**Table S2**: Butterfly species per sampled Forest fragment in southern Bahia, Brazil.

Observação: Disponível mediante solicitação à autora através do e-mail geannepereira@gmail.com.

**Table S3**: Best-supported models (ΔAICc < 2) for each alpha diversity metric. Among them, the most parsimonious model was chosen as the top model. k: number of parameters, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: Difference in AICc relative to the best model, weight: model weight.

**Abundance**

| **Model – Distribution family: Negative binomial** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 183.65 | 0 | 1 |

**Species richness ($^{0}$D)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| **Null model *** | 2 | 154.23 | 0 | 0.45 |
| Forest cover | 3 | 154.74 | 0.50 | 0.35 |
| Number of forest fragments | 3 | 155.95 | 1.72 | 0.19 |

**Species diversity ($^{1}$D)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 145.03 | 0 | 0.73 |
| **Null model *** | 2 | 147.01 | 1.98 | 0.27 |

**Number of dominant species ($^{2}$D)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 133.92 | 0 | 1 |

**Tribes richness ($^{0}$D)**

| **Model – Distribution family: Poisson** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Forest cover | 2 | 98.52 | 0 | 0.51 |
| **Null model *** | 1 | 98.63 | 0.12 | 0.49 |

**Tribes diversity ($^{1}$D)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 84.20 | 0 | 0.51 |
| Forest cover + Number of forest fragments | 4 | 84.31 | 0.11 | 0.49 |

**Number of dominant tribes ($^{2}$D)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 75.93 | 0 | 1 |

**Table S4**: Top models (GDM).

| **Scale** | **Predictor variables** | **Variable relative importance** | **Variable p-value** | **Model p-value** | **Explained deviance** |
|---|---|---|---|---|---|
| **Species** | Forest cover (%) | 26.687 | **0.079** | 0.001 | 21.504 |
| | Number of forest fragments | 2.811 | 0.472 | | |
| | Edge density | 3.356 | 0.496 | | |
| | Geographic distance | 12.483 | 0.119 | | |
| | Vegetation structure (PC1) | 15.527 | 0.154 | | |
| **Tribes** | Forest cover (%) | 10.962 | 0.232 | 0.013 | 23.462 |
| | Number of forest fragments | 65.472 | **0.05** | | |
| | Edge density | 1.828 | 0.585 | | |
| | Geographic distance | 12.483 | 0.119 | | |
| | Vegetation structure (PC1) | 1.037 | 0.649 | | |

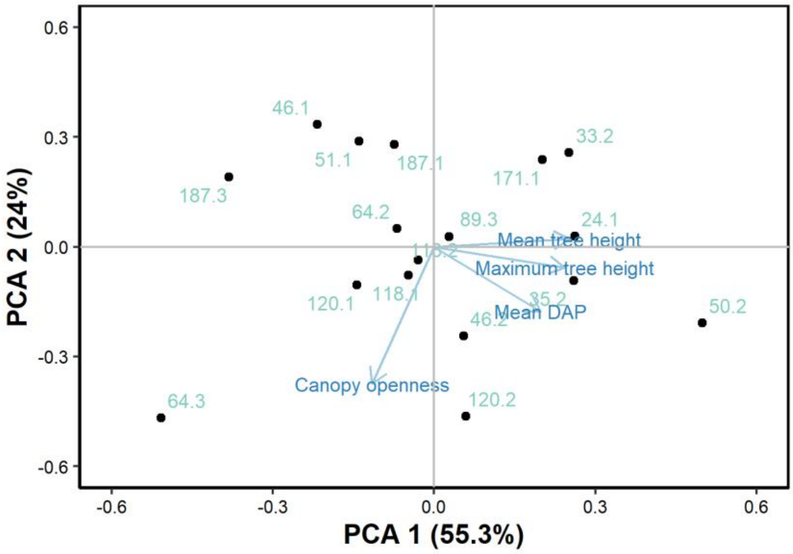


**Figure S1**: Biplot of the first two axes from a PCA ordination of local habitat structure variables across sampling forest fragments.

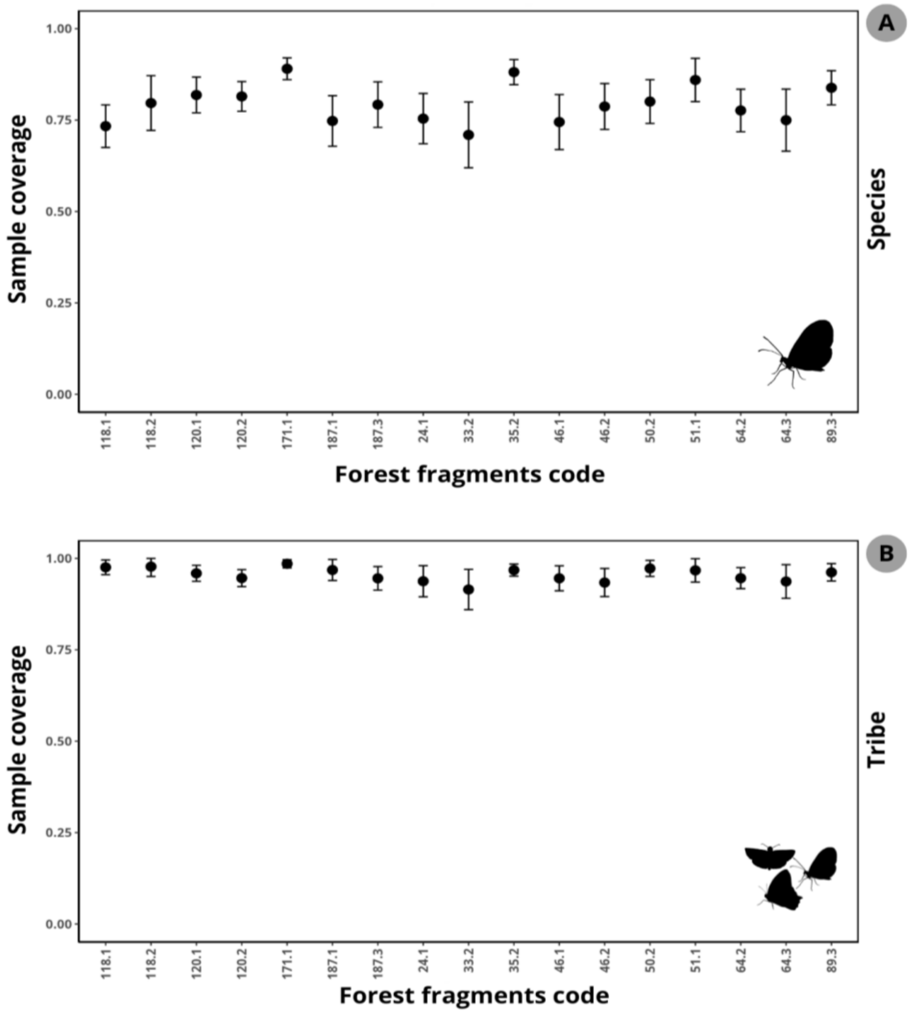


**Figure S2**: Sampling coverage of species (A) and tribes (B) of butterflies) in 17 Atlantic Forest fragments in southern Bahia, Brazil.

**Figure S3**: Heat map of butterfly species abundance by forest fragment in southern Bahia, Brazil. Cluster numbers correspond to the groups identified in Figure 3A**.** Darker shades indicate greater relative abundance of each species at the corresponding site. The numbers on the right indicate the percentage of forest cover measured within a 1 km buffer of each forest fragment.

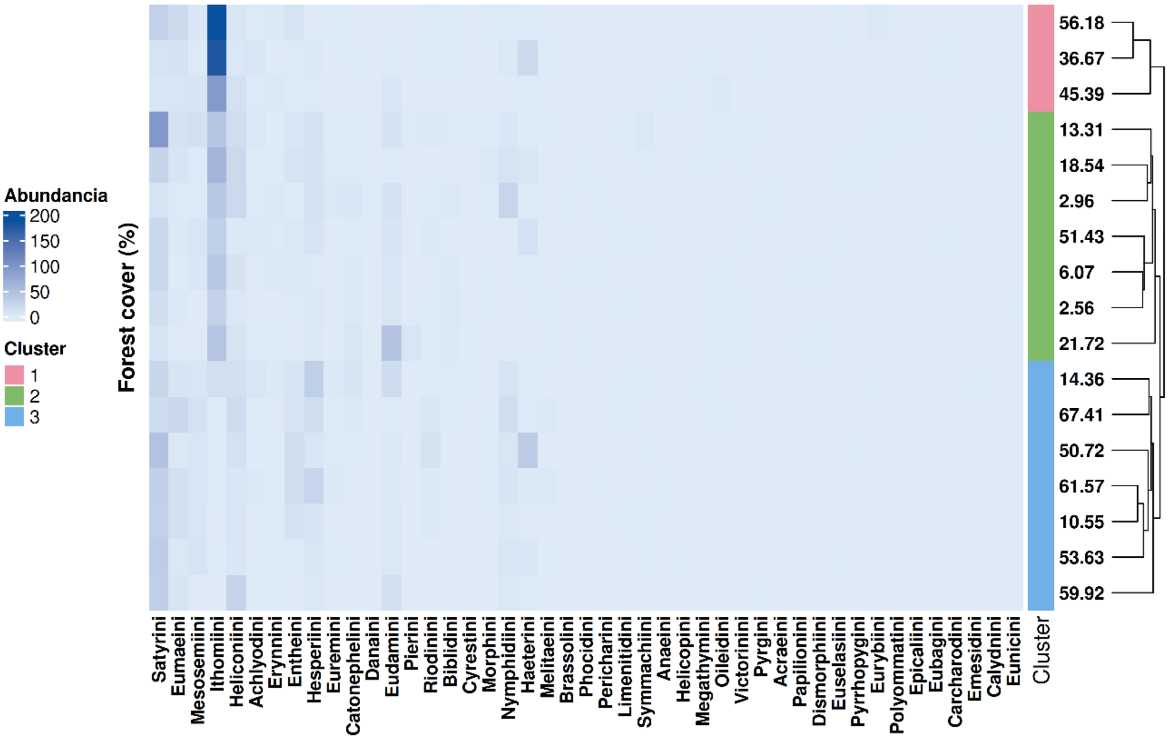
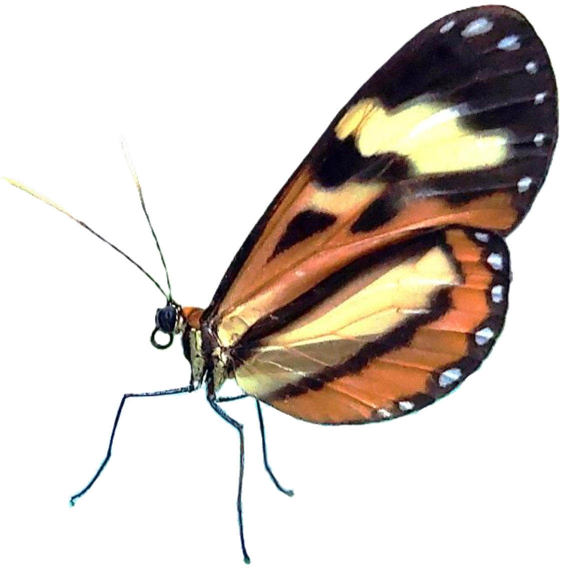


**Figure S4**: Heat map of tribe abundance by forest fragment in southern Bahia, Brazil. Cluster numbers correspond to the groups identified in Figure 3D**.** Darker shades indicate greater relative abundance of each tribe at the corresponding site. The numbers on the right indicate the percentage of forest cover measured within a 1 km buffer of each forest fragment.

## Capítulo 3

# Forest loss or fragmentation *per se*? Drivers of Nymphalidae butterfly diversity in fragmented landscapes

Artigo preparado para submissão na revista *Landscape Ecology*



# Forest loss or fragmentation *per se*? Drivers of butterfly diversity in fragmented landscapes

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## Abstract

### *Context*

Land-use changes driven by intensive agriculture and urbanization are leading causes of global biodiversity loss, with severe consequences in tropical regions, where deforestation rates are highest. These transformations result in structural changes, such as habitat loss and fragmentation, which reduce the size and connectivity of native habitats. Landscape changes also alter the local structure of forest remnants, and these factors may synergistically influence biological diversity.

### *Objectives*

We examined how landscape forest loss and fragmentation *per se* (fragmentation independent of habitat loss), along with local habitat structure, influence the diversity of Nymphalidae butterfly communities in remnants of the Atlantic Forest. We evaluated whether trophic guild (nectar- vs. fruit-feeding) and habitat affinity (forest-dependent vs. disturbance-adapted) mediate these responses.

*Results*

Species richness and diversity were primarily explained by landscape forest cover, which positively affected nectar-feeding and disturbance-adapted species. In contrast, butterfly abundance was mainly driven by fragmentation *per se*, which had a positive effect on most groups, except for forest-dependent species, whose abundance was unaffected.

*Conclusions*

Our findings underscore the importance of considering landscape-scale processes and multiple ecological dimensions when evaluating butterfly responses to habitat changes. The study also highlights the ecological value of forest fragments in highly human-modified landscapes and underscore the importance of considering both forest loss and fragmentation *per se* in conservation planning.

**Keywords**: Fragmentation, Habitat amount, Atlantic Forest, Nymphalidae, Tropical Forest, Edge effect.

## Introduction

Land-use changes driven by intensive agriculture and urbanization are leading causes of global biodiversity loss, with severe consequences in tropical regions, where deforestation rates are highest (Curtis et al. 2018; Jaureguiberry et al. 2022). In 2023 alone, 23.9 million hectares of natural forest were lost, including 3.7 Mha of primary tropical forests (Global Forest Watch 2024). No tropical rainforest remains untouched by human activities (Willis et al. 2004). These transformations result in structural changes, such as habitat loss and fragmentation, which reduce the size and connectivity of native habitats (Haddad et al. 2015). In turn, this limits access to resources, isolates populations, and erodes genetic diversity. Beyond biodiversity loss, these structural changes compromise key ecosystem services, including pollination, nutrient cycling, seed dispersal, and biological pest control (Millennium Ecosystem Assessment 2005; Díaz et al. 2006).

Habitat loss is widely recognized as one of the leading drivers of global biodiversity decline (Brooks et al. 2002). While its ecological effects have been extensively studied, the impacts of habitat fragmentation *per se* (the effects of fragmentation independent of habitat amount) remain less understood and are still subject to considerable debate (Fahrig 2017; Fletcher et al. 2018; Fahrig et al. 2019). However, when disentangled from habitat amount, the effects of fragmentation *per se* are found to be neutral or even positive (Fahrig 2017). Still, decades of empirical evidence consistently show that species diversity across a range of taxa is strongly associated with the maintenance of extensive native habitat at the landscape scale (Püttker et al. 2020). Reductions in forest cover have a detrimental effect on the diversity of several groups (Newbold et al. 2015; Watling et al. 2020), including woody plants (Rocha-Santos et al. 2016), bats (Falcão et al. 2021), mammals (Rios et al. 2021), birds (Morante-Filho et al. 2021), and insects such as dung beetles (Souza et al. 2020) and butterflies (Viljur et al. 2020).

As forest cover declines, structural changes at the landscape scale can lead to profound local modifications within the remaining forest fragments. Continuous forests are replaced by smaller, isolated patches that undergo a series of cascading effects (Tabarelli et al. 2004), including changes in local forest structure (Rocha-Santos et al. 2016). Fragment edges are exposed to stronger winds, higher temperatures, and lower humidity (Magnago et al. 2015). As a result, forest fragments in deforested landscapes tend to exhibit lower tree richness and density, smaller-diameter and shorter trees, reduced basal area, and greater canopy openness (Oliveira et al. 2008; Rocha-Santos et al. 2016). These structural shifts are driving a retrogressive succession process, in which tree assemblages are transformed through the loss of large trees and the increasing dominance of disturbance-adapted species (Santos et al. 2008). This process results in forest communities that retain lower biomass over time, with long-term consequences for ecosystem functioning and the resources available to a wide range of organisms. Also, the microclimatic changes due to the increased light penetration create drier and warmer environments that can benefit certain taxonomic groups whose metabolism depends heavily on solar exposure, such as some reptiles (Pike et al. 2011) or insects like lepidopterans (Weerakoon et al. 2015; Pereira et al. 2017), while simultaneously reducing habitat suitability for more forest-dependent species, including arboreal fauna (Cudney-Valenzuela et al. 2023).

Butterflies are widely recognized as effective bioindicators due to their sensitivity to environmental changes, including subtle shifts in microclimate and vegetation structure (Brown Jr. 1997; Uehara-Prado et al. 2009). Previous studies have demonstrated that both local habitat conditions and landscape-level characteristics significantly influence butterfly communities

(Öckinger and Smith 2006; Viljur et al. 2020). Additionally, several studies have highlighted the importance of considering landscape context when evaluating patterns of butterfly diversity (Öckinger and Smith 2006; Oliver et al. 2010; Brito et al. 2014). However, relatively few studies have specifically assessed the effects of forest loss at the landscape scale, with findings ranging from adverse (Viljur et al. 2020) to neutral effects (Brito et al. 2021). Most existing research has focused on the impacts of patch-scale metrics, such as patch size (Krauss et al. 2003; Soga and Koike 2012; Melo et al. 2019) or land-use change, comparing forested areas with various agricultural matrices (Barlow et al. 2007; Lucey and Hill 2012; Norfolk et al. 2017). Studies that explicitly evaluate the effects of fragmentation *per se*, independent of habitat loss, on butterfly assemblages remain scarce (e.g., Brito et al. 2021). This distinction is crucial, as habitat loss and fragmentation do not always coincide and can have contrasting ecological consequences (Fahrig 2003, 2017), affecting both community-level dynamics and specific functional and trophic groups (Öckinger et al. 2010; Brito et al. 2014).

In this study, we investigate how landscape forest loss and fragmentation *per se*, along with local habitat structure, influence the diversity of butterfly communities in remnants of the Atlantic Forest. We further assess how these factors affect butterfly groups differently based on their trophic and habitat preferences. Focusing on the Nymphalidae family, we aim to identify the main drivers of species richness, diversity, and abundance. We hypothesize that forest loss is the primary determinant of butterfly diversity. Specifically, we predict that greater amounts of remaining forests positively influence butterfly richness and diversity, as increased habitat availability is known to support more species (Fahrig 2013; Viljur et al. 2020). Moreover, we expect differential responses among functional groups: forest-dependent species should decline in response to forest loss whereas disturbance-adapted species might likely benefit. Regarding fragmentation *per se* (measured as edge amount and the number of fragments), we predict a positive influence on butterfly diversity, as fragment edges may create heterogeneous microclimatic conditions that can support high butterfly richness (Lourenço et al. 2019). Finally, we anticipate that local habitat structure further shapes butterfly communities, with forests characterized by more open canopies and larger trees supporting higher butterfly diversity due to increased structural complexity and resource availability (Neal et al. 2024).

## Methods

### *Study area*

The study was conducted in forest remnants of the Atlantic Forest located in southern Bahia, Brazil, within the municipalities of Belmonte, Canavieiras, Mascote, and Una (15˚0'–16˚0' S and 39˚0'–39˚30' W) (Figure 1). The region is one of the three main endemic areas of the Atlantic Forest biome and is characterized by some of the highest deforestation rates. The territory lost 4,717 hectares of native forest in 2024 alone, mainly due to conversion into pasture and agricultural land (SOS Mata Atlântica and INPE 2025). Deforestation in the study area began in the mid-1980s and accelerated during the 1990s due to the cocoa crisis (Rocha-Santos et al. 2017). Currently, the region features a heterogeneous landscape composed of various land uses, including pastures, cacao plantations (*Theobroma cacao*), and rubber tree plantations (*Hevea brasiliensis*) (Pardini 2004). The climate is hot and humid, with no distinct dry season (Alvares et al. 2013), an annual mean temperature of 24°C, and an average annual precipitation of 1,800 mm (Thomas et al. 1998).

The study was conducted in 17 forest fragments that had been previously surveyed by researchers from REDE SISBIOTA, a research project that evaluated the impact of deforestation on biodiversity patterns and processes in southern Bahia (for further details, see Faria et al. 2023, and Table S1). These fragments share similar floristic characteristics but are embedded in different landscapes.

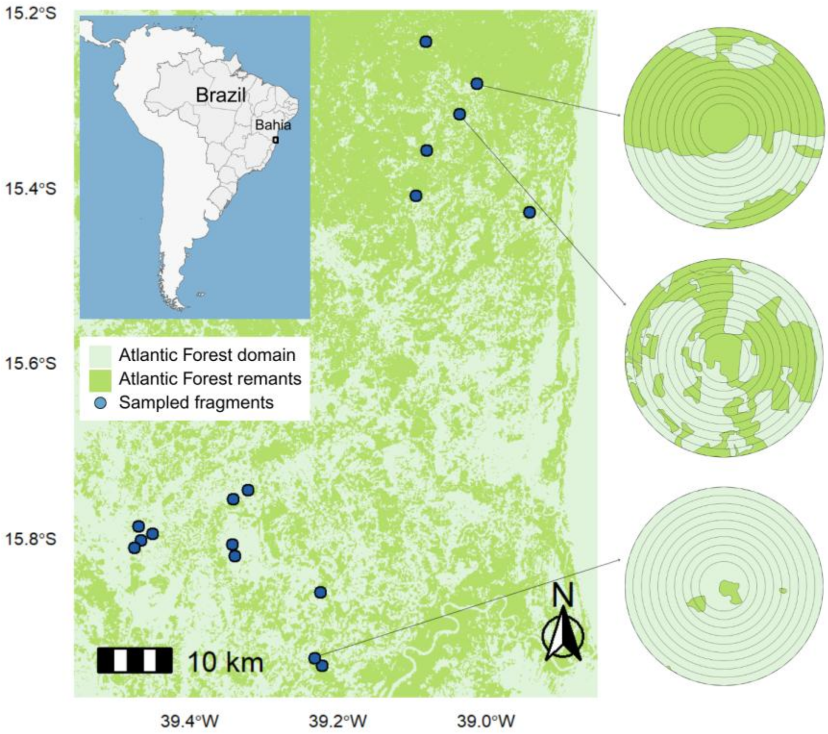

**Figure 1**: Location of the 17 forest fragments surveyed in southern Bahia, Brazil. The sampled fragments are shown in blue. A detail of some of the sampled landscapes is shown on the right. The circles show the entire tested radius (300 to 1,200 m) and highlight the forest cover (dark green areas). The images of the forest cover were obtained from the MapBiomas (2023). Map projection: Albers Equal Area Conic.

### *Butterfly Survey*

Fieldwork was conducted in four campaigns during 2023 (January-February, April-May, July-August, October-November), to capture seasonal variation. In each campaign, each forest fragment was sampled on alternate days for two hours in two time slots, viz., 09:00-12:00, 12:00-15:00 hours, covering the whole period of butterfly activity. Each two-hour sampling involved two researchers walking along pre-existing trails in search of butterflies. Observed individuals were captured using entomological nets, immediately sacrificed, and stored in glassine envelopes for later identification. Each envelope was labeled with the specimen's collection date, time, and sampling forest fragment. We collected individuals from all butterfly families, although we used only Nymphalidae for further analyses. Nymphalidae is the most representative family of butterflies in our study.

In the laboratory, some specimens were mounted with wings spread and secured with entomological pins to facilitate identification. All individuals were identified to the lowest possible taxonomic level using identification guides (Uehara-Prado et al. 2004; Warren et al. 2017), with additional verification provided by specialists as necessary. Part of the material was sent to LABBOR (Unicamp - Campinhas, Brazil), and the remaining specimens are deposited at LABINT, at UESC (Ilhéus – Brazil).

### *Butterfly Classification*

All Nymphalidae species were classified according to their disturbance tolerance as either disturbance-adapted or forest-dependent, and by feeding guild as nectar-feeding or fruit-feeding. To classify disturbance tolerance, we relied on previous studies (Brown and Freitas 2000; Uehara-Prado et al. 2005; Brito et al. 2014; Sant'Anna et al. 2014; Filgueiras et al. 2019; Shirey et al. 2022), as well as on expert criteria. Based in these studies, species reported within the forest interior, regardless of whether they were preserved or secondary forest, were classified as forest-dependent. In contrast, species reported on forest edges, in open areas, or other biomes, excluding those in the Amazon, were classified as disturbance-adapted. For species with no available information in the literature or with ambiguous classification, we assigned the most frequent classification observed among their closest phylogenetic relatives according to TimeTree 5 phylogeny (Kumar et al. 2022; Moura et al. 2024).

### *Landscape predictors*

We used a patch-landscape approach (Fahrig 2013), in which response variables (butterfly richness, diversity, and abundance) were sampled within the forest fragment, and landscape predictors were calculated in multiple concentric buffers ranging from 300 to 1200 m, in 100-m increments, from the center of sampling site in each forest fragment. Using high-resolution satellite imagery, we extracted the percentage of native forest cover, edge density, and the number of forest fragments of each forest fragment to characterize the surrounding landscape (see Faria et al. 2023). These metrics were selected because forest cover (used here as a proxy for habitat amount) is the most important metric of landscape composition. In contrast, the other metrics (edge density, and the number of forest fragments) are commonly used to assess landscape configuration and are strongly associated with habitat fragmentation

(Fahrig, 2003). Buffers smaller than 300 m were deemed unfeasible due to the size of the sampled trails, while those exceeding 1200 m were avoided to prevent spatial overlap between landscapes. When counting the number of fragments, if a single fragment appeared multiple times within smaller buffers, it was counted only once. All spatial analyses were conducted using the R packages *terra* and *tidyterra* (R Core Team 2025; Robert and Hijmans 2025; Hernangómez et al. 2025).

### *Local variables*

To characterize vegetation structure at each forest fragment, we used mean and maximum tree height and mean diameter at breast height (DBH) (data from Rocha-Santos et al. 2017). In addition, we measured canopy openness and vegetation structure. During the initial visit to each sampling forest fragment, hemispherical photographs were taken using a fisheye lens attached to a digital camera. Canopy photographs were captured every 20 m along the trails, at a height of 1.5 m above the ground. The images were processed by calculating the proportion of white and black pixels. The average canopy openness for each sampling forest fragment was calculated by averaging all photographs taken at that forest fragment, providing a single value per sampling event. These data were collected throughout all butterfly sampling periods in each campaign. Image processing was conducted in the R environment (R Core Team 2025).

### *Data analysis*

Butterfly diversity was estimated using Hill numbers (Hill 1973; Jost 2006; Chao et al. 2021). Specifically, we use zero-order diversity ($^0$D), which corresponds to species richness, and one-order diversity ($^1$D), which corresponds to the effective number of abundant species, equivalent to Shannon's exponential diversity. Hereafter, we refer to this measure ($^1$D) as "diversity" (Jost 2006). The Hill numbers was estimated for: (i) all Nymphalidae butterflies, (ii) nectar-feeding, (iii) fruit-feeding, (iv) forest-dependent, and (v) disturbance-adapted species. To minimize bias in diversity estimates caused by variations in sampling coverage across forest fragments, feeding guilds, and habitat preferences, we applied the interpolation–extrapolation protocol of Chao and Jost (2012) to estimate diversity orders for each fragment or fragment–feeding guild/habitat preference combination. All diversities estimates was standardized to a common level of sample coverage, calculated as twice the observed abundance for each forest fragment, with the lowest value serving as the reference (Chao et al. 2014; Hsieh et al. 2016) (Figure S1 and Table S3). Combinations in which a fragment–feeding guild or fragment–habitat preference resulted in less than three species were excluded, due to the sampling coverage was deemed to be inadequate, thus rendering it impossible to estimate diversity. Additionally, fragments with sampling coverage below 0.5 were excluded to reduce noise introduced by undersampling. All diversities estimates were performed using the R package iNEXT (Hsieh et al. 2016; R Core Team 2025).

To assess potential collinearity among the predictor variables (forest cover, edge density, number of forest patches), we computed Spearman's rank correlation coefficients (Quinn and Keough 2002). As no significant correlations were found, none of the variables were excluded. Then, we evaluated the scale of effect, i.e. the spatial scale at which landscape predictors (forest cover, edge density and number of forest patches) most strongly influence the response variables: richness ($^0D$), diversity ($^1D$) and, abundance of (i) all Nymphalidae butterflies, (ii) nectar-feeding, (iii) fruit-feeding, (iv) forest-dependent and (v) disturbance-adapted species. We adopted this approach because the spatial scale at which landscape variables affect ecological responses cannot be determined a priori and may significantly influence the observed relationships (Jackson and Fahrig 2015). To account for this, we fitted generalized linear models (GLMs) for each landscape predictor using Gaussian distributions for $^0D$ and $^1D$, and a negative Binomial distribution for abundance. The response variable was modelled as a function of buffer sizes ranging from 300 to 1200 m, in 100-m intervals. Subsequently, we evaluated the effect of each potential model, with a single explanatory variable, on the response variable and ranked them based on their corrected Akaike Information Criterion (AICc) using the "dredge" function from the MuMin package (Bartoń 2025).

We summarized all local variables (mean and maximum height of tree, DBH, and canopy openness) into a single metric of habitat structure using Principal Component Analysis (PCA). Only the first principal component was retained, which explained 55.3% of the total variance. The first axis of the PCA was negatively related to canopy openness and positively related to mean and maximum tree height and mean diameter at breast height (DBH) (Figure S2 - Table S2).

To evaluate the effect of landscape predictors and habitat structure on Nymphalidae butterflies, we fitted generalized linear models (GLMs) using Gaussian distributions (for $^0D$

and $^{1}D$) and negative binomial (for abundance). The model was inspected to ensure that residuals did not exhibit overdispersion, showed no clear patterns of heteroscedasticity, and followed a uniform distribution (Florian Hartig et al. 2024). Additionally, variables with high variance inflation factors (VIF) were removed (Zuur et al. 2009; Florian Hartig et al. 2024). When the confidence intervals of the VIF values for two or more high-VIF variables overlapped, we tested alternative global models by sequentially removing one variable at a time. We selected the most parsimonious model using AICc. Among the models with $\Delta AICc \leq 2$, we chose the simplest one, based on the principle that simpler models are generally more plausible. When the null model was present among those with the smallest delta, it was selected (Table S4) (Burnham and Anderson 2002; Zuur et al. 2009; Richards 2015). To evaluate fragmentation *per se*, we assessed whether models including a fragmentation variable (either edge density or the number of forest fragments), along with forest cover, yielded a better fit (i.e., lower AIC) compared to models including only forest cover. When this occurs, it indicates that fragmentation has an effect independent of forest cover (Watling et al. 2020).

## Results

We collected a total of 1,605 Nymphalidae individuals, belonging to eight subfamilies (Biblidinae, Charaxinae, Cyrestinae, Danainae, Heliconiinae, Limenitidinae, Nymphalinae, Satyrinae), 18 tribes, and 88 species. Regarding trophic guilds, we collected 39 nectar-feeding species (979 individuals) and 49 fruit-feeding species (626 individuals). We collected 35 forest-dependent species (451 individuals) and 52 disturbance-adapted species (1147 individuals) (Table S5). The most abundant species were *Hypothyris euclea* (Danainae) with 385 individuals (23.9%), followed by *Hermeuptychia* sp (Satyrinae) with 165 individuals (10.2%) and *Amiga arnaca* (Satyrinae) with 89 individuals (5.5%). Among the 88 species recorded, 21 were singletons. No species was recorded in all forest fragments.

Neither, overall Nymphalidae richness nor fruit-feeding species richness ($^{0}D$), were explained by either local or landscape predictors, as the null model ranked among the best models. In contrast, forest cover was the strongest predictor of nectar-feeding and disturbance-adapted species richness, with significant negative relationships ($p = 0.002$ and $p = 0.007$, respectively). For forest-dependent species, edge density best explained richness, with a significant negative relationship ($p = 0.03$) (Figure 2). However, models including only forest cover or combined with edge density were equally plausible, highlighting forest cover -not fragmentation *per se* – as the key driver of forest-dependent butterfly richness (Table S4).

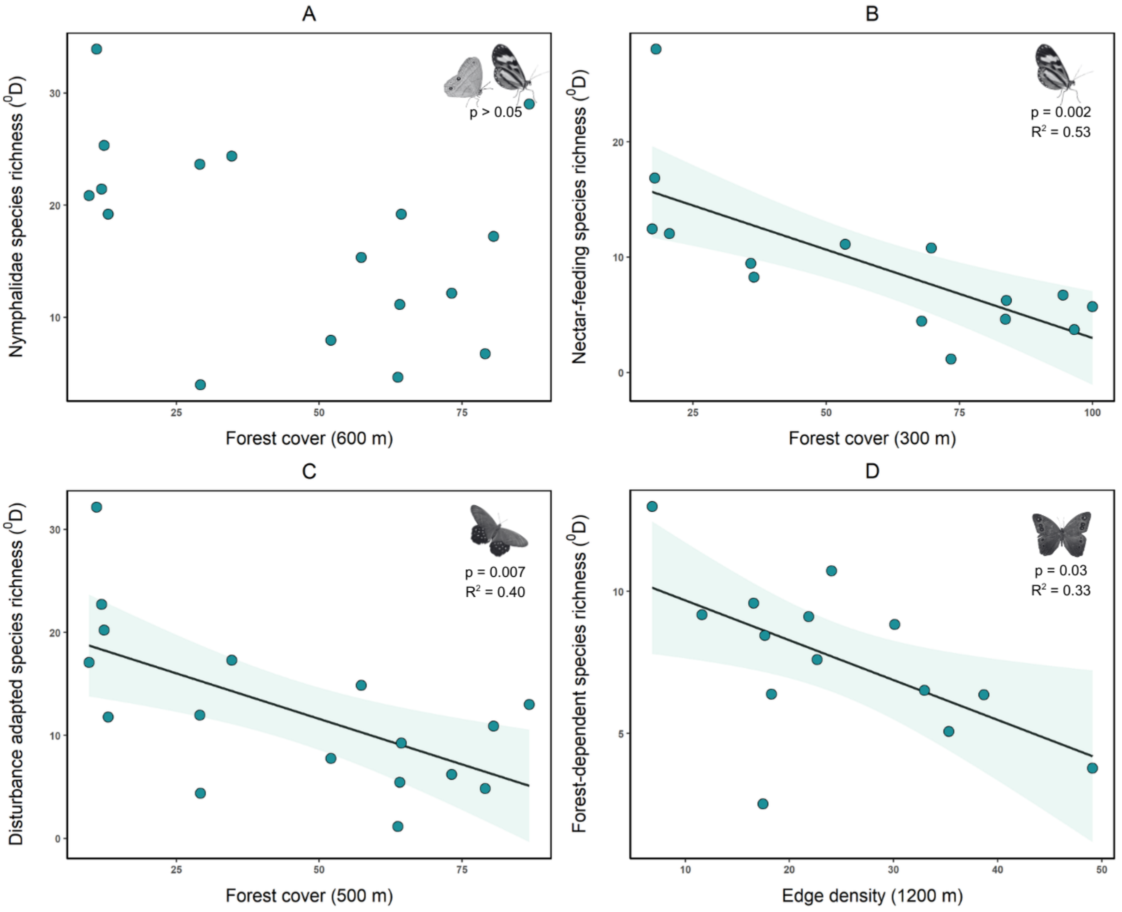

**Figure 2**: Relationships between landscape variables and richness ($^{0}$D) of (A) Overall Nymphalidae species, (B) nectar-feeding species, (C) disturbance-adapted species, and (D) forest-dependent species. Shaded areas around the lines represent the 95% confidence intervals of the models.

Regarding diversity ($^{1}$D), overall Nymphalidae $^{1}$D, as well as $^{1}$D of fruit-feeding and forest-dependent species, were not explained by either local or landscape predictors, as, again, the null model ranked among the best models. In contrast, forest cover was the strongest predictor of diversity ($^{1}$D) for both nectar-feeding and disturbance-adapted species ($p=0.003$, $p=0.014$, respectively), with a negative relationship in both cases (Figure 3).

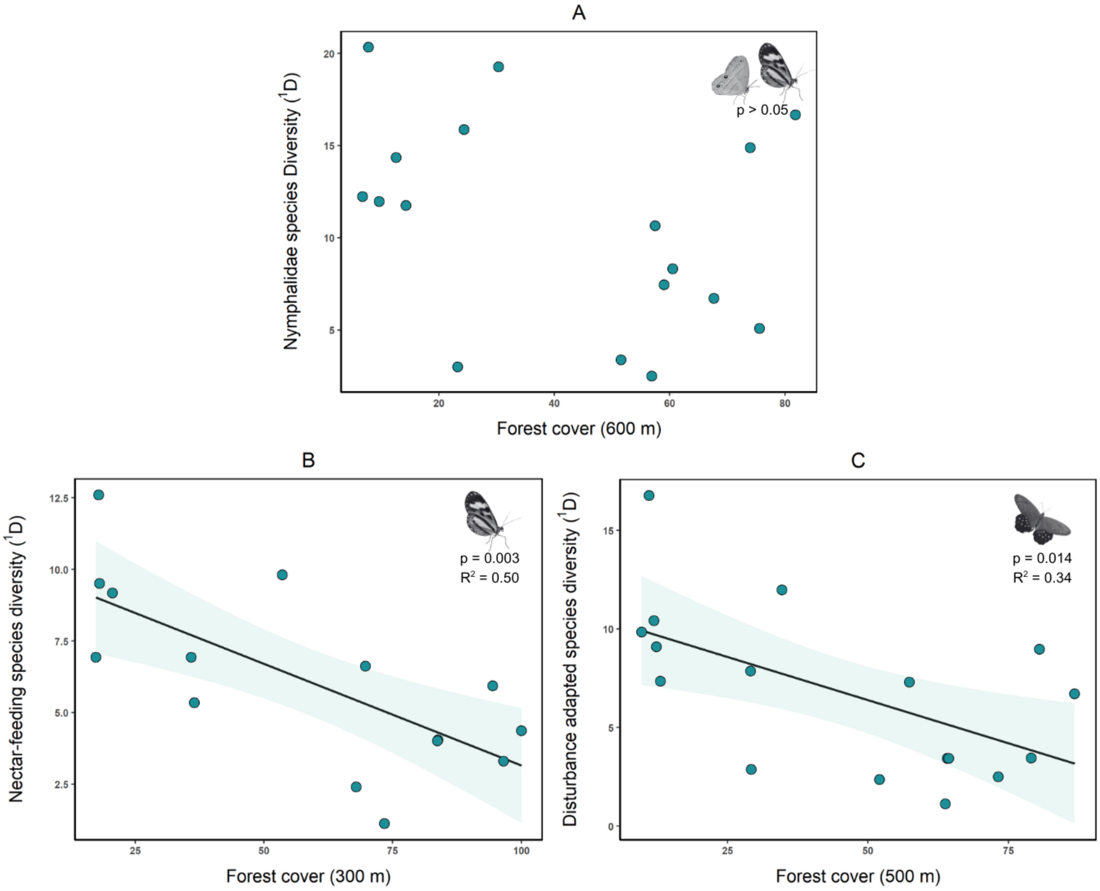

**Figure 3**: Relationships between forest cover and the diversity ($^1$D) of (A) Overall Nymphalidae species, (B) nectar-feeding species, and (C) disturbance-adapted species in our study. The shaded areas around the lines represent the 95% confidence intervals of the models.

Fragmentation *per se* provides the most plausible fit for four out of five models explaining Nymphalidae abundance. The number of forest fragments positively influenced the abundance of overall Nymphalidae ($p < 0.001$), nectar-feeding ($p = 0.002$), and disturbance-adapted species ($p < 0.001$). In contrast, edge density best explained the abundance of fruit-feeding species ($p = 0.002$) (Figure 4).

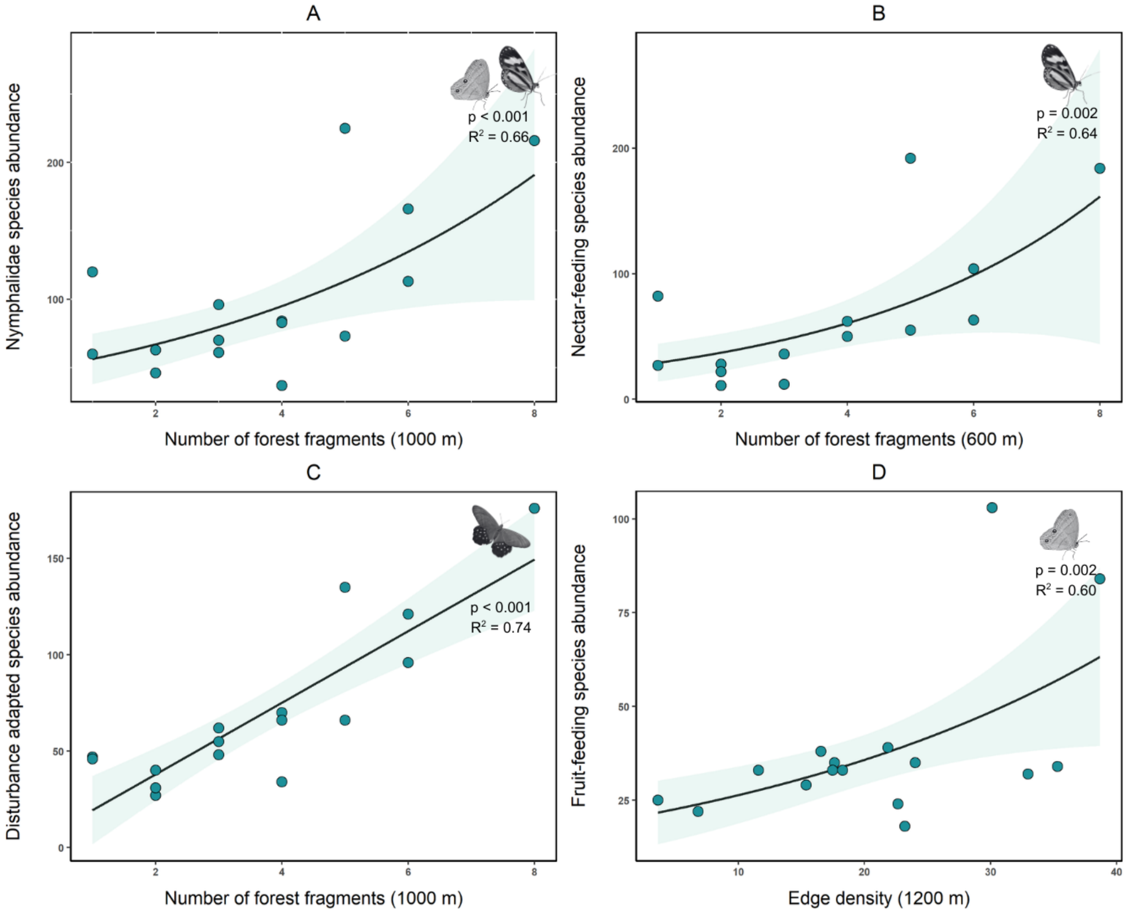

**Figure 4:** Significant relationship between landscape variables and abundance of (A) overall Nymphalidae species, (B) nectar-feeding species, (C) disturbance-adapted species, and (D) fruit-feeding species in our study. The shaded area around the line represents the 95% confidence intervals of the model.

## Discussion

Our results reveal the importance of landscape-scale predictors over local habitat structure in shaping butterfly diversity. Although we did not find significant effects of either local or landscape variables on overall species richness ($^{0}D$) and diversity ($^{1}D$), clear patterns emerged within specific feeding and habitat groups. Forest cover emerged as a negative predictor of richness ($^{0}D$) and diversity ($^{1}D$) for nectar-feeding and disturbance-adapted species. In contrast, butterfly abundance increased with fragmentation *per se*, as more fragmented landscapes supported higher individual numbers across most groups. These findings suggest that habitat loss and fragmentation play distinct roles in shaping butterfly communities.

Fragmentation, rather than being inherently harmful, appears to favor butterfly abundance by creating opportunities for some groups to thrive, particularly in human-modified tropical landscapes.

Our study revealed a rich assemblage of Nymphalidae butterflies, with a well-balanced representation of fruit-feeding and nectar-feeding species. The 88 species recorded are consistent with previous studies conducted in the Atlantic Forest of southern Bahia. For example, Pardini et al. (2009) documented 86 fruit-feeding species using baited traps in the Una municipality region, while Paluch et al. (2016) recorded 87 Nymphalidae species using an entomological net in a reserve, with a similar sampling effort (272 hours in our study; 288 hours in theirs). Despite similar richness, species composition varied considerably: more than half of the species identified by Paluch et al. (2016) were not present in our sample. The most notable differences were found in the tribes Ithomiini and Satyrini, with our study documenting 20 and 38 species, respectively, while Paluch et al. (2016) recorded 7 and 31 species in these same tribes. These findings, combined with our sample coverage level of over 87%, suggest that our results are based on a robust representation of the Nymphalidae diversity in the region and the Brazilian Atlantic Forest.

Our data also showed a higher proportion of disturbance-adapted species (52) compared to forest-dependent species (35), despite both groups being well sampled across the different fragments. Such high proportion contrasts with those from previous studies in the Atlantic Forest which classified species based on habitat affinity, revealing more forest specialists than generalists (Sant'Anna et al. 2014; Filgueiras et al. 2016). We attribute the differences to the large number of Ithomiini butterflies we captured, which represent the majority of nectar-feeding and disturbance-adapted butterfly species. Of the 960 nectar-feeding butterflies sampled, 763 (77%) belonged to the tribe Ithomiini, representing 20 species and 51.3% of the nectar-feeding species richness. Ithomiini butterflies are highly abundant and relatively easy to collect (Willmott and Freitas 2006). Species within this tribe primarily use Solanaceae as larval host plants. In most species, adult males feed on Asteraceae flowers and on withered or dry leaves from Boraginaceae, from which they extract alkaloids that render them unpalatable (Willmott and Freitas 2006). Larvae of *Hypothyris euclea* (Ithomiini), which accounted for 23.9% of the nectar-feeding butterfly abundance, feed on *Solanum asperum*, a common plant in secondary growth vegetation. This species becomes more abundant with increasing habitat isolation and disturbance (Brown Jr and Hutchings 1997). These plant families are common along the edges of our study areas, which likely explains the high representation of this tribe in our samples, as well as the corresponding richness and abundance of disturbance-adapted species.

Nymphalidae species richness and diversity were not affected by either landscape or local-scale predictors. Although butterfly biodiversity is often reported to decline with anthropogenic disturbance (Dirzo et al. 2014), responses can vary considerably across species and contexts. This variability likely reflects differences in ecological traits, such as habitat specialization, mobility, and tolerance to habitat disturbances (Uehara-Prado et al. 2007; Öckinger et al. 2010; Brito et al. 2014; Archaux et al. 2018). While vertebrates are generally more sensitive to habitat loss due to their more complex ecological and physiological requirements (Moreno and Teixido 2025), many invertebrates are more tolerant to degraded environments. Even within butterflies, some studies report stronger responses to local habitat structure (Barlow et al. 2007; Ribeiro et al. 2012; van Halder et al. 2015), while others find that species richness and abundance decline with forest loss and fragmentation (Bossart et al. 2006; Benedick et al. 2006; Bossart and Antwi 2016). The lack of effect in our study for Nymphalidae may be due to the use of overall richness and diversity metrics, which combine species with contrasting ecological traits, potentially masking underlying patterns, evident when analyzed at the level of ecological groups.

Forest cover impacted negatively both the richness and diversity of disturbance-adapted species. A number of studies have documented that landscape changes influence butterfly communities by altering their species composition (e.g. (Uehara-Prado et al. 2009; Vasconcelos et al. 2015; Filgueiras et al. 2016; Archaux et al. 2018; Melo et al. 2019; Wurz et al. 2022). Such changes generally promote an increase in generalist species richness and abundance, while specialist species tend to decline, including endemics (Uehara-Prado et al. 2007; Brito et al. 2014; Vasconcelos et al. 2015; Archaux et al. 2018; Schmitt et al. 2020; Wurz et al. 2022). As a result, mature and extensive continuous forests often harbor lower butterfly richness than forest fragments, but support butterfly communities that are compositionally distinct from those found in fragmented landscapes, usually hosting unique species (Bossart et al. 2006; Wurz et al. 2022). Although most studies typically assess the effects of patch size rather than forest loss at the landscape scale, they support our findings that forest cover influences species richness and diversity of specific groups (disturbance-adapted species). Additionally, the matrix enhances species richness, primarily due to transition zones providing resources for generalist species and less specialized forest species.

Likewise, the richness and diversity of nectar-feeding butterflies was also negatively impacted by forest cover. Notably, two-thirds of the nectar-feeding butterfly species we recorded were classified as disturbance-adapted (26 of 39 species). Thus, the patterns observed for this group are driven mainly by species that thrive in altered environments. In deforested landscapes, the forest structure shrinks (Rocha-Santos et al. 2016), and pioneer plant species dominate, which are the leading resource for generalist butterflies. Furthermore, the remaining fragments in deforested landscapes have few or no forest interior areas, as edge effects can extend up to 100 m into the forest (Bossart and Opuni-Frimpong 2009), what suggests that butterflies adapted to disturbance are benefiting from the abundant floral resources available in forest remnants and transition areas.

As predicted, the density of forest edges was found to negatively influence the richness of forest-dependent butterflies. However, this effect could not be separated from that of forest cover, as the top models included either edge or forest cover. Literature on edge effects reveals both positive and negative responses. Bossart and Opuni-Frimpong (2009) found an adverse effect on the richness of frugivorous butterflies in two of the three sampled areas, whilst a positive edge effect in one area. Surprisingly, the richness of forest-dependent butterfly species was also negatively affected by forest cover. In another tropical forest, in Madagascar, species classified as forest-dependent were also recorded in other habitat types (Wurz et al. 2022). The authors suggested that these occurrences could be attributed to butterflies being attracted to regenerating woody and herbaceous vegetation and suggested that the classification of species as forest-dependent might have been inaccurate due to limited sampling effort in the matrix. However, it is important to note that in our study, species classified as forest-dependent are not necessarily forest-exclusive, and we also included species that occur in secondary forests, which are the most prevalent in our study area. Despite the existence of studies that have classified some butterfly species into categories such as generalists or forest-dependent (e.g., Brito et al. 2014), a comprehensive review is still needed to synthesize the information on the classifications of species from the Atlantic Forest.

Finally, except for forest-dependent butterflies, fragmentation *per se* had a positive effect on butterfly abundance. Species from the Nymphalidae family, as well as disturbance-adapted and nectar-feeding butterflies, benefited from the number of fragments. In highly-fragmented landscapes, habitat isolation is lower, and species can move more easily through the matrix, which facilitates colonization and reduces the likelihood of extinction (Galán-Acedo et al. 2024). Fruit-feeding species showed to be favored by higher edge density. Forest edges typically support a higher butterfly abundance (Bossart and Opuni-Frimpong 2009; Melo et al. 2019; Lourenço et al. 2020) and greater species richness (Schmitt et al. 2020). However, it is important to note that these studies did not isolate the effects of fragmentation *per se.* Here, we show for the first time in the Atlantic Forest that fragmentation *per se* has a positive effect on butterfly abundance. Considering the discussion about habitat amount and fragmentation *per se*, our results corroborate the findings of Brito et al. (2021), indicating that landscape configuration plays a pivotal role in shaping butterfly communities.

## Concluding Remarks

Our findings underscore the importance of analyzing ecological groups separately when studying diversity patterns in tropical butterflies. While species richness ($^0D$) and diversity ($^1D$) were not consistently affected by local or landscape variables, when we focused on ecological groups, clear associations with specific landscape features emerged. Specifically, forest-dependent species richness decreased with fragmentation, whereas nectar-feeding and disturbance-adapted species thrived in more fragmented and deforested landscapes, driven by the availability of host plants and floral resources along forest edges and open areas. Fragmentation *per se* exerted a positive influence on butterfly abundance across most groups, except for forest-dependent species, which remained unaffected. This suggests that fragmented landscapes can support a high abundance of generalist species, but this comes at the expense of losing forest-dependent species. Therefore, integrating the conservation of naturally fragmented areas with broader forest conservation planning could provide a wider conservation opportunity for the diversity of butterflies with different ecological traits. We emphasize the importance of forest remnants in highly modified landscapes, even those with low forest cover, for maintaining rich and abundant butterfly communities. We also highlight the importance of preserving large forest fragments for the conservation of forest species, given the negative effect of edge density on forest-dependent species richness.

## Acknowledgements

We want to thank everyone who assisted us with the fieldwork. We also thank André Freitas, Augusto Rosa, and Eduardo Barbosa for Nymphalidae butterfly identification. And André Freitas and Augusto Rosa for help with butterfly classification. We also thank Larissa Rocha-Santos for the data of vegetation structure. GCNP thanks the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for her doctorate scholarship. We are also grateful to the Fundo Brasileiro para a Biodiversidade (FunBio), the Rufford Foundation, and the Pró-Reitoria de Pesquisa e Pós-Graduação da Universidade Estadual de Santa Cruz for the grants (073.11010.2023.0028633-11) and to Institut Mediterrani d'Estudis Avançats (IMEDEA-UIB) for hosting GCNP for a doctoral internship. Authorization (ICMBio 80610-3) conceived by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/SISBIO).

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# Supplementary Information

# Forest loss or fragmentation *per se*? Drivers of butterfly diversity in fragmented landscapes

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**Table S1**: Landscape information. Landscape variables are presented at a scale of 1000 m.

| Landscape code | Region | Forest cover (%) | Edge density | Number of Fragments | Coordenadas | |
|---|---|---|---|---|---|---|
| | | | | | x | y |
| 187.3 | Belmonte | 67.41 | 14.82 | 2 | -39.22817851 | -15.90208122 |
| 187.1 | Belmonte | 61.57 | 14.83 | 2 | -39.23927474 | -15.89525153 |
| 51.1 | Una | 59.92 | 10.09 | 1 | -39.1422316 | -15.2102857 |
| 171.1 | Belmonte | 56.18 | 11.79 | 5 | -39.24531298 | -15.81874102 |
| 33.2 | Una | 53.63 | 17.08 | 2 | -39.20033391 | -15.34917124 |
| 24.1 | Una | 51.43 | 22.36 | 3 | -39.21892235 | -15.17158382 |
| 89.3 | Una | 50.72 | 26.2 | 3 | -39.04442173 | -15.34817358 |
| 50.2 | Una | 45.39 | 30.74 | 6 | -39.15927313 | -15.24841372 |
| 35.2 | Una | 36.67 | 20.11 | 8 | -39.19594299 | -15.29571857 |
| 46.2 | Belmonte | 21.72 | 17.03 | 5 | -39.50415206 | -15.7754171 |
| 120.1 | Belmonte | 18.54 | 10.68 | 1 | -39.38233338 | -15.72760381 |
| 118.1 | Belmonte | 14.36 | 16.42 | 2 | -39.36872927 | -15.79222376 |
| 120.2 | Belmonte | 13.31 | 17.26 | 6 | -39.36498179 | -15.71507118 |
| 118.2 | Belmonte | 10.55 | 14.1 | 4 | -39.37458604 | -15.78025183 |
| 46.1 | Belmonte | 6.07 | 5.99 | 4 | -39.50533959 | -15.80103967 |
| 64.2 | Belmonte | 2.96 | 4.8 | 4 | -39.48418786 | -15.78179244 |
| 64.3 | Belmonte | 2.56 | 3.5 | 3 | -39.49836171 | -15.79083896 |

**Table S2**: Environmental variables and their correlation with the first axis derived from the PCA ordination.

| Variable | PC1 |
|---|---|
| Mean tree height | 0.601365 |
| Maximum tree height | 0.580513 |
| Mean DAP | 0.473937 |
| Canopy openness | -0.277036 |

**Table S3**: Sample coverage (SC), richness, and abundance by forest fragment. All Nymphalidae butterflies are classified by feeding preference into nectar-feeding and fruit-feeding species and habitat preference into forest-dependent and disturbance-adapted species.

| **Code** | **Nymphalidae** | | | **Fruit-feeding** | | | **Nectar-feeding** | | | **Forest-dependent** | | | **Disturbance-adapted** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **SC** | **Richness** | **Abundance** | **SC** | **Richness** | **Abundance** | **SC** | **Richness** | **Abundance** | **SC** | **Richness** | **Abundance** | **SC** | **Richness** | **Abundance** |
| 171.1 | 0.93 | 32 | 225 | 0.85 | 12 | 33 | 0.95 | 20 | 192 | 0.93 | 16 | 87 | 0.93 | 15 | 135 |
| 64.2 | 0.79 | 30 | 84 | 0.60 | 13 | 22 | 0.86 | 17 | 62 | 0.58 | 8 | 14 | 0.83 | 22 | 70 |
| 46.2 | 0.81 | 23 | 73 | 0.90 | 6 | 18 | 0.78 | 17 | 55 | 0.49 | 5 | 7 | 0.85 | 18 | 66 |
| 118.1 | 0.85 | 26 | 63 | 0.81 | 14 | 35 | 0.90 | 12 | 28 | 0.93 | 10 | 22 | 0.83 | 15 | 40 |
| 118.2 | 0.95 | 7 | 37 | 0.97 | 5 | 29 | 1.00 | 2 | 8 | 1.00 | 1 | 3 | 0.94 | 6 | 34 |
| 120.2 | 0.90 | 39 | 166 | 0.90 | 19 | 103 | 0.89 | 20 | 63 | 0.89 | 14 | 44 | 0.91 | 24 | 121 |
| 120.1 | 0.90 | 32 | 120 | 0.85 | 16 | 38 | 0.93 | 16 | 82 | 0.89 | 19 | 73 | 0.92 | 13 | 47 |
| 187.1 | 0.76 | 19 | 46 | 0.77 | 14 | 35 | 0.75 | 5 | 11 | 0.69 | 10 | 19 | 0.82 | 9 | 27 |
| 187.3 | 0.85 | 19 | 46 | 0.85 | 11 | 24 | 0.87 | 8 | 22 | 0.86 | 9 | 19 | 0.86 | 10 | 27 |
| 46.1 | 0.88 | 24 | 83 | 0.89 | 12 | 33 | 0.88 | 12 | 50 | 0.69 | 9 | 15 | 0.93 | 14 | 66 |
| 64.3 | 0.82 | 22 | 61 | 0.80 | 9 | 25 | 0.84 | 13 | 36 | 0.39 | 5 | 6 | 0.88 | 17 | 55 |
| 24.1 | 0.89 | 20 | 70 | 0.91 | 8 | 34 | 0.87 | 12 | 36 | 0.96 | 7 | 22 | 0.86 | 13 | 48 |
| 51.1 | 0.95 | 11 | 60 | 0.94 | 6 | 33 | 1.00 | 5 | 27 | 0.94 | 4 | 14 | 0.96 | 7 | 46 |
| 89.3 | 0.93 | 19 | 96 | 0.94 | 14 | 84 | 0.85 | 5 | 12 | 0.92 | 10 | 34 | 0.94 | 9 | 62 |
| 50.2 | 0.90 | 19 | 113 | 0.48 | 6 | 9 | 0.94 | 13 | 104 | 0.83 | 6 | 17 | 0.92 | 13 | 96 |
| 35.2 | 0.94 | 24 | 216 | 0.85 | 10 | 32 | 0.96 | 14 | 184 | 0.85 | 12 | 40 | 0.96 | 12 | 176 |
| 33.2 | 0.78 | 15 | 46 | 0.85 | 10 | 39 | 0.49 | 5 | 7 | 0.68 | 8 | 15 | 0.84 | 7 | 31 |

**Table S4**: Top models (with a ΔAICc < 2) for each alpha diversity response variable. The simplest model was selected as the best model. k: number of parameters, AICc: Akaike Information Criterion corrected for small sample sizes, ΔAICc: Difference in AICc relative to the best model, weight: model weight.

## Richness ($^0$D)

### Nymphalidae species richness ($^0$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|
| Edge density | 3 | 125.11511 | 0 | 0.2195836 |
| Forest cover + Number of forest fragments | 4 | 125.49358 | 0.3784677 | 0.1817259 |
| **Null model *** | 2 | 125.56814 | 0.4530331 | 0.1750754 |
| Forest cover | 3 | 125.64463 | 0.5295158 | 0.1685066 |
| Number of forest fragments | 3 | 126.04472 | 0.9296121 | 0.1379549 |
| Comp.1 | 3 | 126.3716 | 1.2564948 | 0.1171536 |

### Nectar-feeding Species richness ($^0$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|
| Forest cover | 3 | 94.821965 | 0 | 0.2897196 |
| Number of forest fragments | 3 | 94.881313 | 0.0593476 | 0.2812488 |
| Forest cover + Number of forest fragments | 4 | 95.102927 | 0.2809616 | 0.251749 |
| Comp.1 + Number of forest fragments | 4 | 95.804302 | 0.9823366 | 0.1772826 |

### Fruit-feeding Species richness ($^0$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|
| Edge density | 3 | 99.135157 | 0 | 0.4384295 |
| **Null model *** | 2 | 99.324737 | 0.1895792 | 0.3987799 |
| Forest cover | 3 | 101.11663 | 1.981469 | 0.1627906 |

### Forest-dependent species richness ($^0$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|
| Edge density | 3 | 70.06476 | 0 | 0.3741327 |
| Forest cover | 3 | 70.787026 | 0.7222657 | 0.260728 |
| Edge density + Forest cover | 4 | 71.386807 | 1.322047 | 0.1931732 |
| Edge density + Number of forest fragments | 4 | 71.619386 | 1.5546253 | 0.1719662 |

### Disturbance-adapted species richness ($^0$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|
| Forest cover | 3 | 116.41191 | 0 | 1 |

## Diversity ($^1$D)

### Nymphalidae species diversity – effective number of abundant species ($^1$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|
| Comp.1 | 3 | 109.30453 | 0 | 0.3030515 |
| Number of forest fragments | 3 | 110.12894 | 0.8244132 | 0.2006769 |
| Edge density | 3 | 110.22225 | 0.9177149 | 0.1915301 |
| Forest cover + Number of forest fragments | 4 | 110.51735 | 1.2128213 | 0.1652554 |
| **Null model *** | 2 | 110.85641 | 1.5518747 | 0.1394861 |

### Nectar-feeding Species diversity – effective number of abundant species ($^1$D)

| Model – Distribution family: Gaussian | k | AICc | ΔAICc | weight |
|---|---|---|---|---|

| | | | | |
|---|---|---|---|---|
| Forest cover | 3 | 73.602015 | 0 | 1 |

**Fruit-feeding Species diversity – effective number of abundant species ($^1D$)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| **Null model *** | 2 | 90.01968 | 0 | 0.4264381 |
| Edge density | 3 | 90.301234 | 0.2815539 | 0.3704396 |
| Number of forest fragments | 3 | 91.502997 | 1.4833176 | 0.2031223 |

**Forest-dependent species diversity – effective number of abundant species ($^1D$)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Edge density | 3 | 60.354325 | 0 | 0.3505864 |
| Forest cover | 3 | 61.518768 | 1.1644429 | 0.1958572 |
| **Null model *** | 2 | 61.814034 | 1.4597091 | 0.1689753 |
| Comp.1 | 3 | 61.99555 | 1.6412253 | 0.1543148 |
| Comp.1 + Forest cover | 4 | 62.334377 | 1.9800518 | 0.1302664 |

**Disturbance-adapted species diversity – effective number of abundant species ($^1D$)**

| **Model – Distribution family: Gaussian** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Forest cover | 3 | 96.650191 | 0 | 0.4038879 |
| Comp.1 + Forest cover | 4 | 96.779465 | 0.1292744 | 0.3786075 |
| Edge density + Forest cover | 4 | 97.888025 | 1.2378346 | 0.2175046 |

## Abundance

**Nymphalidae Abundance**

| **Model – Distribution family: Negative binomial** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 175.67267 | 0 | 1 |

**Nectar-feeding Abundance**

| **Model – Distribution family: Negative binomial** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 152.35687 | 0 | 0.421597 |
| Edge density + Comp.1 + Number of forest fragments | 5 | 152.93435 | 0.5774875 | 0.3158622 |
| Edge density + Comp.1 | 4 | 153.30415 | 0.9472868 | 0.2625408 |

**Fruit-feeding Abundance**

| **Model – Distribution family: Negative binomial** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Edge density | 3 | 135.22961 | 0 | 0.6567378 |
| Edge density + Forest cover | 4 | 136.52719 | 1.2975806 | 0.3432622 |

**Forest-dependent species abundance**

| **Model – Distribution family: Negative binomial** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| **Null model *** | 2 | 123.72553 | 0 | 1 |

**Disturbance-adapted species abundance**

| **Model – Distribution family: Negative binomial** | **k** | **AICc** | **ΔAICc** | **weight** |
|---|---|---|---|---|
| Number of forest fragments | 3 | 151.89048 | 0 | 1 |

**Table S5**: Nymphalidae butterfly species per sample forest fragment. Forest-dependent species (F) and Disturbance-adapted species (D).

Observação: Disponível mediante solicitação à autora através do e-mail geannepereira@gmail.com.

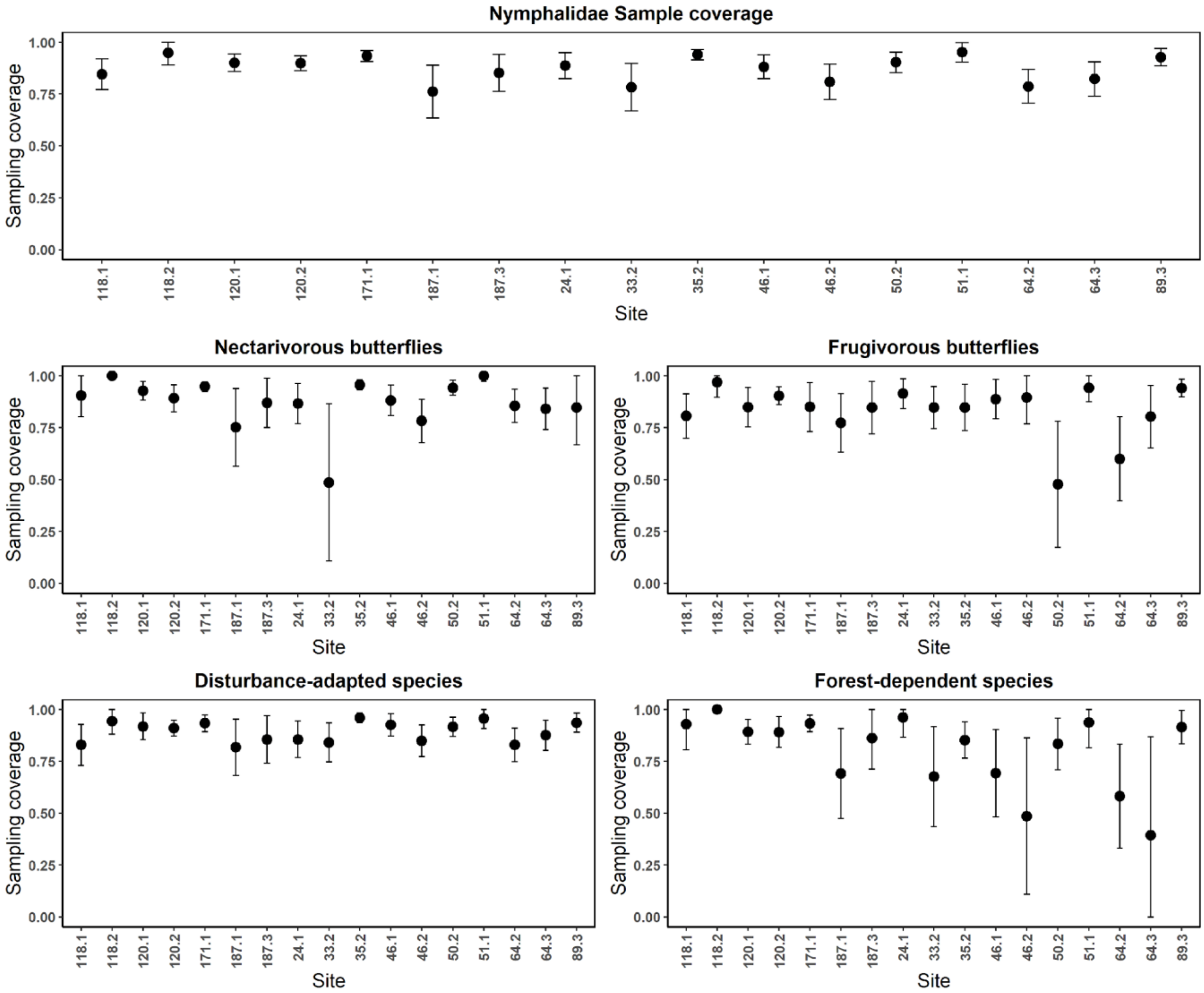

**Figure S1**: Sample coverage by forest fragment. To estimate the Hill numbers of each category, we standardized the samples based on a common sampling coverage of 0.80 for overall Nymphalidae butterflies, 0.82 for nectarivores, 0.75 for fruit-feeding, 0.71 for forest-dependent and 0.87 for disturbance-adapted species.

In the context of forest-dependent species, one forest fragment (118.2) was excluded because it contained a single species, and two forest fragment (64.3 and 46.2) were excluded because they present less than 50 % of sampling coverage, thereby rendering the estimation of diversity impossible. The final dataset, which was used for the analysis of forest-dependent species, consisted of 14 sampling forest fragments, with alpha diversity being estimated at 0.71 sampling coverage. In the context of nectar-feeding and fruit-feeding species, one forest fragment for each was excluded because it presents less than 50 % of sampling coverage (33.2 and 50.2, respectively). For fruit-feeding species, one forest fragment was excluded because it contained only two species (118.2).

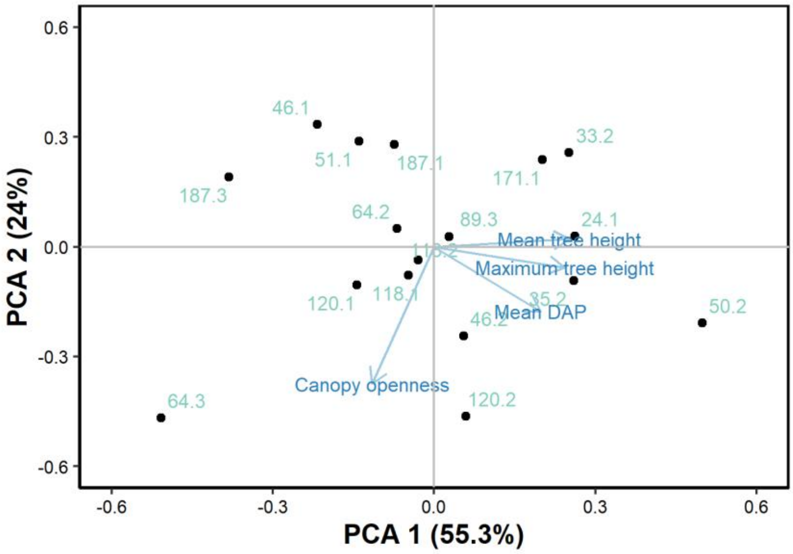

**Figure S2**: Biplot of the first two axes from a PCA ordination of local habitat structure variables across sampling forest fragments.

## Conclusão

No primeiro capítulo, demonstramos que as perturbações antrópicas têm um efeito geral negativo sobre as comunidades de borboletas. No entanto, a riqueza e a abundância de espécies responderam de maneiras contrastantes à essas perturbações. Enquanto a riqueza de borboletas diminuiu em habitats perturbados, a abundância aumentou, particularmente em resposta aos efeitos de borda e mudanças no uso da terra. Essa divergência sugere que pressões antrópicas podem favorecer certas espécies, potencialmente espécies generalistas e adaptadas a perturbações, em detrimento da diversidade geral. Entre os tipos de perturbação analisados, a degradação florestal, a urbanização, o declínio do tamanho das manchas e múltiplas perturbações simultâneas reduziram a riqueza de borboletas, enquanto a urbanização teve um efeito negativo tanto para riqueza quanto para a abundância de borboletas. Essas descobertas ressaltam que a perturbação pode simplificar as comunidades de borboletas, alterando a composição de espécies para conjuntos mais abundantes, mas potencialmente menos diversos.

No segundo capítulo avaliamos os efeitos da perda de habitat, fragmentação e mudanças no habitat local sobre as comunidades de borboletas em paisagens fragmentadas de Mata Atlântica. Encontramos que a fragmentação, medida pelo número de fragmentos florestais na paisagem, influenciou positivamente a abundância de borboletas, corroborando com nossa metanálise. No entanto, esse aumento foi acompanhado por maior dominância de espécies e tribos e na redução da diversidade de tribos. As diferenças na composição de espécies e tribos entre os fragmentos foram impulsionadas principalmente pelo turnover (substituição), incluindo mudanças na abundância relativa de espécies entre os fragmentos amostrados. A cobertura florestal explicou a variação na composição de espécies entre os fragmentos amostrados, enquanto o número de fragmentos florestais foi o preditor mais importante das diferenças na composição de tribos. Com base na variação da composição das comunidades ao longo do gradiente de cobertura florestal, identificamos que paisagens com mais de 45% de cobertura florestal mantêm comunidades de borboletas mais estáveis, com menos substituição e menos mudanças na abundância relativa das espécies, quando comparadas entre si. À medida que a fragmentação se intensificou, a dissimilaridade entre as paisagens aumentou, com o aumento da dominância de poucas tribos, o que resultou em menor diversidade.

No terceiro capítulo nossos resultados revelaram a importância de preditores em escala de paisagem sobre a estrutura do habitat local na estruturação da diversidade de borboletas. Não encontramos efeitos significativos de variáveis locais ou de paisagem na riqueza geral de espécies e diversidade. No entanto, padrões claros emergiram quando avaliamos as guildas tróficas e as preferências de habitat. A cobertura florestal é um preditor negativo de riqueza e diversidade para espécies nectarívoras e adaptadas a perturbações. Em contraste, a abundância de borboletas aumentou com a fragmentação per se, visto que paisagens mais fragmentadas sustentaram números maiores de indivíduos na maioria dos grupos, exceto para espécies dependentes de floresta, que permaneceram inalteradas. Para a riqueza de espécies dependentes de floresta, a densidade de bordas teve um efeito negativo. Essas descobertas sugerem que a perda de habitat e a fragmentação desempenham papéis distintos na formação das comunidades de borboletas.

Em síntese, nossos resultados sugerem que, em geral, as perturbações antrópicas afetam negativamente as comunidades borboletas em florestas tropicais. Embora, paisagens fragmentadas possam suportar uma alta riqueza e abundância de espécies adaptadas a perturbações, isso ocorre à custa da perda de espécies dependentes da floresta, diversidade e equitatividade. Portanto, integrar a conservação de áreas fragmentadas com um planejamento mais amplo de conservação florestal pode proporcionar uma oportunidade mais ampla de conservação para a diversidade de borboletas com diferentes características ecológicas. Ressaltamos a importância dos remanescentes florestais em paisagens altamente modificadas, mesmo aquelas com baixa cobertura florestal, para a manutenção de comunidades de borboletas ricas e abundantes.

**Figura**: Algumas borboletas registradas nos trabalhos de campo realizados em fragmentos de Mata Atlântica no Sul da Bahia, Brasil. (**a - g**) Nymphalidae, (**h - j**) Hesperiidae, (**k - l**) Riodinidae. (**a**) *Amiga arnaca* (Fabricius, 1776), (**b**) *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952), (**c**) *Pierella lena brasiliensis* (C. Felder & R. Felder, 1862), (**d**) *Hermeuptychia* sp. Forster, 1964, (**e**) *Myscelia orsis* (Drury, 1782), (**f**) *Hypothyris euclea* (Godart, 1819), (**g**) *Siproeta stelenes* (Linnaeus, 1758), (**h**) *Burnsius* *orcus* (Stoll, 1780), (**i**) *Calpodes* sp. Hübner, [1819], (**j**) *Telegonus alardus* (Stoll, 1790); (**k**) *Stalachtis susanna* (Fabricius, 1787); (**l**) *Semomesia geminus* (Fabricius, 1793) macho.