UNIVERSIDADE ESTADUAL DE CAMPINAS
Instituto de Biologia

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PADRÕES DE DIVERSIDADE DAS BORBOLETAS FRUGÍVORAS (NYMPHALIDAE) EM DIFERENTES ESCALAS MACROECOLÓGICAS

DIVERSITY PATTERNS OF FRUIT-FEEDING BUTTERFLIES (NYMPHALIDAE) AT DIFFERENT MACROECOLOGICAL SCALES

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Diversity patterns of fruit-feeding butterflies (Nymphalidae) at different macroecological scales

Padrões de diversidade das borboletas frugívoras (família Nymphalidae) em diferentes escalas macroecológicas

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Resumo

Padrões de diversidade são moldados a partir de processos ecológicos cuja contribuição varia de acordo com a escala observada. Para entender a dinâmica e importância relativa destes processos, é necessário investigar a interação entre os padrões e processos em diferentes escalas. A guilda de borboletas frugívoras é bastante empregada em estudos de diversas áreas da ecologia, assim como em atividades ligadas a conservação. Entretanto, o conhecimento acerca da diversidade e os impactos da ação antrópica sob esses organismos ainda são pouco conhecidos. A partir destas lacunas de conhecimento a presente tese objetivou: 1) compilar dados acerca de comunidades de borboletas frugívoras da Mata Atlântica, visando subsidiar análises de grandes padrões de diversidade; 2) em uma escala local, comparar o efeito da fragmentação e da estrutura vertical de florestas na composição filogenética e de espécies de comunidades de borboletas frugívoras; e 3) em escala mais ampla, avaliar o efeito da modificação da paisagem nos padrões de distribuição da riqueza de espécies de borboleta frugívoras da Mata Atlântica. A compilação revelou que os inventários de borboletas frugívoras na Mata Atlântica estão concentrados próximos aos centros de pesquisa, e que a maioria destes são dados históricos não publicados. Nossos resultados ainda demonstraram que processos relacionados a qualidade e quantidade de habitat são importantes fatores estruturadores das comunidades em escala local e regional. Em escala local, a fragmentação e a estrutura vertical de florestas geraram um padrão similar de composição de espécies e de atributos funcionais relacionados ao voo. Isso sugere que um mesmo mecanismo de filtragem decorrente da estrutura do habitat pode estar atuando em diferentes dimensões espaciais. Já em uma escala geográfica regional, a riqueza de espécies de borboletas frugívoras parece estar bastante relacionada com os remanescentes florestais da Mata Atlântica, demonstrando que os fragmentos florestais são capazes de manter uma alta riqueza. Além de coincidirem com os centros de endemismo de outros grupos taxonômicos, os hotspots de riqueza são adjacentes a locais em que a riqueza predita pelos modelos de paisagem é baixa, o que demonstra que o aumento da modificação da paisagem pode levar a perda de espécies. Embora a importância dos processos varie conforme a escala medida, a perda de habitat foi confirmada como um fator determinante da estruturação de comunidades de borboletas frugívoras em diferentes escalas. Em tempos que estabelecemos metas para deter a perda da biodiversidade, promover o planejamento e gestão de conhecimento acerca da diversidade e o impacto causados pela modificação de paisagens naturais têm um papel de destaque.

Abstract

Ecological processes are responsible for shaping diversity patterns and its contribution degree vary according to the scale that they are measured. Investigate the effect of processes in different scales is the key to understand its dynamics and relative contribution in generating patterns. Fruit-feeding butterflies are widely used in many ecological studies and conservations activities as well. The diversity distribution of these organisms are frequently addressed at local scales, but patterns at wider scales and the relative contribution of processes are still poorly understood. Aiming to fill the knowledge gaps, our objectives were: 1) compile data from fruit-feeding butterfly communities of Atlantic Forest, seeking to support analyses of broader diversity patterns. 2) Compare at a local scale, the effect of fragmentation and vertical structure of forests on the phylogenetic and species composition of fruit-feeding butterfly communities. 3) On a broader scale, evaluate the effect of landscape modification on the distribution of fruit-feeding butterfly species richness in Atlantic Forest. The compilation revealed that fruit-feeding butterfly inventories are mostly represented by unpublished historical data, which are concentrated near the butterfly research centers. Our results also demonstrated that processes related to habitat quality and quantity are important structuring factors of local and regional communities. At local scales, the fragmentation and vertical structure of forests generated similar patterns of species composition and flight functional traits distribution. This suggests that habitat structure may act under a similar filtering mechanism in different spatial dimensions. On a regional scale, the fruit-feeding butterfly species richness seems closely related to forest remnants of Atlantic Forest, demonstrating that forest fragments are efficient in maintaining high richness. The richness hotspots location match with endemism centers of other taxa. Moreover, they are located near to sites which landscapes models predicted low richness, which demonstrates that an increasing landscape modification may lead to significant species loss. Although the importance of ecological processes varies according to the observed scale, we confirmed that habitat loss is a determinant factor structuring fruit-feeding butterfly communities at different scales. In times that were established goals for stopping the biodiversity loss, we highlight the importance of diversity knowledge divulgation and management, as well as the prominent role of the impacts caused by natural landscape modification.

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Introdução Geral

"Os conceitos de padrão e escala estão inelutavelmente entrelaçados".

(Hutchinson 1953 apud Levin 1992)

Padrão e escala

Na introdução de seu livro "*Geographical ecology; patterns in the distribution of species*" de 1972, MacArthur escreveu: "fazer ciência é procurar por padrões repetidos...". Padrões são regularidades que observamos na natureza, ou tendências amplamente observáveis (Lawton 1999). Embora a observação de padrões não seja o único *modus operandi* da pesquisa científica em ecologia, é através dela que hipóteses sobre os processos e fatores responsáveis pelo surgimento destes padrões podem ser levantadas. Um padrão bastante estudado e reproduzido nos livros de ecologia é o diagrama climático (de acordo com a precipitação anual e média de temperatura) da distribuição dos biomas terrestres ao redor do planeta (Whittaker 1975). Outro padrão "clássico" é o gradiente latitudinal de espécies, que versa sobre o aumento da riqueza de espécies de diversos grupos de organismos dos polos em direção aos trópicos (Hawkins 2001, Hillebrand 2004, Pianka 1966).

Muitas hipóteses já foram geradas para explicar o gradiente latitudinal de espécies (ver tabela em Willig et al 2003). A hipótese de área geográfica prediz que os trópicos possuem maior riqueza que as outras regiões do globo pois possuem mais área disponível, o que remete a relação existente entre espécie x área (Rosenzweig 1995). Uma área maior pode comportar uma maior diversidade de espécies, habitats e biomas, dessa forma facilitando os processos de especiação e adaptação (Willig et al 2003). Embora já se tenha encontrado evidencias que suportem essa hipótese (Rosenzweig 1995), análises da distribuição de riqueza de mamíferos da América do Norte e Sul apontam que essa hipótese é pouco consistente. Ao remover o efeito da área, a relação entre latitude e riqueza ainda é significativa para ambos continentes (Kaufman & Willig 1998).

Já a regra de Rapoport é um padrão em que o alcance da distribuição das espécies é inversamente proporcional a latitude (Rapoport 1975). Em altas latitudes a variação sazonal é maior e organismos com maior tolerância climática seriam favorecidos pela seleção natural nestas localidades. Já as espécies de latitudes tropicais teriam menor tolerância climática e distribuição mais restrita. Sendo os ambientes nos trópicos mais heterogêneos na perspectiva destas espécies, elas estariam mais propensas a dispersar ao acaso para áreas "desfavoráveis", incrementando a riqueza de espécies. Entretanto, a lógica da regra de Rapoport é aplicável apenas em condições específicas (Rohde 1996), e alguns táxons que apresentam gradiente de riqueza latitudinal sequer se enquadram em sua lógica (Lyons & Willig 1997, Willig & Gannon 1997), o que reduz a chance desta regra ser o principal mecanismo para explicar este gradiente.

A hipótese da produtividade infere que regiões que recebem maior radiação solar tem maior disponibilidade de energia, levando a maior produtividade, biomassa, e consequentemente, a uma maior riqueza (Pianka 1966). Essa alta energia solar também seria responsável por manter habitats mais climaticamente estáveis perto do Equador ao longo do tempo evolutivo. Essa condição também afetaria a resposta fisiológica das espécies à temperatura, segundo a hipótese da energia (Currie 1991). A hipótese cinética relaciona as maiores temperaturas nos trópicos à uma maior velocidade evolutiva, uma vez que temperaturas mais altas acelerariam as taxas de mutação, aumentando a especiação e consequentemente a riqueza nos trópicos (Rohde 1992). Além de taxas evolutivas, outros processos ecológicos também seriam dependentes de alta temperatura, explicando assim a grande diversidade presente nos trópicos (Brown 2014).

Mais recentemente, o modelo “fora dos trópicos” assume que o padrão latitudinal de riqueza de espécies pode ser explicado pela interação de dois processos distintos, especiação e dispersão. Segundo este modelo os diferentes táxons teriam se diversificado preferencialmente nos trópicos e posteriormente expandido suas distribuições geográficas em direção aos polos, entretanto, sem perderem a sua distribuição tropical (Jablonski et al. 2006). Diferente da dicotomia conceitual sobre os trópicos serem considerados um berço ou museu da diversidade, esse modelo assume que os trópicos podem representar ambas as denominações (Jablonski et al. 2006). Embora essa relação tenha sido demonstrada com bivalves marinhos (Jablonski et al. 2013), estudos com mamíferos sugeriram que não há relação entre a taxa de diversificação e latitude (Soria-Carrasco & Castresana 2012).

Muitas outras hipóteses poderiam ser mencionadas, entretanto, muitos dos mecanismos associados às diferentes hipóteses estão correlacionados, o que torna difícil analisar seus efeitos de forma isolada. Sendo assim, é bem possível que nenhum mecanismo sozinho seja capaz de explicar essa variação (Levin 1992, Whittaker et al 2001, Beck et al 2012). Em relação à análise deste e de outros gradientes, é necessário reconhecer que diferentes processos têm diferentes importâncias de acordo com as escalas, e buscar a integração de todos os processos em um só. Sendo assim, mais do que determinar uma escala correta, é necessário entender como a descrição do sistema muda de acordo com a escala (Levin 1992, Blackburn & Gaston 2002).

Macroecologia e comunidades: *Duas visões de um mesmo mundo"*

Uma vez que a ecologia de comunidades é influenciada por uma gama de variáveis que atuam e interagem entre si em diversas escalas, modelos em diferentes escalas são necessários. Em escalas espaciais locais existem inúmeras possibilidades devido a quantidade e complexidade dos fatores, o que torna os sistemas de interesse mais imprevisíveis e as generalizações difíceis de serem percebidas. Ao ampliarmos a escala espacial observada, a importância e imprevisibilidade dos casos individuais é reduzida para uma regularidade de casos que permite estabelecer generalizações sob regras subjacentes mais simples, assim como o diagrama dos biomas proposto por Whittaker (Levin 1992, Lawton 1999). Ainda que metodologicamente a análise de padrões adote uma abordagem reducionista ao delimitar o espaço e o tempo, a visão ampla de sistemas pode revelar níveis mais básicos de organização (Looijen 1998).

A complementariedade das abordagens tradicionais com análises em grande escala permite a identificação do que são consideradas propriedades particulares de indivíduos ou espécies, e o que pode ser regido por processos mais universais (Brown & Maurer 1989). Junto a isso, o desenvolvimento de modelos matemáticos sofisticados, experimentos rigorosos, e avanço das técnicas moleculares auxiliaram também na compreensão da biogeografia histórica e processos de diversificação (Brown 1995). O papel das restrições filogenéticas e condições ambientais do passado passaram a ter uma maior relevância para interpretarmos a resposta dos organismos a alterações ambientais do presente. Tendo em vista que a distribuição atual dos organismos é também dependente de processos evolutivos que ocorreram em uma ampla escala temporal no passado, abordar essas questões requer uma disciplina que consiga explorar a interface destas temáticas de forma integrada (Brown 1995).

A macroecologia como uma área da ecologia foi instaurada no final dos anos 80 por James H. Brown e Brian A. Maurer (Brown 1995, Brown & Maurer 1989). Além de ser relativamente nova, esta disciplina integra diversos métodos da ecologia, incluindo a sistemática, fisiologia, biogeografia e biologia evolutiva (Diniz-Filho et al 2006). Segundo os autores a macroecologia busca por padrões gerais em escalas geográficas locais a globais, e o desenvolvimento de hipóteses que expliquem esses padrões. Os estudos focados em escalas geográficas locais captam processos ecológicos que estruturam as comunidades de forma pontual, o que é equivalente a enxergar apenas uma parte de um sistema com boa resolução, mas não o sistema todo. Por sua vez, um enfoque macroecológico em escalas geográficas amplas, proporciona uma visão global dos padrões e processos, mas os detalhes ficam pouco nítidos (Diniz-Filho et al 2006). Entre os recorrentes temas em estudos macroecológicos estão por exemplo, os gradientes latitudinais de espécies (Hawkins et al 2007), análises de padrões temporais e espaciais de riqueza (Adler et al 2005), estrutura filogenética de comunidades (Wiens et al 2010), processos em escala de metacomunidades (Leibold et al 2004), partição de diversidade (Tuomisto 2010), e substituição (turnover) de espécies (Shurin 2007).

A macroecologia tem sido bem-sucedida ao descrever padrões gerais, entretanto não o suficiente para inferir predições causais precisas e únicas. Como exemplo, voltando aos gradientes latitudinais de riqueza de espécies, alguns autores têm sugerido que a compreensão desse padrão é dependente de uma hierarquia, da filtragem do pool regional de espécies pelos fatores efeitos históricos e evolutivos até os mecanismos que determinam a ocorrência das espécies em escala de comunidade (Beck et al 2012, Cornell & Harrinson 2014, Ricklefs 2004). O pool regional compreende uma dada área biogeográfica que é de uma ordem de grandeza espacial maior que as comunidades locais. Devido a isso, sua origem teoricamente receberia uma maior contribuição de processos de grande magnitude espacial e temporal (biogeográficos), como eventos geológicos, tectônica de placas, e história evolutiva dos organismos (Jenkins & Ricklefs 2011). A estrutura de comunidades locais, por sua vez, além de dependerem dos processos regionais (macroecologicos), seriam mais afetadas por mecanismos de menor escala como filtros ambientais, limites de dispersão ou interações interespecíficas (Ricklefs 1987). Além disso, propriedades como as interações ecológicas dependentes de densidade, e a abundancia das espécies seriam medidas com mais precisão em comunidades locais (Willig et al 2003, Cavender-Bares et al 2009).

Borboletas como objeto de estudo

A ordem Lepidoptera é a segunda maior ordem entre os insetos com cerca de 16% de todas as espécies (Aguiar et al 2009). Essa ordem é composta por borboletas e mariposas, sendo que cerca de 20.000 de borboletas já foram descritas (Beccaloni & Gaston 1995, Brown & Freitas 1999). As borboletas pertencem à superfamília Papilionoidea, a qual se subdivide em sete famílias: Hedylidae, Hesperiidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae e Nymphalidae (Heikkilä et al 2012, 2015). O conhecimento acerca da taxonomia e ecologia de borboletas é extenso quando comparado aos demais insetos (Thomas 2005), o que tem contribuído para o entendimento de aspectos gerais de ecologia, evolução, biogeografia e conservação (Bonebrake et al 2010).

Segundo os hábitos alimentares dos adultos, as borboletas podem ser divididas em duas guildas principais: 1) espécies nectarívoras, que consomem primariamente o néctar das flores, e em alguns casos pólen, como recurso, e 2) espécies frugívoras, que se alimentam principalmente de frutas em decomposição, exsudação de plantas e excremento e carcaças de mamíferos (DeVries 1987). As borboletas frugívoras são representadas por alguns grupos da família Nymphalidae, e compreendem cerca de 50-75% da fauna de ninfalídeos dos neotrópicos, sendo taxonomicamente e ecologicamente diversificadas em ambientes tropicais (Brown 2005). Além disso, são facilmente amostradas com armadilhas atrativas permitindo a padronização de protocolos amostrais (Freitas et al. 2014). As borboletas frugívoras têm sido empregadas em estudos que comparam diferentes graus de perturbação (Shahabuddin and Terborgh 1999, Fermon et al. 2000, Barlow et al. 2007, Uehara-Prado et al. 2007, 2009, Ribeiro & Freitas 2012), efeito de borda (Bossart and Opuni-Frimpong 2009), restauração ecológica (Sant`anna et al. 2014), e em programas de monitoramento (Pozo et al. 2008; Costa-Pereira et al. 2013).

Assim como muitos outros grupos de organismos, em escala global as borboletas apresentam um gradiente latitudinal de diversidade, com mais espécies ocorrendo nos trópicos em comparação com as zonas temperadas (Shields 1989). Entretanto, ao observar padrões de riqueza em diferentes escalas, outros mecanismos (contemporâneos ou históricos) têm sido inferidos. Os padrões de riqueza já foram relacionados a grandes eventos climáticos do passado, como a retração das glaciações e teoria dos refúgios climáticos do Pleistoceno para um gênero de borboleta na América do Sul (Brown et al 1974). Ao testar hipóteses históricas e gradientes espaciais para este mesmo gênero (Heliconius), Rosser et al (2012) concluíram que o gradiente de riqueza de espécies pode ser explicado em parte pela variação das taxas de especiação e extinção. No Reino Unido e na América do Norte a disponibilidade de luz solar (hipótese da energia) já foi inferida como fator determinante dos padrões de riqueza (Turner 1987, Kerr et al 1998). No Canadá, Kerr et al (2001) apontaram que a diversidade de habitats mantém a riqueza de borboletas mais do que a evapotranspiração. Já para a região oeste/central da Europa e norte da África, um balanço entre a disponibilidade hídrica e energética foi apontada como a mais parcimoniosa para explicar o gradiente de riqueza. E ainda, que estes dois fatores atuam de forma indireta afetando a produtividade de plantas, ou diretamente na fisiologia das borboletas (Hawkins & Porter 2003). Mais recentemente, utilizando uma abordagem filogenética, Hawkins & DeVries (2009) testaram que o gradiente de riqueza de espécies de borboletas da América do Norte pode ser explicado pela hipótese do conservantismo de nicho tropical. Essa hipótese se baseia na premissa de que as espécies atuais se originaram em ambientes de condições tropicais, e que devido a inércia filogenética, existe uma barreira evolutiva para a colonização de áreas temperadas (Wiens & Donoghue 2004).

Estudos de comunidades em escalas locais já reconhecem a íntima relação das borboletas com o tipo de vegetação (New et al 1995), e alta fidelidade a microhabitats (Simonson et al 2001). A alteração de ambientes naturais pode desencadear em mudanças nos parâmetros de diversidade das borboletas, levando as populações a entrar em declínio e a diminuição da riqueza (Brown & Freitas 2000, Lawton et al 1998). Em alguns casos, a riqueza de espécies de borboletas em florestas pode vir a aumentar com a perturbação, em virtude da hipótese do distúrbio intermediário (Connel 1978, Wood & Gillman 1998). Outros trabalhos demonstraram que o corte seletivo pode reduzir o número de espécies localmente (Hill et al 1995), ou também não causar nenhum efeito específico sob esse parâmetro (Ribeiro & Freitas 2012). A resposta das comunidades de borboletas à distúrbios no habitat são diversas, o que dificulta o estabelecimento de um consenso geral. A delimitação da escala para abordar a questão e do grupo de borboletas pode levar a subestimativas do efeito da perda de habitat (Bonebrake et al 2010, Koh 2007). Por exemplo, estudos em pequenas escalas possuem uma tendência maior a registrar um aumento da diversidade comparando áreas não perturbadas com perturbadas do que estudos de grandes escalas (Hill & Hamer 2004). Já a comparação entre estudos que utilizam delimitações taxonômicas distintas, pode se tornar enviesada dado os atributos específicos de cada espécie, como dispersão a afinidade com o habitat (Horner-Devine et al 2003, Spitzer et al 1993).

Para que a conservação da diversidade tropical de borboletas seja efetiva é necessária a utilização de múltiplas abordagens em termos de escala. E em contrapartida a conservação das borboletas em regiões temperadas, as regiões tropicais ainda carecem de uma maior abrangência de dados de distribuição, e que sejam potencialmente comparáveis, para que se obtenha um maior conhecimento da real dimensão de toda sua diversidade ecológica. Em função do curto prazo e da otimização dos custos de monitoramento, determinados grupos ou espécies têm sido utilizadas como indicadoras de qualidade de habitat ou como representantes de outros grupos biológicos (Gardner et al. 2007). Neste sentido, dados os estudos disponíveis e as características presentes nas borboletas frugívoras, esta guilda parece ser modelo de estudo promissor para o desenvolvimento dessas atividades.

Contextualizando

A Mata Atlântica ocorre em um gradiente latitudinal ao longo da costa brasileira, estendendo seu território até algumas áreas do Paraguai e Argentina (Morellato e Haddad 2000, Tabarelli et al 2010). Localizada nas regiões mais populosas do país, a Mata Atlântica vem sofrendo historicamente com a pressão de distúrbios antrópicos e exploração de recursos naturais (Laurance 2009). Ações conservacionistas necessitam prover respostas rápidas das alterações e possíveis impactos causados sob os ambientes naturais. Invertebrados são cada vez mais utilizados em estudos que avaliam mudanças e perda de habitats, pois costumam ser bons indicadores e sensíveis a estes efeitos. Grupos de insetos, mais especificamente as borboletas, representam um excelente modelo para avaliar a dinâmica da comunidade em ambientes modificados. Em um contexto macroecológico, é de suma importância conhecer os padrões de diversidade destes organismos, para que possamos relacionar as alterações nestes padrões com possíveis distúrbios no ambiente. Para entender as reais dimensões da diversidade, a forma como está organizada, e o papel dos processos no estabelecimento de padrões são necessárias abordagens que levem em consideração a integração de diferentes escalas geográficas, analisando parâmetros de diversidade, história evolutiva e atributos funcionais dos organismos.

Objetivo geral

A presente tese tem como principal objetivo investigar padrões de diversidade das borboletas frugívoras em diferentes escalas macroecológicas utilizando métricas de comunidades. A tese está dividida em três capítulos:

Capítulo 1 – Neste capítulo montamos e disponibilizamos uma base de dados de comunidades de borboletas frugívoras da Mata Atlântica, a partir da compilação de estudos disponíveis na literatura e inventários históricos não publicados. Descrevemos a distribuição das diferentes categorias taxonômicas e discutimos a distribuição geográfica dos inventários bem como a necessidade de amostragens em locais com defasagem de informação.

Capítulo 2 – Neste capítulo testamos o efeito da fragmentação e da estrutura vertical de florestas na composição de assembleias de borboletas frugívoras da Mata Atlântica. São comparados os padrões de composição de espécies, estrutura filogenética e funcional das borboletas frugívoras, gerados por processos locais que ocorrem em duas dimensões distintas do espaço, mas que representam filtros abióticos semelhantes.

Capítulo 3 – Neste capítulo descrevemos o padrão de distribuição da riqueza de espécies de borboletas frugívoras da Mata Atlântica em uma escala geográfica regional através da modelagem de nicho, utilizando variáveis climáticas e de paisagem. Discutimos a contribuição individual do clima e da paisagem nos padrões obtidos e de que maneira nossos resultados podem contribuir para a conservação da diversidade deste organismo.

Capitulo 1: Artigo original no formato da revista a ser submetido (Ecology)

ATLANTIC BUTTERFLIES: A DATASET OF FRUIT-FEEDING BUTTERFLY COMMUNITIES FROM THE ATLANTIC FORESTS

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Introduction

Approximately 18,000 species of butterflies (Lepidoptera: Papilionoidea) have been described so far (Shields 1989, van Nieukerken et al. 2011). Most of the known diversity is concentrated in tropical areas, with more than 7,800 species present in the Neotropics (7,780 described species listed in Lamas 2004). Butterflies are probably the best known group of insects in terms of taxonomy and ecology (Thomas 2005), and their historical contribution to the development of scientific fields such as ecology, evolution and conservation are widely recognized (Bates 1862, Wallace 1865, Fisher et al. 1943, Gilbert and Singer 1975, Boggs et al. 2003). Moreover, some butterfly groups have intimate associations with other taxa and rapidly respond to disturbance in habitat conditions, which are characteristics of good biological indicators (Brown & Freitas 2000, Barlow et al. 2007).

Butterflies can be roughly divided into two guilds based on the main food resources of adults: (i) the nectar-feeding guild that gains most of its nutritional requirements from flower nectar; these species are almost exclusively flower visitors, being dominant in practically all butterfly assemblages worldwide. (ii) The fruit-feeding guild that obtains its comparable nutritional requirements from rotting fruits and fermented plant sap, and that is seldom or never observed visiting flowers (DeVries 1987, Freitas et al. 2014). In Neotropical habitats, this latter guild is represented by species from the Nymphalidae subfamilies Satyrinae, Biblidinae, Charaxinae and some species of Nymphalinae (comprising a polyphyletic group of genera previously treated as tribe Coeini) (Freitas & Brown 2004, Wahlberg et al. 2009). Fruit-feeding butterflies can be easily captured through standardized methods using bait traps, which allow the identification and releasing of specimens unharmed (Freitas et al. 2014). Bait-attracted butterflies can comprise 50-75% of all Neotropical Nymphalidae richness, depending on the locality (Brown 2005). As a result, butterfly-trapping data have been successfully employed in studies comparing the degree of habitat disturbance among sites (Fermon 2000, Uehara-Prado et al. 2007, Ribeiro and Freitas 2012), studies of population ecology (Grotan et al. 2012), patterns of diversity and distribution (DeVries and Walla 2001, Ribeiro and Freitas 2011), environmental monitoring and conservation research (Brown 1991, Pozo et al. 2008, Santos et al. 2016).

The Atlantic Forest Biome is considered a global hotspot for conservation, with a history of threat from landscape modification, climate change, and invasive species (Myers et al. 2000, Mittermeier et al. 2011, Bellard et al. 2014, Joly et al. 2014). This biome is composed of two main types of phytophysiognomies: the Ombrophilous Forest and the Semideciduous Seasonal Forest (Morellato & Haddad 2000). In addition, other vegetation types are found in the regions of contact with the Cerrado (Brazilian savanna), the Pampa (Brazilian grasslands), the Pantanal (a large seasonally flooded plain in central Brazil) and the Caatinga (seasonal xeric forest) domains (Ribeiro et al. 2009). Despite its great diversity, heterogeneity and high level of endemism, Atlantic Forest remnants account for less than 16% of its original distribution, with 80% of patches smaller than 50 hectares and poorly connected to larger forests remnants (Ribeiro et al. 2009).

In this study, we compiled information (species presence records) on fruit-feeding butterfly communities from more than a hundred localities in the Atlantic Forest biome. The present dataset contains 279 fruit-feeding butterfly species, representing 122 communities geographically distributed throughout the Atlantic Forest in Brazil and neighboring Argentina. Our priority was the reliability of data, and we therefore confirmed all species records and updated all the taxonomic nomenclature. The ATLANTIC BUTTERFLIES dataset represents a major effort to compile species lists of fruit-feeding butterfly communities for the Neotropical region, aiming to fill a knowledge gap about the distribution of this indicator group in the Atlantic Forest hotspot.

METADATA

CLASS I. DATASET DESCRIPTORS

A. Dataset identity:

Title: ATLANTIC BUTTERFLIES. A Dataset of Fruit-Feeding Butterfly Communities from the Atlantic Forests.

B. Data set and metadata identification codes:

Suggested Data Set Identity Codes:

ATLANTIC_BUTTERFLIES_sites.csv

ATLANTIC_BUTTERFLIES_species.csv

ATLANTIC_BUTTERFLIES_references.csv

C. Data set description

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Abstract:

Butterflies are one of the best-known insect groups and they have been the subject of numerous studies in ecology and evolution, especially in the tropics. Much attention has been given to the fruit-feeding butterfly guild in biodiversity conservation studies, due to the relative ease with which taxa may be identified and specimens sampled using bait traps. However, there remain many uncertainties about the macroecological and biogeographical patterns of butterflies in tropical ecosystems. In the present study, we gathered information of fruit-feeding butterfly species in local communities from Atlantic Forests of South America. The ATLANTIC BUTTERFLIES dataset –which is part of ATLANTIC SERIES datapapers – results from a compilation of 145 unpublished inventories and 64 other references, including articles, theses and book chapters published from 1949 to 2018. In total, the dataset contains 7,062 records (presence) of 279 species of fruit-feeding butterflies identified with taxonomic certainty, from 122 study locations. The Satyrini is the tribe with highest number of species

(45%) and records (30%), followed by Brassolini, with 13% of species and 12.5% of records. The ten most-common species correspond to 14.2% of all records. This dataset represents a major effort to compile inventories of fruit-feeding butterfly communities, filling a knowledge gap about the diversity and distribution of these butterflies in the Atlantic Forest. We hope that the present dataset can provide guidelines for future studies and planning of new inventories of fruit-feeding butterflies in this biome. The information presented here also has potential use in studies across a great variety of spatial scales, from local and landscape levels to macroecological and biogeographical research. We expect that such studies be very important for the better implementation of conservation initiatives, and for understanding the multiple ecological processes that involve fruit-feeding butterflies as biological indicators.

D. Key words: Atlantic Forest, biodiversity hotspot, butterfly communities, Lepidoptera, Neotropical region, Nymphalidae

E. Description:

The dataset was organized based on the delimitation of the Atlantic Forest biome resulting from the union of the following limits (*sensu* Muylaert et al. in review): 1) World Wildlife fund - WWF (Olson et al. 2001); 2) Ministry of the Environment of Brazil ("Ministério do Meio Ambiente" in Portuguese, IBGE 2017a); 3) the Atlantic Forest law (provides for the use and protection of native Atlantic Forest vegetation, as well as other measures, IBGE 2017b); and 4) Ribeiro et al. (2009). The dataset is mainly composed of unpublished data from the personal archives of Prof. Dr. Keith Brown Jr., collecting expeditions and research from the LABBOR group (Laboratório de Ecologia e Sistemática de Borboletas at Unicamp, Campinas, Brazil), and other institutions or personal contributors (69.4%). Scientific articles, book chapters and theses comprised 64 references (30.6 %).

Although theses and dissertations are not peer-reviewed publications, they are valuable sources of species lists and their content is only available in the repositories of universities and institution catalogs. In total, the present dataset consists of 7,062 specimen records, for 279 species distributed among 122 studied locations (Figure 1).

We compiled data for what we call here fruit-feeding butterflies "*sensu lato*", which include Nymphalidae species from the following subfamilies: Satyrinae, Charaxinae, Biblidinae (including Eubagini, a clade that is not usually sampled with bait traps), and some Nymphalinae (the bait-attracted species in 'Coeini'). More details are given in the "Taxonomy" section. Museum records (except in a single case explained below) were not included since museum collections do not represent exhaustive sampling of communities, and the resulting data would thus contain many incompletely sampled communities. Additionally, museum records would require a huge effort of verification to achieve the level of taxonomic reliability of the remainder of our dataset. For several early lists prepared by Prof. Dr. Keith Brown Jr. the voucher specimens were located, examined and identified whenever possible (all material is deposited in the ZUEC - Museu de Zoologia da Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil).

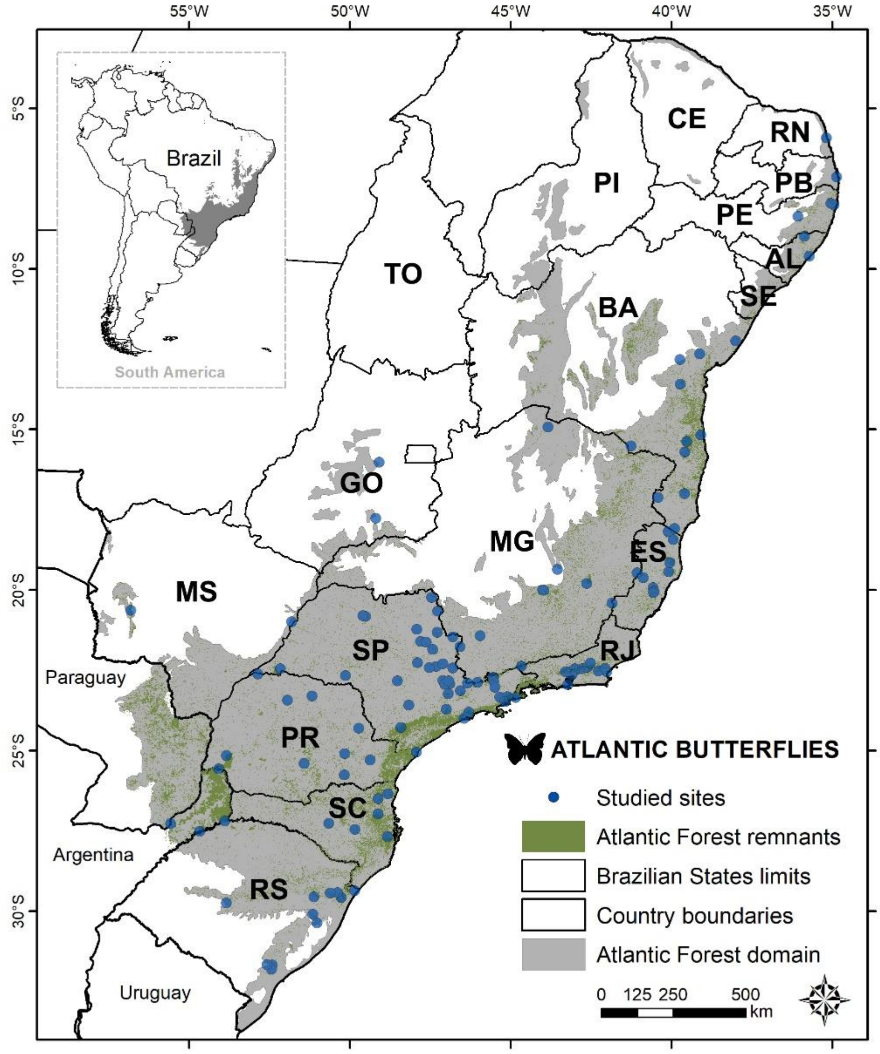

Figure 1. Distribution of the study sites in the ATLANTIC BUTTERFLIES dataset. The limit of Atlantic Forest Biome according to Muylaert et al., in review. The abbreviations of Brazil states are as follows: AL = Alagoas, BA = Bahia, CE = Ceará, ES = Espírito Santo, GO = Goiás, MG = Minas Gerais, MS = Mato Grosso do Sul, PB = Paraíba, PE = Pernambuco, PI = Piauí, PR = Paraná, RJ = Rio de Janeiro, RN = Rio Grande do Norte, RS = Rio Grande do Sul, SC = Santa Catarina, SE = Sergipe, SP = São Paulo, TO = Tocantins.

Most of the sampled communities are located in São Paulo state (n=37; 30%), followed by Rio Grande do Sul (n=13; 10%) and Rio de Janeiro (n=13; 10%), representing ca. 50 % of all communities in the dataset (Figure 2). The high concentration of communities sampled in these states may be due to the following reasons: First, the majority of unpublished data derives from Brown's scientific legacy. His expeditions covered many South American locations, from the 1960s until 2006. However, his research group was based in São Paulo state, at the University of Campinas (UNICAMP). Thus, most sampling effort is concentrated in the south of Brazil, simply as a consequence of logistics. Subsequent studies carried out by members of the Butterfly Laboratory Group (LABBOR) at UNICAMP followed this same trend, concentrating studies in São Paulo state, with a few exceptions (see Ribeiro & Freitas 2012).

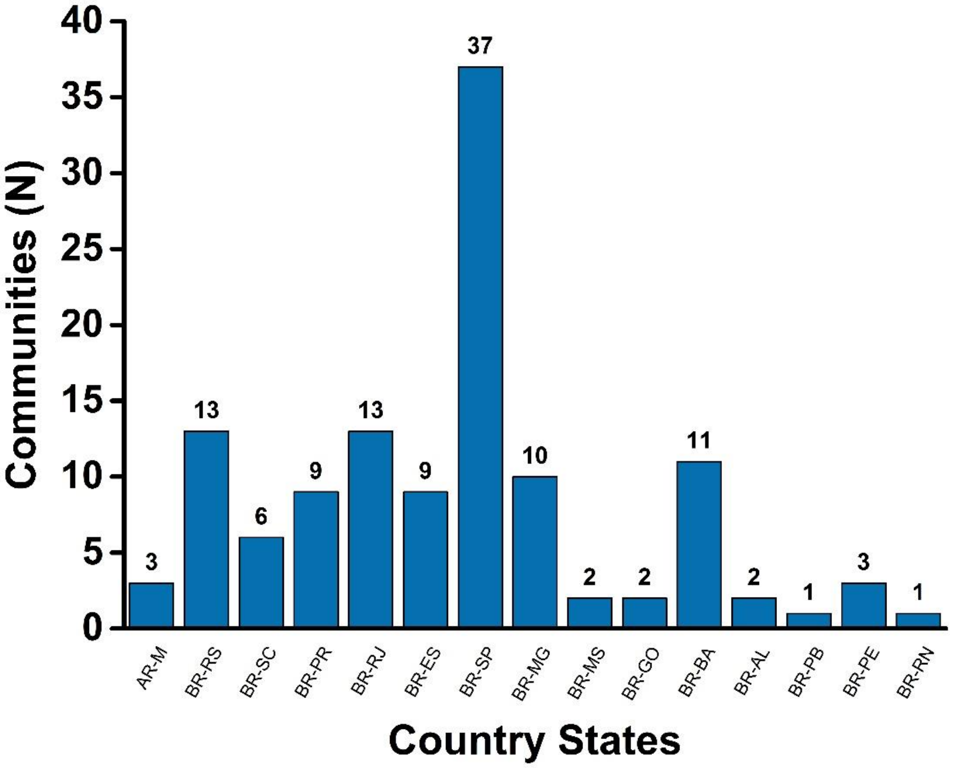

Figure 2. Number of communities sampled per country-state in the ATLANTIC BUTTERFLIES dataset, from a total of 122 communities. The abbreviations of states are

as follows: AR-M = Misiones, BR-AL = Alagoas, BR-BA = Bahia, BR-ES = Espírito Santo, BR-GO = Goiás, BR-MG = Minas Gerais, BR-MS = Mato Grosso do Sul, BR-PB = Paraíba, BR-PE = Pernambuco, BR-PR = Paraná, BR-RJ = Rio de Janeiro, BR-RN = Rio Grande do Norte, BR-RS = Rio Grande do Sul, BR-SC = Santa Catarina, BR-SP = São Paulo. The countries were abbreviated as AR = Argentina and BR = Brazil.

Although many localities have samples of fruit-feeding butterfly assemblages, it is notable that there is an absence of information in several areas of the Atlantic Forest, as evidenced in Figure 1. These areas correspond to eastern Minas Gerais State (MG), the southern region of Mato Grosso do Sul (MS), and the boundaries between the Atlantic Forest with dry forests in the interior of MG and Bahia (BA) states. In addition, there are no lists of sampled locations from Paraguay. The lack of information on butterfly diversity increases even more when other butterfly groups are considered, or when the compilation of studies is expanded to other ecosystems. Since butterflies are one of the best-studied insect groups, it is clear that there is a need for more inventories, as well as the organization of consistent databases for other butterfly (and moth) groups, and indeed insects in general.

The tribes with the most records were Satyrini (30%), Brassolini (12.5%) and Anaeini (9.3%). In addition, these same three tribes have the highest number of species recorded in our dataset (Figure 3). The relationship between high numbers of records and species richness probably explains this pattern. Satyrini and Brassolini are part of Satyrinae, the most species-rich butterfly subfamily in the Neotropical region, with approximately 1,200 described species (Lamas 2004).

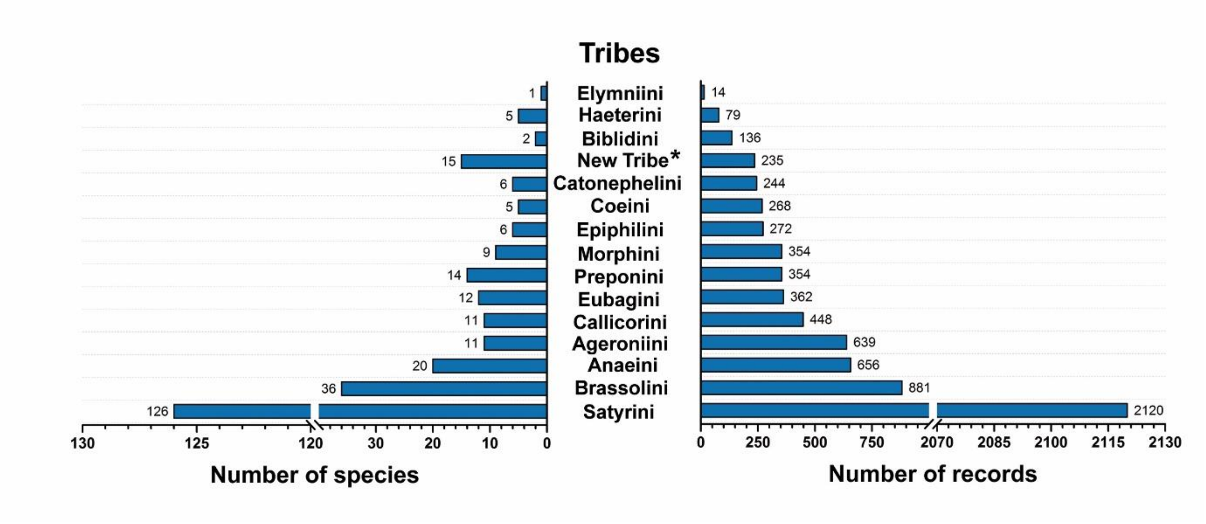

Figure 3. **Representativeness of the tribes in the ATLANTIC BUTTERFLIES dataset.** Number of species records in each tribe (left bars) and absolute frequency of tribes (right bars) based on the 7,062 records of fruit-feeding butterfly species. “New tribe” refers to the genus *Eunica* (see Taxonomy section).

The ten most frequently recorded species represent about 14.2% of total records (Figure 4). The three most recorded species were *Hermeuptychia hermes* (Satyrinae), *Hamadryas amphinome* and *Biblis hyperia* (Biblidinae). These three species have a wide geographical distribution and occur in different habitat types, such as forest fragments, trails, parks and even city squares. The genus *Hermeuptychia* represents a species complex that, by definition, is a group of related species characterized by unclear boundaries due to their phenotypical similarities (Sigovini et al. 2016). Until recent advances in the delimitation of species using DNA sequence data (Seraphim et al. 2014), most records of *Hermeuptychia* species in the Atlantic Forest were referred to as “*Hermeuptychia hermes*”. In this case, and as in other cryptic species, the taxa were lumped under a single name in our dataset (see Taxonomy section).

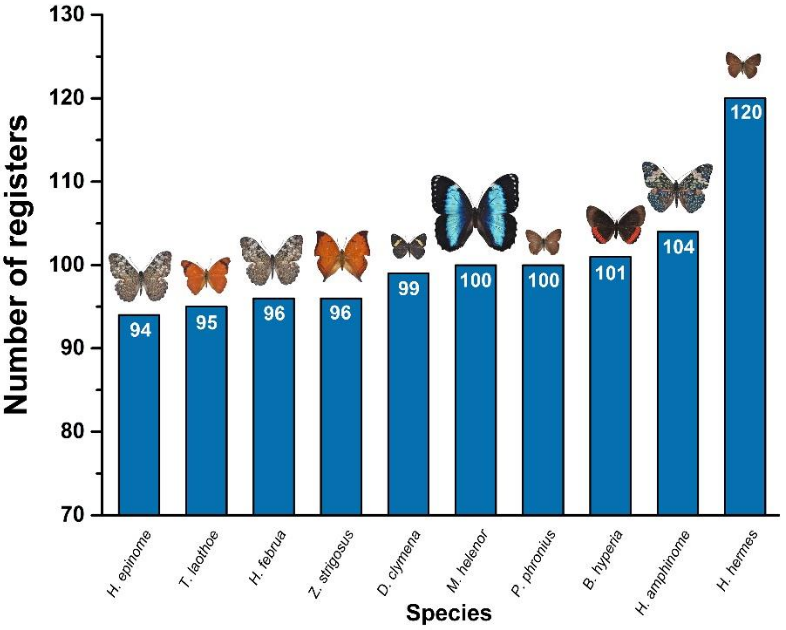

Figure 4. **Representativeness of the ten most frequently recorded species in the ATLANTIC BUTTERFLIES dataset.** Number of records of each fruit-feeding butterfly species in the 7,062 record dataset. The species and containing tribes include: *Hermeuptychia hermes** (Satyrini), *Hamadryas amphinome* (Ageroniini), *Biblis hyperia* (Biblidini), *Paryphthimoides phronius** (Satyrini), *Moprho helenor* (Morphini), *Diaethria clymena* (Callicorini), *Zaretis strigosus* (Anaeini), *Hamadryas februa* (Ageroniini), *Temenis laothoe* (Epiphilini), *Hamadryas epinome* (Ageroniini). * Both *Hermeuptychia hermes* and *Paryphthimoides phronius* consist of four and two lumped similar species, respectively (see Table 1).

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

Identity: A compilation of fruit-feeding butterfly communities of the Atlantic Forest Biome.

Originators: The ATLANTIC BUTTERFLIES project was coordinated by Jessie P. Santos and André V. L. Freitas, from University of Campinas (UNICAMP), and the database was assembled with help from all the other authors. This is part of the ATLANTIC SERIES, led by Mauro Galetti and Milton Ribeiro, from São Paulo State University (UNESP), Brazil.

Period of Study: Data sampling ranged from 1949 to 2018.

Objectives: The aims of this data paper were: (i) compile the information available in the Portuguese, Spanish, German and English literature about sampled sites of butterfly communities in the Atlantic Forest, focusing on fruit-feeding butterflies, and taxonomic revision; (ii) communicate the current state of knowledge on the fruit-feeding butterfly communities of the Atlantic Forest biome; and (iii) provide data for future sampling efforts, testing of hypotheses at a great variety of scales –from local to landscape, regional and macroecological perspectives–, and contribute to conservation decisions involving these important biological indicators.

Abstract: Same as above.

Sources of funding: The compilation of this dataset was supported by São Paulo Research Foundation (FAPESP) grants 2011/50225-3, 2013/50297-0 (AVLF) and 2013/50421-2 (MCR), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) fellowships (JPS), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), grants 563332/2010-7, 303834/2015-3, 421248/2017-3 (AVLF), 150319/2017-7, 312045/2013-1 (MCR) and 312292/2016-3 (MCR), National Science Foundation (NSF), DEB-1256742 (AVLF); and Procad/CAPES project 88881.068425/2014-01 (MCR).

B. Specific subproject description

Site description:

We adopted a broad delimitation of the Atlantic Forest Biome following Muylaert et al. (in review) – see Figure 1 – which encompasses several ecotone regions, thus ensuring the more comprehensive inclusion of butterfly inventories in regions wherever Atlantic Forest occurs. The Atlantic Forest occurs across an extensive latitudinal gradient in coastal Brazil, extending west to inland areas of Brazil, Paraguay and Argentina (Morellato & Haddad 2000, Tabarelli et al. 2010). Around 92% of its original distribution was located along the Brazilian coast, sharing complex limits with other domains such as the Cerrado (Brazilian savanna), the Pampa (Brazilian grasslands), the Pantanal (a large seasonally flooded plain in central Brazil) and the Caatinga (seasonal xeric forest) (Ribeiro et al. 2009, Ribeiro et al. 2011). The Atlantic Forest comprises tropical and subtropical evergreen and semideciduous forests with highly heterogeneous environmental conditions, and other minor ecosystems such as oceanic islands, coastlines, rocky shores, dunes and coastal sand forests (known locally as "restingas"), mangroves and marshes, and high-altitude grasslands and swamps (Morellato & Haddad 2000).

Today, about seventy percent of the Brazilian population (~145 million people) are settled in areas originally covered by the Atlantic Forest (IBGE 2013). Thus, several anthropogenic activities, including logging, agriculture, development of pasture, and urban expansion have contributed to the degradation of the ecosystem (Tabarelli et al. 2005, 2010). Due to anthropogenic disturbance, coupled with the high rates of endemism and diversity, the Atlantic Forest has acquired the status of a biodiversity hotspot (Myers et al. 2000, Mittermeier et al. 2011). In addition, the Atlantic Forest is one of the hotspots most vulnerable to global warming, climate change, land use modification, and invasive species (Bellard et al. 2014).

Dataset source:

Data were gathered from three main sources: (i) unpublished lists of Prof. Dr. Keith S. Brown Jr and other members of the LABBOR group (Laboratorio de Ecologia e Sistemática de Borboletas); (ii) articles and theses in online academic databases (e.g., ISI Web of

Knowledge, Scielo, Scopus, Google Scholar); and (iii) other unpublished butterfly species lists from other research groups and collaborators.

Compilation methods:

Our dataset results from the compilation of fruit-feeding butterfly species recorded in a number of localities in the Atlantic Forest. We selected all available publications, irrespective of sampling method employed (entomological nets, bait traps or both), or taxonomic range (all Nymphalidae or the fruit-feeding guild only). To decrease bias and uncertainty in species taxonomy, we disregarded papers, theses, and other publications whose specimens could not be checked, or those based on a single butterfly species. Every study site received an individual identification code and was classified according to its specific location (Country, State, Municipality and Location), including its geographic coordinates (latitude, longitude). Geographic coordinates are presented with a value of precision in meters, including the values 10, 100, and 1,000, which represent an estimate of the maximum distance between the georeferenced point and the point at which the species was actually recorded. When localities could not be georeferenced more with greater precision than 1000 m, the field value is "Not precise". A further field contains the total protected area of conservation units containing study sites, where relevant. Missing information about a study site was indicated as “NA” in each dataset field.

Butterfly communities were compiled from the following literature: Almeida et al. (1986), Araujo (2016), Beirão (2016), Bellaver et al. (2012) Beltrami et al. (2014), Biezanko (1949), Brito et al. (2014), Brown (1992), Brown and Freitas (2003), Brown and Mielke (1968), Camargo (2006), Cardoso (1949), Carneiro et al. (2008), Carreira (2015), Castro (2008), Corso and Hernandez (2012), Dessuy and Morais (2007), Dolibaina et al. (2011), Ebert (1969), Filgueiras (2015), Francini et al. (2011), Freitas et al. (2016), Fucilini (2014), Garcia-Salik et al. (2014), Graciotim and Morais (2016), Gomes-Filho (2003), Gueratto (2018), Iserhard and Romanowski (2004), Iserhard et al. (2010), Marchiori (2012), Melo (2014), Mielke (1994), Mielke and Casagrande (1997), Mielke et al. (2011), Neves and Paluch (2016), Nunez-Bustos (2008), Nunez-Bustos (2009), Nunez-Bustos et al. (2011), Paluch et al. (2011), Paluch et al. (2016), Pedrotti et al. (2011), Pereira et al (2017), Ribeiro (2006), Ribeiro et al. (2012), Richter 2018, Santos et al. (2011), Santos et al. (2017), Schantz (2000), Silva et al. (2010), Silva et al. (2012), Silva et al. (2015), Soares et al. (2011), Soares et al. (2012), Spaniol and Morais (2015), Teixeira (2003), Teixeira (2005), Thiele et al. (2014), Uehara-Prado et al. (2004), and Zacca et al. (2011).

Taxonomy:

All species records had their taxonomic classification revised and updated, mostly following the classification presented in Lamas (2004), Freitas & Brown (2004), and Wahlberg et al. (2009) (see Warren et al. 2017 for images of most Neotropical taxa). For some specific clades, the taxonomy was modified following recent studies (e.g. Ortiz-Acevedo et al. 2017, Barbosa et al. 2015, Freitas et al. 2014, 2015, Zacca et al. 2013). We discarded taxonomically uncertain records in species lists where specimens could not be examined, such as [genus followed by “sp.”, “cf” species]. A single case of “ca” species was included (“*Paryphthimoides_ca_difficilis*”) since this represented an undescribed taxon (T. Zacca et al. in prep.). The genus *Eunica* was classified within the Catonephelini by Lamas (2004), but was here placed in “New Tribe” according to Freitas et al. (in prep.).

Species recently described, with the name revalidated, or discovered as cryptic species complexes, were lumped under a single taxon name (see Table 1). In all cases, we adopted the name most frequently used in previous literature and included in the dataset. We took this decision to maintain species records where it was not possible to verify identifications, instead of discarding the data. For example, all four Atlantic Forest species from the genus *Hermeuptychia* (Seraphim et al. 2014) were lumped under the name *Hermeuptychia hermes*. In the case of *Praepedaliodes*, since several new cryptic species have been described recently (Pyrcz et al. 2018), it is not possible to know which species were recorded in some old lists without preserved material available (e.g. Soares et al. 2011). All cases of lumped taxa in the present dataset are presented in Table 1.

Table 1. List of fruit-feeding butterfly taxa that were lumped under single species names. This measure was adopted to avoid discarding information from species records in old lists where it was not possible to verify taxonomy from voucher specimens. The left column contains the valid and actual names of taxa belonging to species complexes. The column at the right has the single name representing the records of species complexes in the present dataset.

Taxon	**Species name in dataset**
Hermeuptychia hermes *Hermeuptychia atalanta* *Hermeuptychia fallax* *Hermeuptychia gisella*	*Hermeuptychia_hermes*
Praepedaliodes phanias *Praepedaliodes francinii* *Praepedaliodes landryi* *Praepedaliodes duartei* *Praepedaliodes granulata*	*Praepedaliodes_phanias*

Praepedaliodes pawlaki *Praepedaliodes sequeirae* *Praepedaliodes zaccae*	
Euptychoides spp. (several undescribed species)	*Euptychoides_castrensis*
Pharneuptychia spp. (several undescribed species)	*Pharneuptychia_pharella*
Paryphthimoides phronius *Paryphthimoides eous*	*Paryphthimoides_phronius*
Paryphthimoides poltys *Paryphthimoides vestigiata*	*Paryphthimoides_poltys*
Pareuptychia ocirrhoe *Pareuptychia hesionides*	*Pareuptychia_ocirrhoe*

C. Data limitations and potential enhancements

The compilation of butterfly community data, including gathering the maximum number of species records possible and insuring taxonomic reliability, is a challenging mission for two main reasons. Firstly, many locations do not have a considerable number of butterfly inventories available in literature, or simply do not have any. For a better understanding of butterfly diversity in Atlantic Forest, future inventories should invest in filling the sampling gaps presented here. Secondly, the taxonomy is obviously dated in all lists made before the publication of the Checklist of Neotropical Butterflies (Lamas 2004), and in most of the few lists published subsequently. New molecular techniques applied in systematic research have brought substantial taxonomic modifications, affecting the precision of several records due to taxonomic uncertainty in older species lists. In the present dataset, we have tried to minimize the loss of information by lumping two or more species under a single name. Additionally, we reviewed all species aiming to avoid false positive records, or inconsistencies in species distribution.

Most studies in the dataset have different sampling efforts, methods, and taxonomic scope. This results in differences in the number of collectors, number of traps, bait types, sampling duration, and target groups. Most bait trap studies have their focus specifically on fruit-feeding butterflies (*sensu* Freitas et al. 2014), meaning that some taxa may be omitted, such as the facultative fruit-feeders in the species-rich genus *Dynamine* (Biblidinae: Eubagini), *Mestra* spp. (Biblidinae: Biblidini), some canopy dwelling *Morpho* (Satyrinae: Morphini), and non-feeding *Brassolis* (Satyrinae: Brassolini). In the present data paper, we decided to include all of the above species for the sake of taxonomic completeness.

This dataset is an effort to assemble the great majority of information about fruit-feeding butterfly communities sampled in Atlantic Forest. Even if not as extensive as the metadata of better-studied groups, it represents the best information available for butterfly communities in this biome. Recently fruit-feeding butterflies have been used as an indicator group in monitoring programs to evaluate the effectiveness of conservation units in Brazil (Costa-Pereira et al. 2013, Santos et al. 2016). Realizing the full potential of implementing this type of initiative depends on prior knowledge of the diversity and distribution of indicator species. Motivated by the important role played by this fraction of the butterfly fauna in ecological research, we designed the dataset to: i) encourage the execution of butterfly inventories and the proper publication of records; ii) provide original information on the species richness of Atlantic Forest butterflies; and iii) encourage the investigation of macroecological and biogeographical patterns through an approach using multiple groups that includes butterflies.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: July 2018

Latest archive date: July 2018

Metadata status: Last updated 10 July 2018, version submitted

Data verification:

Species records in each community were confirmed, and the taxonomy checked. Most geographic coordinates represent an approximation of the survey locality reported in decimal degrees (Datum WGS 84) using maps, coordinates provided by personal information of authors, or publications. The precision of the georeferenced location was indicated using several categories of precision.

B. Accessibility

1. Storage location and medium: The original ATLANTIC BUTTERFLIES dataset can be accessed in the ECOLOGY repository. Updated versions of this dataset and some extra information for both ATLANTIC BUTTERFLIES and other ATLANTIC SERIES datasets can be accessed at https://github.com/LEEClab/Atlantic_series

2. Contact persons: Jessie Pereira dos Santos (jessiepereira@gmail.com), André Victor Lucci Freitas (baku@unicamp.br), Thadeu Sobral-Souza (thadeusobral@gmail.com), or Milton Cezar Ribeiro (miltinho.astronauta@gmail.com).

Copyright restrictions: None.

Proprietary restrictions: Please cite this datapaper when using the current data in publications or teaching events.

Costs: None.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

We divided the dataset into three complementary files. The first (ATLANTIC_BUTTERFLIES_sites.csv) describes the characteristics of the sampled localities. The second (ATLANTIC_BUTTERFLIES_species.csv) contain species locality records (presence only), with taxonomic categories and information (class, order, family, subfamily, tribe, genus, species, and species authors). The third (ATLANTIC_BUTTERFLIES_references.csv) contain the references cited, the type of reference and the authors.

A. Data set file

Identity: `ATLANTIC_BUTTERFLIES_sites.csv`

Size: 17 columns and 123 rows records, including header row, 24 KB**.**

Format and storage mode: comma-separated values (.csv)

Header information: See column descriptions in section B.

Alphanumeric attributes: Mixed.

Data anomalies: If no information is available for a given record, this is indicated by “NA”.

Identity: `ATLANTIC_BUTTERFLIES_species.csv`

Size: 9 columns and 7,063 rows records, including header row, 789 KB**.**

Format and storage mode: comma-separated values (.csv)

Header information: See column descriptions in section B.

Alphanumeric attributes: Mixed.

Data anomalies: If no information is available for a given record, this is indicated by “NA”.

Identity: `ATLANTIC_BUTTERFLIES_references.csv`

Size: 6 columns and 210 rows records, including header row, 41 KB**.**

Format and storage mode: comma-separated values (.csv)

Header information: See column descriptions in section B.

Alphanumeric attributes: Mixed.

Data anomalies: If no information is available for a given record, this is indicated by “NA”.

B. Variable information

1) Table 2. Site information in the ATLANTIC BUTTERFLIES dataset. Description of the fields related with the study site of the ATLANTIC_BUTTERFLIES_sites.csv.

Type of information	**Variables**	**Description**	**Levels**	**Example**
SITE INFORMATION	**Sites_ID**	Identification code for each study site	bor1001-bor1122	bor1048
	Country	English name of the country	Brazil, Argentina	Brazil
	State	State or Province of the study site based on the geographic coordinates	15	Sao Paulo
	Municipality	Municipality of the study site based on the geographic coordinates	112	Campinas
	Study Location	Local name of the study site(s) based on the information in the references	122	Parque Nacional do Itatiaia
	Latitude	Corrected and transformed coordinates of latitude in decimal degrees (Datum WGS84)	decimal degree	-22.8219

	Longitude	Corrected and transformed coordinates of longitude in decimal degrees (Datum WGS84)	decimal degree	-47.10806
	Precision	Coordinate precision of the study site (meters)	10	30
	Reserve Area	Area of Reserves, Parks, Conservation Units sampled in study locations	Ha	10.653
	Altitude	Meters above sea level range reported in the reference paper or obtained later based on the corrected coordinates	0 to 2600	570-600
	Altitude1km	Altitude in meters above sea level, from the Hydro-1K dataset (United States Geological Survey – USGS, 2001. HYDRO 1K: Elevation Derivative Database. Available from: <http://edc.usgs.gov/products/elevation/gtopo30/hydro/namerica.html>) on May 5th	1 to 2534	950
	A_mean_temp	Annual mean temperature. WorldClim v. 1.4., in Celsius degrees, available in http://www.worldclim.org/version1. Access on May 5th, 2017.	9.38 to 25.8	26.4

	A_rainfall	Annual rainfall. WorldClim v. 1.4., in mm, available in http://www.worldclim.org/version1. Access on May 5th, 2017.	632 to 2902	200
	Olson200gr	Olson bioregion (Olson et al. 2001), represented by G200_REGIO column of the shapefile wwf_terr_ecos	3	Atlantic Forests
	Olsoneconame	ECO_NAME column of the shapefile wwf_terr_ecos available in WWF website (Olson et al. 2001).	14	Caatinga
	Ribeirovegtype	Type of vegetation sensu Ribeiro et al. (2009)	10	Floresta Estacional Decidual
	BSRs	Type of biogeographical sub-regions (BSRs) sensu Ribeiro et al. (2009)	9	Serra do Mar

2) Table 3. Species information in the ATLANTIC BUTTERFLIES dataset. Description of the fields related to fruit-feeding butterfly species records of the ATLANTIC_BUTTERFLIES_species.csv.

Type of information	**Variables**	**Description**	**Levels**	**Example**
SPECIES INFORMATION	**Sites_ID**	Identification code for each study site	bor1001-bor1122	bor1048

	Class	Taxonomic class	Insecta	Insecta
	Order	Taxonomic order	Lepidoptera	Lepidoptera
	Family	Taxonomic family	Nymphalidae	Nymphalidae
	Subfamily	Taxonomic subfamily according to Wahlberg et al 2009	4	Satyrinae
	Tribe	Taxonomic tribe according to Wahlberg et al 2009	15	Brassolini
	Genus	Taxonomic genus	86	Morpho
	Species	Taxonomic species	279	Caligo_arisbe
	Species Authors	Name and year of the species' authors	125	(Linnaeus, 1758)

3) Table 4. Reference information in the ATLANTIC BUTTERFLIES dataset.

Description of the fields related to the reference information of the ATLANTIC_BUTTERFLIES_references.csv.

Type of information	**Variables**	**Description**	**Levels**	**Example**
REFERENCE INFORMATION	**Sites_ID**	Identification code for each study site	bor1001-bor1122	bor1048
	Ref_number	Number of each reference	0001-0209	0020
	Authors	Name of the authors	66	Brown
	Type	Type of reference publication	5	Article
	References	Complete reference with the name of authors, title, year, and publication	61	Unpublished data

	Voucher specimens	Collection, Museum, or other location which specimens are deposited	31	Museu de Zoologia Adao Jose Cardoso, Universidade Estadual de Campinas

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

1. Data request history: None

2. Data set updates history: None

3. Data entry/verification procedures

G. History of data set usage:

Santos (2018) used part of this dataset to investigate the effects of landscape and climate in the patterns of fruit-feeding butterfly species richness in the Atlantic Forest Biome.

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Capítulo 2: Artigo original no formato da revista a ser submetido (Oikos)

Fragmentation and vertical structure of forests engender similar patterns on fruit-feeding butterfly assemblages

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Abstract

Forest structure and processes associated to habitat change are expressed in distinct spatial dimensions, and comparisons between the patterns they generate allow elucidating its triggering factors and possible impacts. In the present study, we used two datasets of fruit-feeding butterfly assemblages from Atlantic forest sites, to test the effect of fragmentation and vertical forest structure on assembly patterns. We compared taxonomic and phylogenetic composition in relation to continuous and fragmented samples in one site and canopy and understory in another. We also used the body size, and two indexes t based on morphological measures to explore the relation of flight traits with the habitats. We found alterations in species composition between continuous and fragmented areas as well as for understorey and canopy, but in both cases did not imply in phylogenetic structuration. Butterfly species that inhabit continuous and understorey forests had larger and slender bodies, and a lesser wingbeat flight. We detected a moderate phylogenetic signal for forewing length, but the sign was not detected in metacommunity structure. Our results demonstrated congruent patterns of species and trait distribution generated by fragmentation and forest vertical structure, suggesting that both may act through a similar mechanism of selection. However, the difference of traits and species composition between vertical strata had better statistically support than the comparison between continuous and forest fragments. We associated this discrepancy to a distinction in community response time, since habitat change from understorey to canopy are more abrupt than to forest reduction caused by fragmentation. Nevertheless, fragmentation represent a physiological filter to closed-forest species at long term, implying in serious loss of local diversity. Our study demonstrated that different habitat gradients can generate similar patterns, and highlights the implications of our findings for conservation, since the fragmentation is a gradient resultant from anthropic disturbance in natural systems.

Introduction

Habitat structure can be defined as the arrangement of biotic or abiotic matter across horizontal and vertical physical space, and is an important component of ecological studies (McCoy and Bell 1991, Beck 2000). The impact of habitat structure on organisms still can extends beyond the ecological time, which potentially lead to evolutionary changes in morphology, behaviour and other traits due to prolonged interaction of organisms with physical structure (McCoy and Bell 1991). Therefore, understand how changes in the habitat structure affect the composition of species assemblages is a key step for biodiversity management and conservation.

In forest ecosystems, plant communities are the main components of the physical structure of habitats, thus influencing the distribution of animal species and interaction between them (Cramer and Willig 2002, Brose 2003, Hamer et al. 2003). The intensification of human activities have been unceasingly converting large expanse of habitats into a number of small patches isolated from each other by a matrix of distinct habitats (Laurance & Williamson 2001, Fahrig 2003). Forest fragmentation processes increases the proximity of interior forests with its edges, which lead to the emergence of edge effects (Saunders et al. 1991, Murcia 1995, Broadbent et al. 2008). The edge effects impact the forest habitat structure, altering microclimates (Willians-Linera et al. 1998) thus promoting changes in plant and animal species composition (Willians-Linera et al. 1998, Baker et al. 2007).

The forest ecosystems also have multiple vertical layers of vegetation, and this vertical complexity is one of the main factors contributing to the higher diversity of tropical forests (King et al. 2006, Moffett 2013). The variation of environmental variables such as luminosity, temperature and humidity on vertical dimension generate a great diversity of niches. Therefore, the differential occupation of these niches result in changes of species composition between understorey and the canopy forests. This phenomenon is known as vertical stratification and is recognized for several zoological taxa (Basset et al. 2003, Vieira et al. 2003, Walther 2002, Grimbacher & Stork 2007).

The guild of fruit-feeding butterflies (i.e. feeding on fermented fruits and exudates) represents a significant portion of butterfly diversity in tropical forests (DeVries 1987, Freitas et al. 2014).). They are considered an excellent model group for ecological studies, environmental monitoring and conservation practices (Bonebrake et al. 2010, Brown 1991, Santos et al. 2016). The patterns of butterfly assembling in response to fragmentation are commonly associated to species-specific responses to hostplant availability, dispersion capacity and behaviour (Shahabuddin & Terborgh 1999, Benedick et al. 2006, Uehara-Prado et al. 2007, Filgueiras et al. 2016). Likewise, differences in species composition of fruit-feeding butterflies in forest vertical strata are addressed to environmental variation, but potential biological hypothesis cannot be discarded (Fermon et al. 2005, Molleman et al. 2006, Fordyce & DeVries 2016, Santos et al. 2017).

Biotic and abiotic factors drive the differences of butterfly life history traits in fragmented landscapes, thus playing an important role in assembly processes. This suggests that the habitat conditions may operate as an environmental filter in butterfly trait evolution (Pavoine et al. 2014). For example, large bodied butterflies seem to be more vulnerable to fragmentation processes, being more frequent in the interior of continuous forests (Shahabuddin and Ponte 2005, Uehara-Prado et al. 2005, Benedick et al. 2006). In the case of vertical distribution, larger butterflies are predominantly sighted in the forest understorey (DeVries 1988, Schulze et al. 2001, Graça et al. 2017). Therefore, the species composition of butterflies in fragmented or continuous landscapes, and canopy or understory of forests may reflect the adaptations of its morphological traits.

Morphological traits like wing and body size are related to the flight performance of butterflies (Chai 1990, Chai & Srygley 1990, DeVries et al. 2010). Given the importance of flight for the adults, we may expect that the butterfly species have adaptations to specific habitat types. However, phylogenetic constraints may also play a role in the assembly patterns since species traits such as hostplant use or phenotype are often fixed along clades (Schulze et al. 2001). In this way, we hypothesized that species with certain set of traits related to continuous forest habitats will be more prevalent in understory species, whereas species living in the canopy will have similar traits to those living at the edge of fragments. In the present study, we compared the effects of forest fragmentation and vertical structure in the assembly patterns and trait evolution of fruit-feeding butterflies.

We aimed to answer the following questions: (I) Are forest fragmentation and forest vertical structure two equivalent habitat filters? If so, both habitats will generate similar species and traits assembly patterns. (II) Are the differences in fruit-feeding butterfly assemblages between fragmented and continuous areas or canopy and understorey strata dependent of phylogenetic relatedness? If they are, then we may expect that more related species would co-occur (phylogenetic clustering) in a certain habitat type. (III) Habitat structure determines the variation of morphological traits, or this is an indirect effect due to the phylogenetic relatedness?

Methods

Sampling areas

The present study compares two distinct datasets based on a same sampling protocol in two areas of Atlantic Forest in São Paulo state, southeastern Brazil. The first study was conducted in the municipality of Cotia (23°35’; 23°50’S, 46°45’; 47°45’W) at four sites inside of a continuous large forest area (Morro Grande Reserve), and four forest fragments. The altitude varies from 800-1000 m and the average annual temperature is 20.4 ºC. Five bait traps suspended 1.8 m above ground and distant at least 20 m for each other composed each sampling unit (hereafter SU). The total sampling effort was of 32.00 trap-days, from November 2001 to May 2002. More details about study site, sampling and general results can be found in Uehara-Prado et al. (2007).

The second study was carried out in a continuous forest at Serra do Japi Biological Reserve (23°13’S, 46°56’ W), in the municipality of Jundiaí. The altitude varies from 700 m to 1300 m and average annual temperature is 19ºC. In this site, six SUs consisting of ten traps distant 20 m from each other and alternating between understorey (1.5 m above the ground) and canopy (ca. 12m above the ground) were stablished. The sampling effort totalized 28.00 trap-days, from October 2011 to September 2012. More details about study site, sampling and general results can be found in Santos et al. (2017).

Morphological traits

Selective forces such as habitat use and predation influence the flight behaviour of butterflies, wherefore morphological traits related to flight may reflect the ecologic adaptations. (Chazot et al. 2016, Rossato et al. 2018). We selected five morphological traits, and from these we obtained a few indexes that represented characteristics of flight performance: 1) forewing length (*Fw*), 2) hindwing length (*Hw*), 3) thorax width (*Tw*), 4) thorax length (*Tl*), and 5) body length (*Bl*). Each trait value was defined as the mean of each trait measured from 3 to 5 male individuals per species. *Fw* and *Hw* were measured from the base of wing insertion to apex, *Tw* as the distance between forewing insertions in the thorax, and *Bl* was measured from the tip of thorax to tip of abdomen (Chai & Srygley 1990). We used the *Fw* as an indirect measure of butterfly body size. The other measures were used to obtain the following indexes: (1) a thorax index ($TI = Tl / Tw$) as a proxy of body shape (from slender to stout, as the index change from higher to lower values) and flight speed (where higher index values represent slower flights). (2) Wing shape index ($WI = Fw / Hw$), a proxy of type of flight, from deeper wingbeats and larger stroke amplitudes (lower values) to smooth wingbeat and smaller amplitudes (higher values).

Statistical Analysis

To explore the patterns of species composition between the fragmented and continuous areas of Morro Grande, and vertical strata in Serra do Japi we performed a correspondence analysis (CA). The CA is a multivariate ordination method used to explore the relationship between variables (Legendre & Legendre 1998). The two main axes generated in CA are responsible for concentrating most data variance, and the distribution of species and samples in ordination space allow interpret the association patterns between them. The statistical support for the distinction of species composition between samples was accessed with PERMANOVA. The comparison of butterfly trait variation between fragmented and continuous areas in Morro Grande, and canopy and understory forest in Serra do Japi was assessed using the t test or

Welch's t test in cases of unequal variances. In this comparison we did not remove the taxonomic relatedness of species (the average trait was calculated using the species presence on samples and its abundance-weighted). These analyses were performed using the PAST software (Hammer et al. 2001).

Phylogenetic trees

The phylogenetic relationships of fruit-feeding butterflies were reconstructed using the package phytools in R Language (Revell 2017). We used the Nymphalid family tree available on Wahlberg et al. 2009 to estimate the divergence time of species in our trees. We pruned the branches corresponding to species that were absent from our dataset and included the species that are absent in the original tree using the topologies from specific taxonomy literature and specialist consulting (Freitas & Wahlberg unpublished). Nodes created by the insertion of absent species on the original tree had their lengths estimated from half of the original branch length. In total, we built two trees, one to each community (Supplementary material Appendix 1, Fig. A1).

Phylogenetic analyses

The data matrices of species abundance, the pairwise phylogenetic distances of species and environmental variables for each community were submitted to the phylogenetic fuzzy weighting method, which result in a matrix (P) describing phylogeny-weighted species composition of the communities (Pillar & Duarte 2010, Debastiani & Pillar 2012). To evaluate the influence of fragmentation and vertical stratification on taxonomic and phylogenetic structure of assemblages, principal coordinates of phylogenetic structure (PCPS) were generated (Duarte 2011, Debastiani & Duarte 2014). The axes obtained from PCPS represent phylogenetic eigenvectors, which means a phylogenetic gradient across the metacommunity (Debastiani & Duarte 2014). The PCPS axes were used in a generalized linear model (GLM) and the significance is tested confronting the estimated parameters against those obtained using null models. One null model (site shuffle) is a classical permutation-based procedure assuming independence between communities and sites. The site shuffle consists of computing a statistic test based on the association between each PCPS axis and predictor variables. The sampling units are freely permuted and at each permutation, a null test statistics is computed. As long as the proportion of permutations in which the null test statistics exceeded the observed, is defined the probability of obtaining the observed statistic by chance. This procedure will capture the influence of the environmental gradient on both phylogenetic and species composition (Duarte et al. 2016).

The second null model (taxa shuffle) permutes the phylogenetic relationships and then estimates the GLM parameters to build the distribution under the null hypothesis (similar to site shuffle). However, it consists in the free permutation of the terminal tips (species) across the phylogenetic trees to generate random phylogenetic relationships, and compute pairwise null phylogenetic distances among species. In the case of GLM, null PCPS are calculated from null matrices at each permutation step. The null PCPS are then submitted to procrustean adjustment, and fitted values between observed PCPS and null PCPS are obtained. Each selected adjusted null PCPS were used as response variable in GLM using environmental variables as predictor. Finally, the F null values and the probability under the null hypothesis is calculated.

The observed values are independently compared with those generated by both null models. If the observed value is unlikely to be generated under the null hypothesis of the site shuffle model, this suggests that the environmental affects the distribution of species. Thereafter, the taxa shuffle model is examined, and if null hypothesis is rejected, it can be concluded that the effect of environmental on structuration of communities is dependent of phylogenetic relatedness among species (Duarte et al. 2016). These analyses were conducted using the packages PCPS and SYNCSA (Debastiani & Pillar 2012, Debastiani & Duarte 2014).

Functional analysis

To detect the presence of phylogenetic signal on *FL*, *TI* and *WI* indexes, the K statistic value for both communities was calculated. The K statistic calculate the degree of phylogenetic constraint in species resemblance (Blomberg et al. 2003, Molina-Venegas and Rodriguez 2017). The K values vary from 0 to >1: Values close to 0 indicate no phylogenetic signal (the trait has evolved independently of phylogeny); values close to 1 indicate trait evolution according to the Brownian motion (i.e. random walk divergence in species resemblance); values >1 reflect that close relatives are more similar than expected under Brownian motion (strong phylogenetic signal).

To understand the role of body size in communities sorting along habitat types, we calculated the community-weighted mean (CWM) using the forewing length, and plotted against the first CA axis of each habitat case (fragmentation and vertical strata).

We used a null model approach to test the influence of environment on species and trait composition (Duarte 2017, Peres-Neto 2017). Similar as used for the PCPS axes, this method uses permutation models to test the effect of habitat structure on CWM variation, and on species composition dependent of CWM. First, the communities are freely permuted (site shuffle) to capture the influence of environment in species and functional composition. In the second round of permutations (trait shuffle), the species composition is fixed and trait values are permutated to compute the statistics. If null hypothesis is rejected in this subsequent model, then it can be concluded that the influence of environment on species distribution is dependent of the trait similarity between them. This analysis was performed using the SYNCSA package. To visualize the evolution of forewing length throughout the phylogeny, we mapped and plotted this trait in the estimated phylogeny of communities. We used a comparative phylogenetic method of ancestral reconstruction based on a maximum likelihood approach (Revell 2013). According to this approach, it is assumed that traits evolved within the Brownian motion, where the expected difference between any two species is proportional to the time of divergence from the most recent common ancestor (Felsenstein 1985). Although the uncertainty of estimates, this method is useful for visualizing the direction of evolutionary changes to the most recent nodes in a phylogeny (Schluter et al. 1997, Revell 2013).

Results

A distinction between the composition of assemblages of fragmented and continuous areas was detected in Morro Grande (Figure 1, F = 3.21; p = 0.029). The axis 1 and 2 of CA described respectively 27.7 and 20.9 percent of variation. For the community from Serra do Japi, species composition presented differences between canopy and understorey (Figure 2, F = 8.73; p = 0.002). The first and second CA axis were responsible for 35 and 18 percent of variation respectively.

When communities were phylogeny-weighted, an overlap of SUs from fragmented and continuous forest areas was detected in PCPS ordination (Figure 3A). Using the first four PCPS axes to test the effect of environmental gradient on species and phylogenetic composition, the null hypotheses could not be rejected for either of the two models (Table 1). In Serra do Japi, understorey and canopy samples are segregated on the phylogenetic ordination space (Figure 3B). The site shuffle model was significant for PCPS1, confirming the effect of vertical gradient on assemblage structure. However, there was no phylogenetic structuring accordingly to the taxa shuffle model (Table 1). Third PCPS axis was chosen to be represented in ordination graph due to its marginal value for the effect on phylogenetic structure, according to the taxa shuffle model at this axis (Table 1).

Functional traits responses

In the continuous areas of Morro Grande, butterflies presented higher means of forewing length and higher values of wing shape and thorax indexes, although only the difference in forewing length was statistically supported (Table 2). Correlating CWM with the first axis of CA we found forewing length was greater in continuous than in fragmented communities (Figure 4A). The forewing length presented a K value near to the random divergence between species, while WI and TI indexes presented weak phylogenetic signals (Table 3). The forest fragmentation influenced the distribution of species and butterfly size, since smaller butterflies are more frequently associated to fragments, but the difference of species distribution between continuous and fragmented forests was independent of trait variation according to trait shuffle model (Table 3).

In Serra do Japi, understorey butterflies presented significantly higher means of forewing length, higher values of wing shape and thorax indexes compared to canopy (Table 2). The forewing length presented a K value indicating an evolution according to the Brownian motion, but the other traits (wing and thorax indexes) evolved independently of phylogeny (Table 3). The understorey community presented higher forewing length (CWM) than the canopy community (Figure 4B). The forest vertical structure affected the distribution of species and all traits measured, but similar to the effect of fragmentation, species variation was not mediated by the trait variation (Table 3).

The mapping of trait evolution showed that small forewing lengths are concentred mainly in the tribe Satyrini, and greater lengths are restricted to Brassolini and Morphini (Supplementary material Appendix 1 Fig. A2). The map showed that the common ancestor of Morphini, Brassolini and Satyrini clade probably had an average size. Therefore, the species size as we known are may related to evolutionary processes that are relatively more recent in time. Despite the species composition from both sites not being exactly similar, the pattern of forewing length evolution between the communities trees were congruent.

Discussion

In the present study, we tried to understand the effect of habitat structure on patterns of butterfly species assembling and in the evolution of functional aspects of fruit-feeding butterflies. The fragmentation have promoted a distinction of species composition as well as the vertical structure of forest. However, the absence of phylogenetic signal for species composition in the different habitats demonstrated that these patterns were shaped independently of evolutionary history. Our results still showed a consistent pattern: *i.e.* butterflies are smaller in the canopy and forest fragments, and larger in the understory and continuous forest landscapes. All morphological traits measured presented moderated to weak phylogenetic signals, and particularly not mediated the difference in species composition. The habitat structure in both vertical and horizontal dimensions have promoted changes in species composition and led to differences of butterfly size in these habitats. Nevertheless, the similarity between the assembly patterns suggests that habitat structure in vertical and horizontal dimension is a potential environmental filter acting through similar mechanism of selection.

Although the difference in butterfly assembly between habitats, this same pattern was not expressed on phylogeny. The non-segregation of butterfly lineages may arose from the co-occurrence of more distantly related species that share similar traits associated to its habitats (Pavoine et al. 2014). The measured traits in our study presented moderate to weak phylogenetic signals, then its distribution in habitats might be due to convergence, and independent of phylogenetic relatedness. Thus, we assert that trait adaptation explain the distribution of butterflies in habitats, more than phylogenetic constraints would do. Our results agreed with previous studies that demonstrated the relation of morphological traits related to the flight and vertical strata (Graça et al. 2017), and in butterfly life traits with fragments (Pavoine et al 2014).

We cannot discard the contribution of ecological niche and trait lability on the assembly responses (Cavender-Bares et al. 2009). If traits involved in habitat specialization are labile and the close relative specialize for different niches, then it is possible that environmental filtering produce a pattern of phylogenetic overdispersion (Ackerly et al. 2006, Cavender-Bares et al. 2009). However, other processes beyond environmental filter can be indirectly associated to the habitat structure in our study case, such as competition. Although the processes responsible for assembly patterns in horizontal and vertical dimensions were not specifically identified, the similarity of responses induced suggests that they might represent the same ecological mechanism.

Butterflies traits and the habitat structure

As mentioned before, abiotic and biotic factors are pointed as the main determinants of the species distribution in a given habitat. Its importance in species filtering is may related to their impact in butterfly traits.

Sunlight is an important factor associated to thermoregulation activities of butterflies (DeVries 1988, Ribeiro & Freitas 2010, Turner et al. 1987), and the sunlight exposure levels are dependent of vertical and horizontal structure of forests (Hill et al 2001, Montgomery & Chazdon 2001). Several butterfly species search for forest gaps and to the exposed canopy for sun basking, maximizing its flight performance at low energetic costs (Srygley & Chai 1990). However, this behaviour cannot be extrapolated to all butterfly assemblage. Morphini and Brassolini species are more frequently associated to the interior of forests (Figure 1). The same trend is expected in relation to the vertical dimension, which this these tribes were more registered in the understory (Figure 2). Darker and larger butterflies are more prevalent in cool and closed-canopy forests than in adjacent hot open areas (Xing et al. 2016). Interestingly, owl butterflies (genus *Caligo*) and other Brassolini with crepuscular habits raise their body temperature through shivering instead of exposing themselves to sun basking (Srygley 1994, Freitas et al. 1997). The preference of Morphini and Brassolini to the understory of continuous areas probably contributed to increase the body size in these areas. This could consequently drive other functional differences between understory/continuous and canopy/fragment assemblages.

Biotic factors may benefit species with a specific set of traits such as larger forewing lengths and slender bodies. Our functional indexes indicate that butterfly species occurring in understory and continuous landscapes have lower average flight speed and wing beating frequencies. Butterfly species adapted to use canopy forests need higher speed flights to avoid fast predators such as birds. Consequently, these species will have stouter bodies due to the well-developed muscles that allow them to perform stronger and faster flights. As well as favour these flight attributes, the exposed habitats may help these species to reach the temperature needed for perform its flight activities faster than shaded habitats usually would do. Conversely, species with slender bodies and smoother flights will be more successful in habitats such as the understory of forests. Since shaded habitats would have limited sunlight penetrance, the cost for thermoregulation and maintenance of fast flights would be higher. Therefore, the evolution of butterfly traits seems correlated to more than a single factor. Understand the interaction between factors from different natures and the responses generate from them requires an integrative approach.

Similar, but different: Conservation implications

In general, the statistical differences between measured traits were consistently supported when comparing assemblages across the vertical strata but not for assemblages in representing different fragmentation levels. This difference could be related to differences on the nature of processes acting in vertical and disturbance dimensions. While the changes in the abiotic conditions seems more abrupt among vertical forest structure, the same is unexpected in relation to continuous and fragmented landscapes. Forest fragments contain a combination of interior and edge tolerant species (see Filgueiras et al. 2016). Moreover, the forest canopy is in direct contact with the air matrix above, so it resemble more a forest edge than a forest fragment properly. Forest fragment edges are in constant contact with contrasting matrices that could represent a barrier to many species. The resemblance of patterns generated by fragmentation and vertical structure, suggests that this type of disturbance may impair populations of shaded understory species due to the increased exposure of shaded forest habitats through time. Since fragmentation processes are directly related to anthropic activities, its constant increasing will reduce the natural habitats for species bearing traits linked to forest environments.

Other human disturbances such selective forest logging impact fruit-feeding butterfly communities (Ribeiro & Freitas 2012). The removal of large trees alter the structure of forest canopy, allowing more penetrance of light, which consequently modify microclimate conditions in understory. The changes in vegetal structure also increase the growth of pioneer plant species and decreasing of shadowy plants (Silva et al. 1995). Regardless the nature of these processes, the understory fauna ends up being more susceptible to habitat change resultant of them. At the speed that anthropic activities have been advancing over natural landscapes, forest habitat changing can lead to the extinction of typical understory species, and consequently a significant diversity loss.

Concluding remarks

Our study demonstrated that fragmentation and vertical structure of forests are structuring butterfly assemblages in distinct dimensions of space. Its similar effects suggest that both act through similar mechanism of selection. We found that butterflies from canopy had smaller and stouter bodies and more vigorous and faster flights. This same trend was found for butterfly traits in forest fragments despite it was not so clear than for vertical strata. Despite the moderate phylogenetic signal found for forewing length, habitat structure is not selecting specific lineages, which demonstrate that the selection of traits and species composition in habitats are independent of phylogeny. We emphasize the importance of life history traits in determining habitat use for fruit-feeding butterflies. Furthermore, the present study reveals important insights about potential impacts of habitat modification on tropical butterfly diversity.

Acknowledgements

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Table 1. Models testing the effect of fragmentation (Morro Grande) and vertical stratification (Serra do Japi) on phylogenetic composition of fruit-feeding butterfly assemblages. Models were tested using the four first axes obtained in the analysis of Principal Components of Phylogenetic Structure (PCPS). Site shuffle captures the influence of the environmental gradient on both phylogenetic and species composition. The taxa shuffle permutes the phylogenetic relationships and test if the structuration of communities is dependent of phylogenetic relatedness among species.

Morro Grande			Models	
Axis	R² adj	Eigenvalues	Site shuffle	Taxa shuffle
PCPS 1	0.040	0.330	0.269	0.515
PCPS 2	0.001	0.098	0.502	0.62
PCPS 3	0.070	0.059	0.257	0.283
PCPS 4	0.001	0.047	0.412	0.349
Serra do Japi				
PCPS 1	0.619	0.434	0.004*	0.533
PCPS 2	0.001	0.297	0.63	0.653
PCPS 3	0.132	0.103	0.15	0.064
PCPS 4	0.001	0.094	0.591	0.385

Table 2. Student T and Welch T tests comparing means of functional traits (measured in millimetres) of fruit-feeding butterfly assemblages between continuous and fragmented areas (Morro Grande), and between understory and canopy (Serra do Japi). Comparisons were performed calculating mean trait values using the weighted abundance of butterfly species, disregarding the phylogenetic relatedness.

	Functional traits means (mm)		
	Forewing length	Wing index (WI)	Thorax index (TI)
Morro Grande			
Fragmented areas	5.03	0.18	0.33
Continuous areas	7.19	0.23	0.45
T value	-2.49	-2.01	-2.18
Permutation (p) value	0.039*	0.092	0.058
Serra do Japi			
Canopy	3.98	0.16	0.30
Understory	8.12	0.25	0.48
T value	-3.34	-2.13	-2.42
Permutation (p) value	0.004*	0.045*	0.027*

Table 3. Phylogenetic signal (K statistic) calculated for functional traits and indexes of fruit-feeding butterfly communities from Morro Grande (fragmented vs continuous areas) and Serra do Japi (understorey vs canopy). Null models were calculated to detect the effects of both environmental gradients on forewing length variation (Site shuffle) and of trait on species distribution along gradients (Trait shuffle).

			Models		
	K statistic	p values	F values	Site shuffle	Trait shuffle
Morro Grande					
Forewing length (Fw)	1.04	0.001*	6.21	0.012*	0.125
Thorax index (TI)	0.17	0.063	0.00	0.937	0.962
Wing index (WI)	0.42	0.001*	4.09	0.019*	0.204
Serra do Japi					
Forewing length (Fw)	1.00	0.001*	35.64	0.002*	0.157
Thorax index (TI)	0.21	0.03*	26.01	0.002*	0.215
Wing index (WI)	0.46	0.001*	29.15	0.003*	0.185

Figure legends

Figure 1. Correspondence analysis (CA) of sampling units from Morro Grande, testing the differences of fruit-feeding butterfly assemblages between continuous (closed squares) and fragmented (open squares) areas. Butterfly species with more than 10 individuals were represented with images and code names (first letter of the genus and the three first letters of species).

Figure 2. Correspondence analysis (CA) of sampling units from Serra do Japi, testing the differences of fruit-feeding butterfly assemblages between understorey (closed squares) and canopy (open squares) strata. Butterfly species with more than 10 individuals were represented with images and code names (first letter of the genus and the three first letters of species).

Figure 3. Principal coordinates of phylogenetic structure ordination, which explore the phylogenetic structure of communities across habitat structures. A) Principal coordinates of phylogenetic structure (PCPS) of fruit-feeding butterfly assemblages in continuous (closed squares) and fragmented areas (open squares) in Morro Grande. No trend of lineage segregation was found in relation to fragmentation filter B) Principal coordinates of phylogenetic structure (PCPS) of fruit-feeding butterfly assemblages in understorey (closed squares) and canopy (open squares) in Serra do Japi.

Figure 4. Correlations between community-weighted mean (CWM) of forewing length of fruit-feeding butterflies and first axis of correspondence analysis to explore the relation of this trait with fragmentation (Morro Grande) (A) and vertical stratification (Serra do Japi) (B). Continuous areas and understorey samples = closed squares; Fragmented areas and canopy samples = open squares.

Supplementary material Appendix 1 Fig. A1. Phylogenetic relations between fruit-feeding butterfly species from Morro Grande (A) and from Serra do Japi (B). The branch colours refer to fruit-feeding butterfly subfamily and tribes. Satyrinae: Satyrini (brown), Brassolini (purple), Morphini (blue); Charaxinae (red); Biblidinae: Ageroniini, Catonephelini, Epiphelini, Callicorini (grey); Coeini (orange).

Supplementary material Appendix 1 Fig. A2. Map of forewing length evolution in fruit-feeding butterfly clades from Morro Grande (A) and Serra do Japi (B). Warmer colours mean smaller wing sizes.

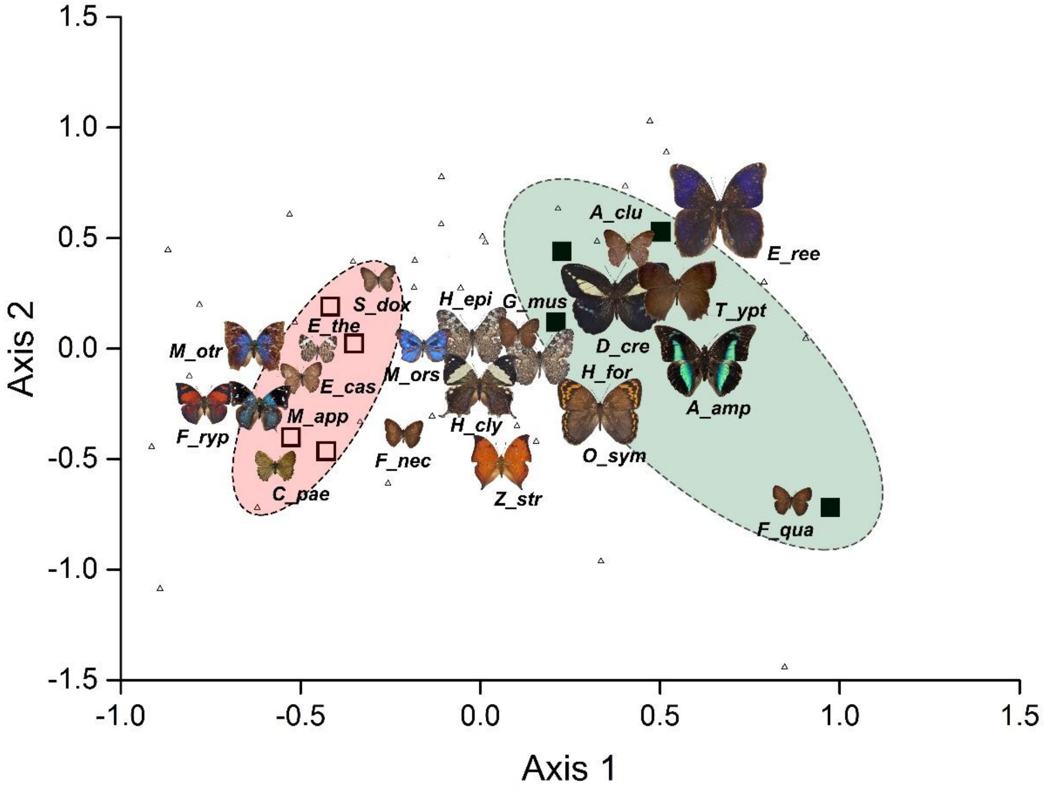
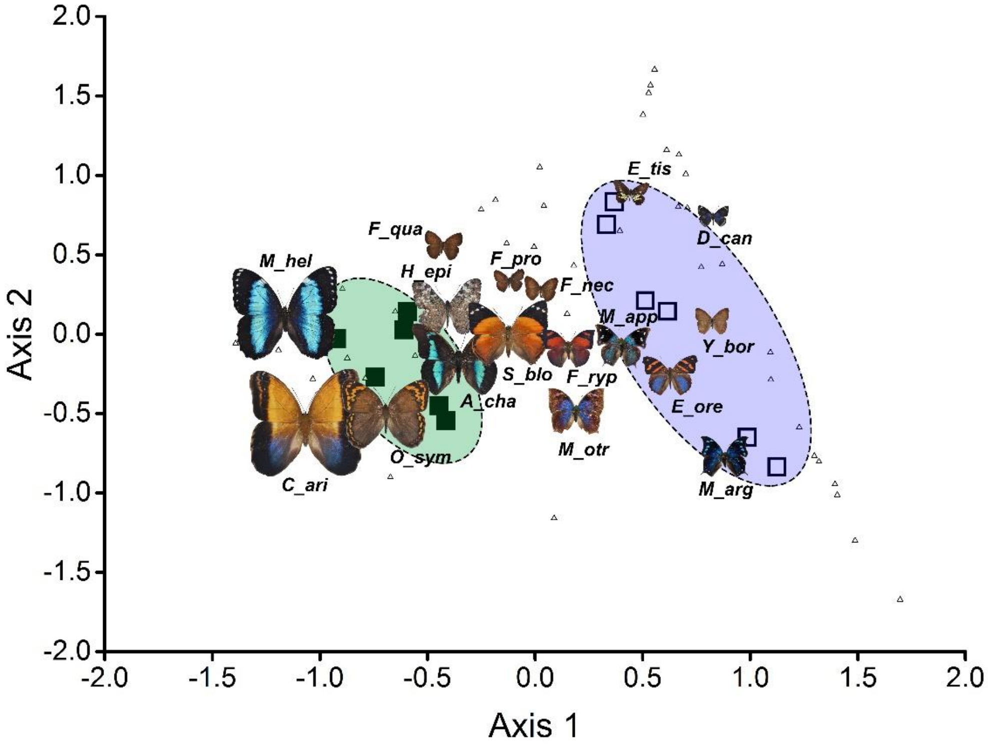


Figure 1.


2.0
1.5
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Axis 1
E_tis
D_can
F_qua
M_hel
H_epi
F_pro
F_nec
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Y_bor
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E_ore
M_otr
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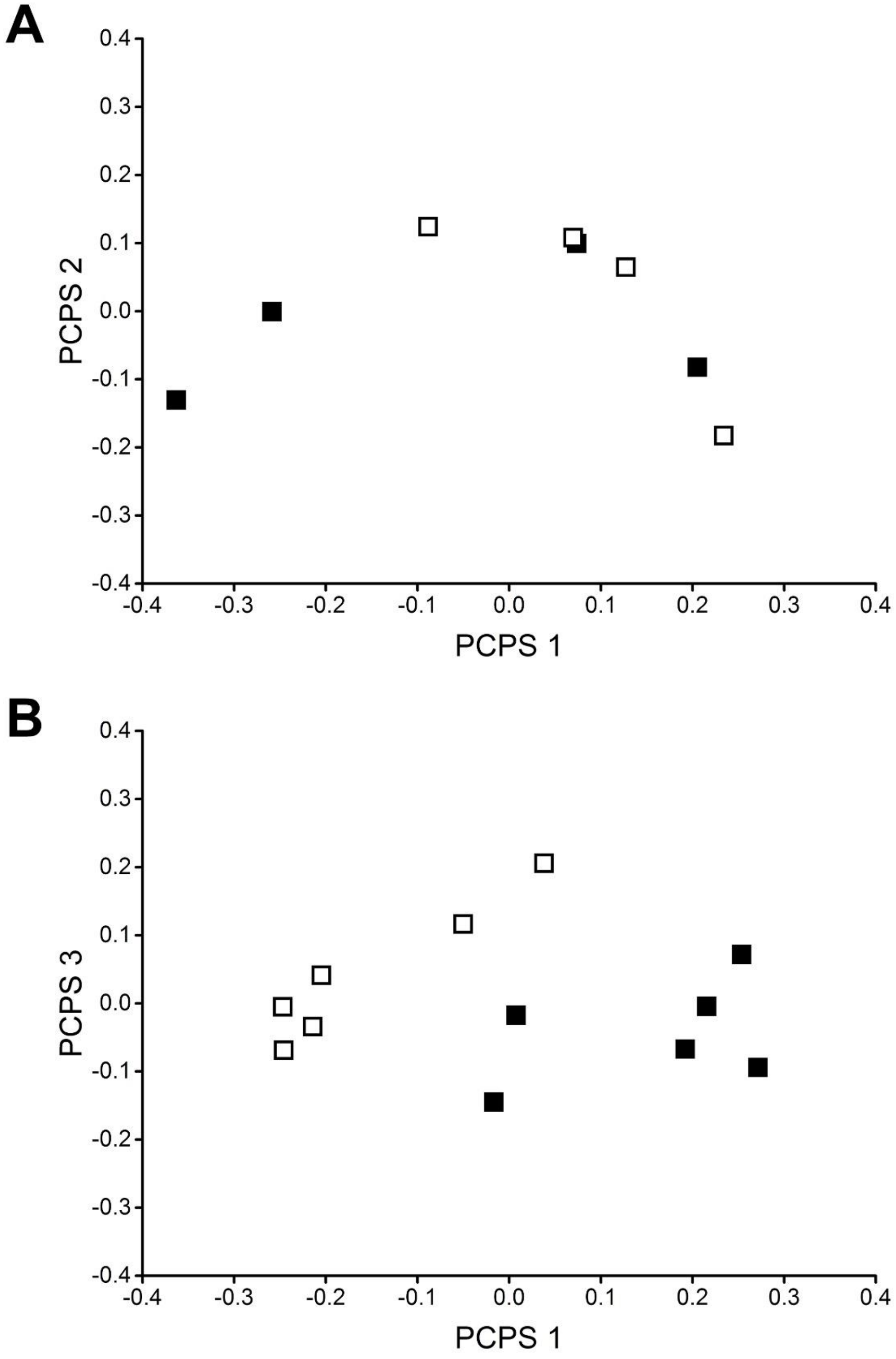
C_ari
M_arg

Figure 2.


A
PCPS 2
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
PCPS 1
B
PCPS 3
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
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PCPS 1

Figure 3.

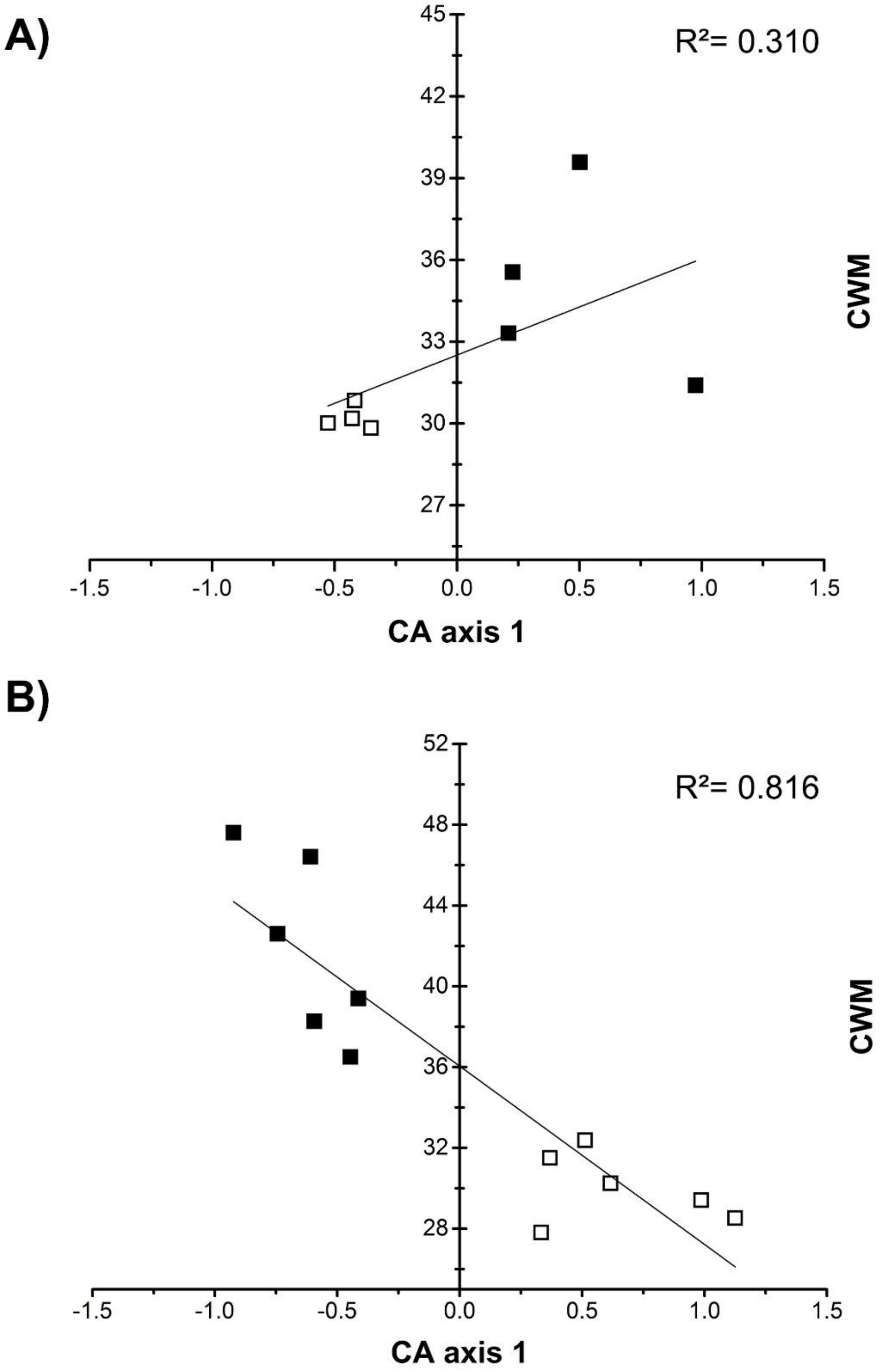
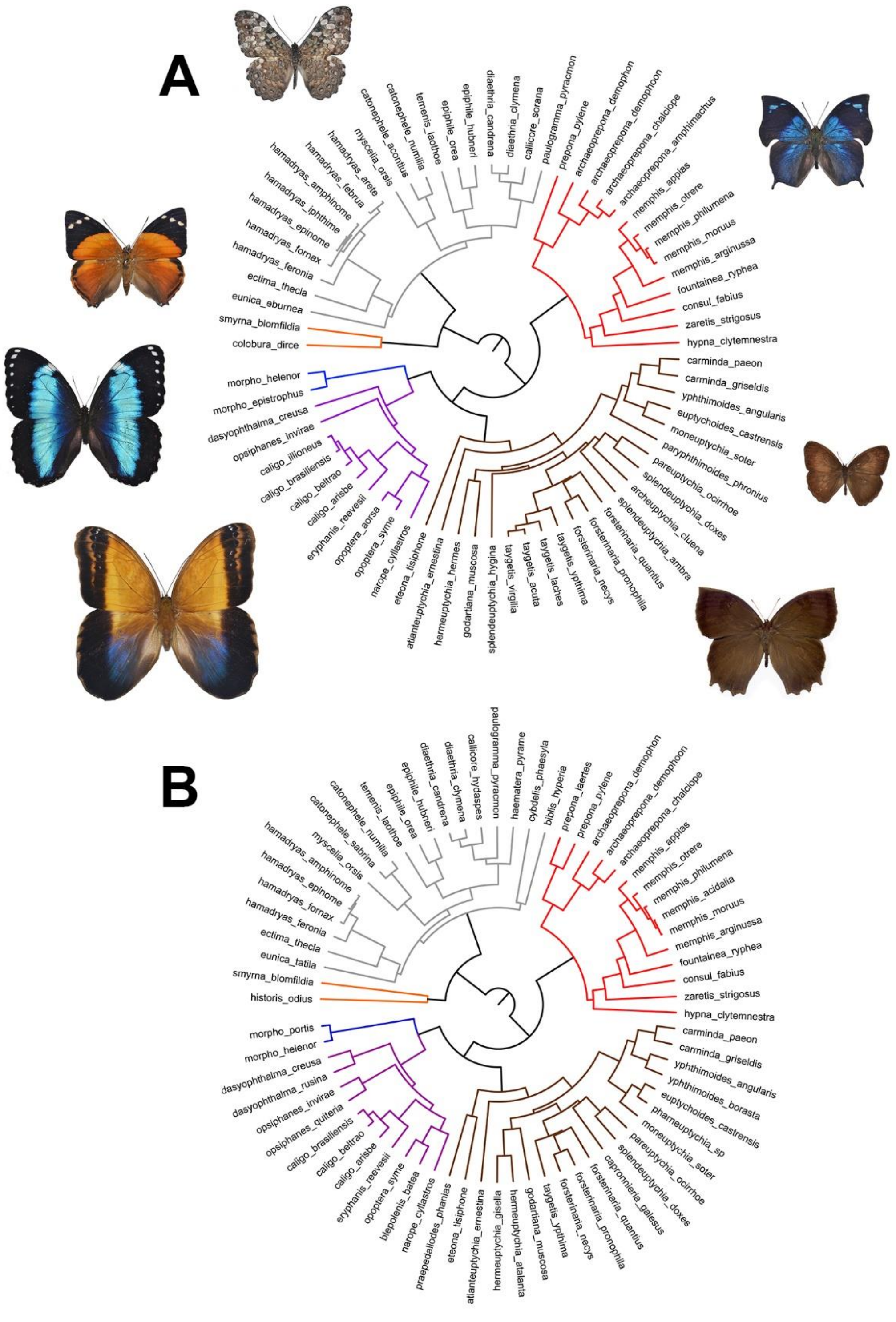
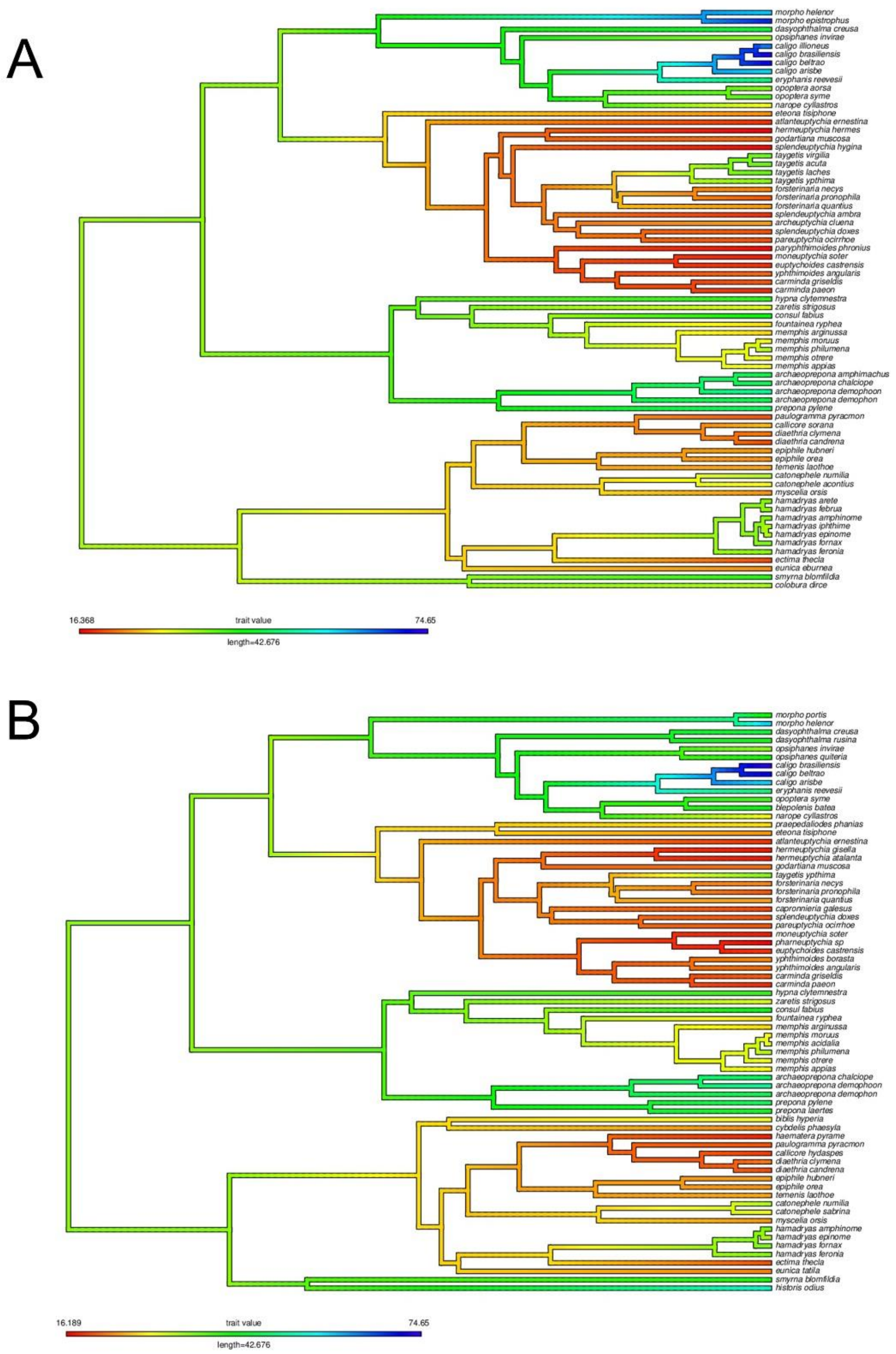

A)
R²= 0.310
45
42
39
36
33
30
27
CWM
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
CA axis 1
B)
R²= 0.816
52
48
44
40
36
32
28
CWM
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
CA axis 1

Figure 4.



Supplementary Material Fig A1.



Supplementary Material Fig A2.

Capitulo 3: Artigo original no formato da revista a ser submetido (Diversity and Distributions)

The effects of landscape modification on species richness of fruit-feeding butterflies in the Atlantic Forest

Jessie Pereira Santos[1], Thadeu Sobral-Souza[2], Maurício Humberto Vancine[2], Milton Cezar Ribeiro[2], Keith S. Brown Jr.[1] & André Victor Lucci Freitas[1]

Abstract

Aim Assess the geographical pattern of fruit-feeding butterfly species richness in the Atlantic Forest (AF) based on ecological niche modelling (ENM) combining climate and landscape variables; we evaluate the effect of landscape modification on the fruit-feeding butterfly species richness and propose conservation guidelines for the Atlantic Forest biome based on the obtained results.

Location Brazilian Atlantic Forest.

Methods We used ecological modelling niche (ENM) to generate maps of fruit-feeding butterfly species richness in the Atlantic Forest. The dataset contains 5094 registers of 270 butterfly species, distributed in 88 local communities. Both climate and landscape models were analysed separately to understand its contributions to the pattern of richness distribution. Then, an EcoLand map was generated to evaluate the effect of landscape modification on butterfly species richness. The EcoLand cells were categorized to better define conservation strategies based on different richness combinations.

Results The areas predicted as hotspots of species richness coincided with the main endemism centres of Atlantic Forest butterflies. However, the richness patterns predicted by climate and landscape were not always congruent. In general, the landscape model predicted higher species richness than climate model. The EcoLand confirmed the importance of landscape for the maintenance of diversity since the location of richness hotspots match with that of forest remnants. Additionally, several areas where climate predicted high richness but landscape predicted as low are located near the richness hotspots pointed by both models. This pattern highlight the potential impact of the advance of landscape modification on butterfly diversity.

Main conclusions Our models confirmed the importance of forested landscapes to the maintenance of high butterfly species richness. The availability of natural habitats seems to be a determining factor for butterfly richness maintenance, thus confirming the landscape modification as the prime threat to its conservation.

Keywords

Atlantic Forest, butterflies, conservation, diversity, modelling, species richness.

Introduction

Climate and landscape changes are widely recognized as the most important threats to biodiversity and ecosystem services (Titeux et al 2017). Over the last decades, extensive human activity have been altering the dynamics and ecosystems functioning, thus impacting biodiversity and society wellbeing (Cardinale et al 2012, Hooper et al 2012). Recent evaluations also have indicated that anthropogenic climate disruption and destruction of natural habitats are the main drivers of species decline (Dirzo et al 2014). Therefore, understand biodiversity distribution patterns is an important step towards identifying priority areas and propose more efficiently conservation policies (Margules & Pressing 2000, Myers et al 2000).

Mapping areas that contains higher species richness is a traditional method used for the establishment of priority areas for conservation (Ceballos & Ehrlich 2006, Jenkins et al 2013). However, this approach may not result in a comprehensive species coverage, since species with restricted distributions will not necessarily be not included in conservation networks distributed under these richness criteria (Nobrega & De Marco 2011, Veach et al 2017). The recent increase of consistent databases (Bello et al 2017, Bovendorp et al 2017, Muylaert et al 2017) added to the advance of distribution modelling techniques, has allowed to fill the distribution gaps of species that are rare or have limited available information (Nobrega & De Marco 2011, Siqueira et al 2009). Ecological niche modelling (ENM) is a methodological approach that perform a mathematical reconstruction or prediction species distributions. The ENMs infer relationships between environmental variables and species occurrence points to predict habitat conditions to the survival of populations of each species. Thus, niche-based models may represent a suitable and effective method to consider the species richness distribution in conservation planning (Costa et al 2010).

The niche parameters in ENM analysis are traditionally estimated using abiotic conditions, since the climate is a driver of species distributions (Soberón & Nakamura 2009). Conservation studies have given focus to the impacts of climate change and on the prediction of future biodiversity scenarios (Titeux et al 2017). On the other hand, the consequences of land use change is a topic recently incorporated in ENM. Landscape modification through habitat fragmentation is associated to major biodiversity changes, including species loss and local persistence (Haddad et al 2015, Thompson et al 2017). Changes of climate conditions occur in broader temporal scales when compared to landscape modification. In this sense, if climate and landscape encompass assembly mechanisms from different temporal scales, a framework integrating both categories of environmental variables would unravel their relative contribution to diversity distribution.

The Atlantic forest (hereafter AF) domain occurs along a latitudinal gradient in the Brazilian coast, extending its territory until west to inland areas of Paraguay and Argentina (Morellato e Haddad 2000, Tabarelli et al 2010). More than 70% of Brazilian population inhabit within Atlantic Forest domain, thus its ecosystems have been suffering due to human disturbance and overexploitation of its natural resources for centuries (Laurance et al 2009). Therefore, given its high level of species endemism and high degree of threaten, the AF is considered a hotspot of biodiversity (Myers et al 2000). One hypothesis to explain the high levels of endemism in the AF predicts that climatic regions that remained stable across historic climate fluctuations served as refuges for forest species (Carnaval & Moritz 2008, Graham et al 2006). However, such predictions generally employ only climatic data to model the diversity in the AF, thus neglecting other factors related to landscape ecology (i.e. forest cover, connectivity) (Carnaval & Moritz 2008, Metzger 2001).

Tropical butterflies are considered good models for ecology studies due to its sensitivity to environmental changes (Bonebrake et al 2010). More specifically, the guild of fruit-feeding butterflies whose adults primarily feeds on rooting fruits, are employed as model organisms for environmental monitoring and conservation (Barlow et al 2007, Freitas et al 2014, Ribeiro & Freitas 2012, Santos et al 2016). Although the occurrence of butterflies is mainly dependent on abiotic conditions, the habitat type and factors associated with the landscape are determinants of its diversity distribution. Then, we hypothesize that beyond climate suitability, the highest fruit-feeding butterfly richness would be concentrated in the available forest remnants, especially due to their dependence on forest food resources. In the present study, we modelled the distribution of fruit-feeding butterfly species in the AF using climate and landscape variables, aiming to elucidate its patterns of richness distribution. We seek to understand how is the richness of fruit-feeding butterfly distributed in the Atlantic Forest and if patterns predicted by climate and landscape congruent. Based on our results, we also tried to identify priority areas for conservation and made some suggestions of mitigation actions and study approaches under environmental change scenarios.

Methods

Study area

The Atlantic Forest (AF) roughly comprises two major vegetation types: the coastal Atlantic Rain Forest and the Atlantic Semi deciduous Forest (Morellato & Haddad 2000). Based on a non-objective analysis of distribution of three biological groups (birds, primates and swallowtail butterflies), Silva & Casteleti (2003) proposed a division of the AF in five sub regions (considered endemism centres), namely: 1) Bahia, 2) Brejos Nordestinos, 3) Pernambuco, 4) Diamantina, and 5) Serra do Mar, and in three transitional regions: 1) São Francisco, 2) Araucaria forest and 3) Interior forests (Figure 1), a scheme that has been followed by Ribeiro et al (2009) and several other subsequent authors since then. Within each of these sub regions, large extensions are of degraded or fragmented forests, with most remaining habitats restricted to riparian forests and steep slopes (Ribeiro et al 2009, Tambosi et al 2014). Currently, the AF is considered a hotspot of biodiversity (Myers et al. 2000) and one of three Earth biomes particularly vulnerable to global changes (Bellard et al 2014).

Species Database

The occurrence points of fruit-feeding butterflies in AF were obtained from a huge unpublished database from KSB (from 1964 to 2006) with recent contribution by AVLF for some localities (from 1988 to the present) and JPS (from 2008 to the present). In addition, several available published butterfly species lists were also included in our dataset (Appendix 1). We compiled the presence registers of what we call "*lato sensu* fruit-feeding butterflies", which also include some facultative fruit-feeding or nectar feeding butterfly species belonging to the selected clades and not usually sampled with bait traps. The taxonomy and nomenclature follow Lamas (2004), updated after Warren et al. (2017). For several of the old lists by KSB, voucher specimens have been located, spread and identified whenever possible (material deposited in the Zoology Museum, Unicamp). In some cases, cryptic species complexes recently unveiled by modern molecular techniques were lumped on a single name for comparative purposes (e.g. all similar species of *Hermeuptychia* were lumped as

Hermeuptychia hermes in our database). The final occurrence dataset contains 5094 registers of 270 fruit-feeding species, distributed in 88 localities along the entire AF (Figure 1).

Predicting fruit-feeding butterfly richness in Atlantic Forest

We used ecological niche modelling (ENM) techniques to predict geographical patterns of fruit-feeding butterfly species richness on the AF. The ENMs procedures consists on using three information sources: i) known occurrence of a given species, ii) environmental layers and iii) mathematical algorithms (Franklin 2009, Peterson et al 2011).

We conducted the ENM analysis based in two different predicting variables: i) models based on climate variables and ii) models based on landscape metrics. We used the 19 bioclimatic variables available at *WorldClim* database (www.worldclim.org, Hijmans et al 2005) and cut for Atlantic Forest delimitation proposed by Ribeiro et al (2009) following the Barve et al (2011) criteria for background delimitation. To select the less-correlated variables, we performed a factorial analysis using *Varimax* rotation (see method used in Sobral-Souza et al 2015, 2017). Five explanatory variables were selected from factorial analysis: mean diurnal range, isothermality, mean temperature of warmest quarter, precipitation of wettest quarter, precipitation of driest quarter. These variables summed explained 94.3% of the variation within 1km²-cell size resolution in the AF (Table 1). We assumed the premise that forests habitats are important as food sources for fruit-feeding butterflies, as well as in promoting its dispersion through different regions. Thus, we selected forest cover percentage, habitat homogeneity taxa, and functional connectivity– assuming 200m as the limit of dispersion (following Ribeiro et al. 2012) as landscape variables. All these variables were obtained from Jorge et al (2013).

We modelled the 146 Atlantic Forest butterfly species represented by at least 10 occurrence points. The remaining 124 species with less than 10 occurrences points were summed to the final map of richness, being only counted in the cell where it was originally registered. We used distinct mathematical algorithms to infer species distribution since each one adopts specific premises. The combined use of algorithms increases the reliability of final models considering a wide range of distributional patterns (Araújo and New 2007, Diniz-Filho et al 2009). We conducted the ENMs based on four algorithms of distinct modeling methods: two presence-only methods; envelope score - Bioclim (Nix 1986), and Domain (Gower distance, Carpenter et al 1993); and two machine-learning methods (presence-background records) - Support Vector Machines (SVM) (Tax and Duin 2004) and Maximum Entropy - MaxEnt (Phillips and Dudik 2008). All algorithms were built in "dismo" R-package (Hijmans et al 2015) except for the SVM that was built in "kernlab" R-package (Karatzoglou et al 2004).

The occurrence points of each species were partitioned into two distinct subsets, 75% and 25% for model training and validation, respectively, randomized 10 times to provide less biased models. In total, we built 40 models for each species (10 times x 4 algorithms). For each model we used the maximum sensitivity and specificity threshold according to Liu et al (2016) recommendation. Additionally, we used this threshold to evaluate models based on True Skilled Statistic (TSS) value, which ranges from -1 to 1. Models with TSS values negative or near-zero indicate predictions not different from randomly generated model, whereas models with values closer to 1 are close to perfect agreement (Allouche et al 2006). To predict species distribution maps, we conducted an ensemble forecast approach (Araújo & New 2007). Through ensemble method, the different algorithm maps were overlapped. Thus, we obtained a final consensus map for each species, by computing frequencies from all algorithms. The cell values of final distribution maps show the standardized frequencies of predicted presences combining all generated models.

Finally, to create a fruit-feeding butterfly richness map we inferred the lowest-presence-threshold (LPT) (Pearson et al 2007) for each species map to transform the continuous frequencies into a binary map (0 for absence and 1 for presence). Adding up all species binary maps we obtained the predicted number of species occurrence (richness) of fruit-feeding butterflies in each cell of AF delimitation. All modeling steps described above were followed to build a climate-based and a landscape-based map, thus resulting in one map of climate-richness and another of landscape-richness.

Predicting conservation issues and landscape effects in AF butterfly richness

To understand the effects of landscape modifications in species richness we conducted an EcoLand analysis (more details in Figure 2). For this, we extracted the cell values from climate and landscape richness maps and plotted in a XY graph in which the x-axis represent the climate predicted richness, and in the y-axis the landscape predicted richness. Then, we established thresholds to categorize the amount of species richness: low richness (less 0.25 of total richness), intermediate richness (between 0.25 and 0.75 of total richness) and high richness (greater than 0.75 of total richness). The relation between richness categories of climate and landscape models into XY graph were then categorized into the following combinations: i) areas with high richness predicted by both climate and landscape; ii) areas with high richness predicted by climate but intermediate richness predicted by landscape; iii) high richness predicted by climate but low richness predicted by landscape; iv) intermediate richness predicted by climate but high richness predicted by landscape; v) intermediate richness predicted by both climate and landscape vi) intermediate richness predicted by climate but low richness predicted by landscape; vii) low richness predicted by climate but high richness predicted by landscape; viii) low richness predicted by climate but intermediate richness predicted by landscape; and viii) low richness predicted by both climate and landscape. Each predicted richness combination received a specific color and was mapped, thus allowing the identification of these locations in the AF. The EcoLand map was then used for proposing conservation strategies based on the richness scenarios.

Results

Climate model

The climate model predicted that areas with higher species richness have approximately 140 species, and areas with lowest richness have at least seven to 20 species. According to the climate projections, the hotspots of species richness should be concentred in three main regions in the "Serra do Mar sub region" of Silva & Casteleti (2003): 1) the complex region including the Serra do Mar and Serra da Mantiqueira in São Paulo (SP) and Minas Gerais (MG) states, 2) a large portion of the Rio de Janeiro (RJ) State, starting in a narrow coastal stripe in the south of the state, to a broad area in the north of the state, and 3) the montane region of Espírito Santo (ES) south of the large Doce river basin (Figure 3). The areas with lower predicted species richness are located in the transitions to the Cerrado savannas and in the "São Francisco transitional sub region" of Silva & Casteleti (2003). In some areas the climate models predicted a richness lower than the actual observed richness (ex: Iguaçu National Park).

Landscape model

The landscape model predicted from 130 to 145 fruit-feeding butterfly species in the areas with highest species richness, whereas localities with lower species richness presented a minimum of 40 species. A large area where at least 120 species are predicted to occur was established in the southern portion of Atlantic Forest, encompassing the interior and coastal regions of Santa Catarina (SC), Paraná (PR) and São Paulo states. Nevertheless, areas with highest species richness predicted by landscape model mostly overlap the hotspots predicted by climate models (Figure 4). The Iguaçu National Park, where approximately 120 species have been effectively recorded, also presented a high predicted species richness according to the landscape model, different from what had been predicted by the climate model. The interior of São Paulo presented a few areas with more than 100 predicted species, in spite of samplings in this region did not registered these richness values. The western of São Paulo near the boundaries with Mato Grosso do Sul (MS) and Minas Gerais (MG) presented low richness according to the landscape model. Following the coast, a large discontinuity of higher predicted species richness was found between north Rio de Janeiro and south Espírito Santo.

Atlantic Forest EcoLand

According to the EcoLand model, we found three large patches with high species richness predicted by both climate and landscape (red areas in Figure 5). The first extends from the south (the "Araucaria transitional sub region of Silva & Casteleti, 2003), following all the extension to southeast reaching the Rio de Janeiro (RJ) state. The second patch encompasses most of the montane region of Espírito Santo state (ES) and south of Bahia (BA). The third extends from north of Bahia (BA) to northeast, reaching the Pernambuco state (PE) (Figure 5). The EcoLand showed that some large areas in the AF present high species richness as predicted by the landscape, but not for climate (the orange areas in Figure 5). These areas include the south portion of the AF (PR and SC states) and a large region in the interior comprising the states of Minas Gerais (MG) and Bahia (BA). Most areas with high predicted species richness according to climate but low predicted richness for landscape (dark green area in Figure 5) are close to the hotspots of species richness (the red areas). These areas include the interior of São Paulo (SP), the borderland between Rio de Janeiro (RJ) and Espírito Santo (ES), and the "Pernambuco sub region" of Silva & Casteleti (2003). The regions with low predicted values of species richness according to climate (light green, light blue and yellow areas in Figure 5) are mostly concentrated near the southwestern edge of the AF in the south, in the transition to the Cerrado savanna domain, and in the San Francisco sub region.

Discussion

In the present study, we modelled the species richness of Atlantic Forest fruit-feeding butterflies based on climate and landscape variables. We found that species richness hotspots overlap with the centres of endemism recognized for Atlantic Forest butterflies. Moreover, the hotspots are mostly coincident with forest remnants and surrounded by localities with low richness as predicted by landscape models (Figure 5). The EcoLand approach proved to be useful for unravel the relative contribution of climate and landscape in species richness distribution. Our results bring important insights about the importance of including landscape variables in ENM analysis. Additionally, highlights the role of the landscape processes on patterns of species richness distribution of Atlantic Forest butterflies.

The fruit-feeding butterfly richness hotspots coincided with the centres of endemism proposed for several other biological groups such as birds (da Silva et al 2004), amphibians (Carnaval et al 2009), and mammals (Costa et al 2000). More specifically, these hotspots reflect the three main centres of endemism of Atlantic Forest proposed for butterflies (Brown 1979, 1987, Tyler et al 1994). Although the centres of endemism for butterflies were established based on the geographic distribution of local races (subspecies), it is quite interesting that our results are coincident with them. There is not a single hypothesis to explain the distribution of diversity patterns of butterflies or other organisms in Neotropical Forests, and the inferences are frequently taxon-dependent (Sobral-Souza & Lima-Ribeiro 2017). The hypothesis of rivers as barriers already were evoked to explain the discontinuities observed in the two sides of the Doce and São Francisco rivers (Carnaval & Moritz 2008, Carnaval et al 2009). Nevertheless, our models showed that the species richness hotspots overflow the rivers, reducing the explanatory power of this hypothesis in relation to species richness patterns. Future studies addressing the spatial species turnover in relation to Doce River are necessary to determine if the communities from each margin are composed by distinct unities.

As demonstrated by the EcoLand model and the forest remnants map, high butterfly richness and forest remnants are overlapped, suggesting a high landscape influence. Some clades of fruit-feeding species are strictly associated to forested habitats and to specific forest vertical strata (DeVries et al 1997, Ribeiro & Freitas 2012, Santos et al 2017). Large patches of forest are critical for providing resources for butterflies, especially host plant availability for caterpillars (Horner-Devine et al 2003, Koh 2007). Additionally, forest cover mainly provide suitable microclimate and food resources for fruit-feeding butterflies, which importance increase in dry seasons (Horner-Devine et al 2003). Intermediate disturbance may lead to an increase in the local species richness, since landscapes that are more heterogeneous would allow the coexistence of species with distinct ecological requirements. However, the proximity to forest patches (source areas) may be critical for the improvement of connectivity and species dispersion, improving the persistence of population of many forest species (see next section).

Implications for conservation

Based on the distribution of richness predicted by our models, we propose conservation practices and future study approaches for Atlantic Forest diversity. The frequency distribution of cells in the EcoLand model indicates that areas with higher species richness predicted by landscape are more preponderant than areas with high richness predicted by the climate (Figure 6). Despite the landscape suitability to high richness, these regions have colder temperatures and high precipitation indexes or high temperatures and low rainfall in the driest quarter (orange and yellow cells respectively in Figure 5). In a future scenario of climate change, these landscapes could represent suitable habitats to harbour high species richness (Figure 7). These areas also have a few forest remnants, and as the case of the "Araucaria sub region", are near the hotspots where the great forest remnants are located. Therefore, they are important areas for the implementation of ecological corridors to improve the connectivity among these areas.

The areas with high species richness predicted by both, landscape and climate (red cells) are priority places for conservation of fruit-feeding butterflies (Figure 7). These areas could act as refuges and sources for species diversity besides the quite disturbed surrounding landscapes. A good example is the landscape in the Serra do Mar sub region (Silva & Casteleti 2003). According to Tambosi et al (2014), this sub region has an intermediate resilience (ability to recover from local species losses) given its connectivity and suitability for forest restoration. In addition, the presence and extension of conservation units in this sub region call the most attention. However, some of the heaviest populated urban regions are also in this sub region, resulting in high pressure and anthropogenic disturbance. We suggest that a management plan for the entire region should prioritize the protection of the larger forest remnants. The establishment of permanent corridors with smaller forest fragments would be important especially in the "Bahia sub region", where forests have been extensively destroyed in the last decades, and are now persisting as a plethora of small fragments.

The areas with highest species richness predicted by climate but low richness according to landscape (dark green in figure 5) are most closely located to the predicted richness hotspots. This means that butterfly richness severely decreased due to landscape modification. Long-term restoration plans could expand the extension of suitable habitats for maintaining a high diversity of butterflies. However, these areas harbour some of the densest urban centres of the AF (especially in the southeast and northeast), which means that forest restoration would be less effective and highly expensive. Therefore, a careful evaluation of any restoration plan is needed, considering the resilience of the system, aiming for the better use of strategies in terms of efficiency and cost.

In the regions where both landscape and climate predicted low species richness, the perspectives of gaining diversity through restoration or conservation practices are equally low. In addition to the inauspicious climate for supporting high butterfly richness, the landscape presents a general lack of forest cover and low connectivity, preventing the dispersion and maintenance of viable populations of many butterfly species. Nevertheless, more than diversity maintenance, investing in restoration at these localities may be important for restoring basic ecosystem services, such as water flow, soil erosion and greenhouse gases emission (Tambosi et al 2014).

Sampling effort implications

According to the EcoLand, there is not a single Atlantic Forest spot expected to have less than seven fruit-feeding butterfly species as predicted by climate. This result has important methodological implications concerning the sample sufficiency. Many studies involving fruit-feeding butterfly samplings aim to understand the effect of environmental changes on diversity and composition of communities. A frequent question is related to data reliability, or simply how much sample effort is required to obtain a truthful picture of local communities (Graça et al 2017). Based on the predictions of our models, local inventories in AF with less than seven fruit-feeding (including species of *Dynamine*, see methods) species fit in one of two scenarios: 1) inventories are preliminary or possibly undersampled; 2) the area is naturally poor for fruit-feeding butterflies richness, such as the highland grasslands and the pampa biome.

According to landscape results, none locality would have less than 40 fruit-feeding species, but the sampled points used in our models may lead to a bias in the undersampling assumption. Most of these points came from relatively well-sampled locations or associated with natural landscapes and conservation units. Unfortunately, samplings that address urban landscapes or agricultural matrices are a minority or simply scarce (Brito et al. 2014). Therefore, the prediction of species richness to these landscapes types may have been overestimated. Although the amount of each landscape type contemplated in samplings points is unknown, we reinforce the importance of long-term studies to obtain more completeness samples and consequently better-supported response patterns.

Conclusions

The present study aimed to unravel the patterns of species richness distribution of fruit-feeding butterflies. Through the association between climate and landscape models, we propose strategies for future studies and conservation efforts based on results obtained for this indicator group. Our results confirmed that hotspots of fruit-feeding butterfly species richness are coincident within endemism centres recognized for Atlantic Forest butterflies and other groups of plants and animals. The presence of forest remnants is an important predictor of higher richness for fruit-feeding species since the hotspots most overlap forest remnants areas. The EcoLand model showed that landscape maintained higher richness in localities where climate is not suitable to maintain a higher number of species. This scenario was the most frequent found in AF, followed by regions of low richness predicted by landscape and intermediate by climate. Regions with low richness estimated in landscape model are found mainly near the hotspots, which suggests a potential negative impact of land-use on these diversity sources. The evaluation of forest remnants resilience is an important step to promote restoration activities aiming the expansion of natural habitats and connectivity. Our results highlight the importance of conserving natural habitats as sources of diversity as well as the recuperation of ecosystem services front of a global change scenario.

Acknowledgements

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Table 1. The factorial analysis results for climate variables selection using AF delimitation with 1km² cell-resolution. The bold values are correspondent to select variables as well as the cumulative variation.

Climate variables	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Annual Mean Temperature	0.90	0.36	-0.12	-0.16	0.14
Mean Diurnal Range	0.02	0.28	0.14	**0.93**	0.16
Isothermality	0.32	0.71	-0.02	0.02	**0.57**
Temperature Seasonality	-0.36	-0.67	0.08	0.40	-0.48
Maximum Temperature of Warmest Month	0.92	0.14	-0.22	0.27	0.03
Minimum Temperature of Coldest Month	0.74	0.26	-0.24	-0.53	0.18
Temperature Annual Range	-0.21	-0.22	0.12	0.92	-0.21
Mean Temperature of Wettest Quarter	0.77	0.39	0.07	-0.02	-0.05
Mean Temperature of Driest Quarter	0.78	0.20	-0.25	-0.25	0.26
Mean Temperature of Warmest Quarter	**0.97**	0.14	-0.14	-0.06	-0.04
Mean Temperature of Coldest Quarter	0.81	0.45	-0.13	-0.25	0.23
Annual Precipitation	-0.26	-0.76	0.55	0.04	0.07
Precipitation of Wettest Month	-0.03	0.18	0.87	0.04	0.15
Precipitation of Driest Month	-0.29	-0.94	-0.10	-0.01	-0.02
Precipitation Seasonality	0.24	0.87	0.24	0.09	0.16
Precipitation of Wettest Quarter	-0.04	0.17	**0.89**	0.02	0.12
Precipitation of Driest Quarter	-0.28	**-0.95**	-0.09	0.02	-0.01
Precipitation of Warmest Quarter	-0.27	-0.09	0.90	0.17	-0.24
Precipitation of Coldest Quarter	-0.27	-0.09	0.90	0.17	-0.24
SSloadings	5.717	4.92	3.828	2.455	0.996
Proportion	0.301	0.259	0.201	0.129	0.052
Cumulative	0.301	0.56	0.761	0.89	**0.943**

Figure legends

Figure 1. Distribution of Atlantic Forest, its biogeographical sub regions (adapted from Silva & Casteleti 2003), and the forest remnants (Ribeiro et al 2009). The occurrence points represent the communities included in the original database. The Brazilian state names are abbreviated as follow: AL = Alagoas, BA = Bahia, CE = Ceará, ES = Espírito Santo, GO = Goiás, MA = Maranhão, MG = Minas Gerais, MS = Mato Grosso do Sul,
PE = Pernambuco, PB = Paraiba, PI = Piauí, PR = Paraná, RN = Rio Grande do Norte, RS = Rio Grande do Sul, SC = Santa Catarina, SE = Sergipe, SP = São Paulo, TO = Tocantins.

Figure 2. Framework demonstrating the steps of EcoLand (Sobral-Souza in prep) analysis. The first step consisted in modelling the distribution of each butterfly species according to climate variables using different algorithms. The ensemble method overlaps the maps from all algorithms and constructs a final consensus map for each species. From threshold values, the species suitability is converted in presence of species at each cell. These presences are summed to generate the distribution map (a). The same procedure is performed to landscape modelling, using landscape variables (b). Finally, the species richness predicted by the landscape in each cell was plotted against richness predicted by climate. The relation between richness values was categorized. In the EcoLand map, these cell categories were identified in geographical space, assisting the understanding of the relative contribution of each variable in the species richness distribution (c).

Figure 3. Distribution of fruit-feeding butterfly species richness in Atlantic Forest according to the climate model. Warmer colours indicate areas with larger predicted species richness. Circles represent each sampled community and its size the number of species registered.

Figure 4. Distribution of fruit-feeding butterfly richness in Atlantic Forest according to the landscape model. Dark green regions represent the areas with larger predicted species richness. Circles represent each sampled community and its size the number of species registered.

Figure 5. Fruit-feeding butterfly richness distribution in Atlantic Forest according to the EcoLand model, which considers both the climatic and landscape variables. Circles represent each sampled community and its size the number of species registered. The colour scheme indicates the different combinations between climate and landscape richness predictions. High predicted richness according to climate and landscape (red); high richness predicted by climate and intermediate richness predicted by landscape (dark green); intermediate richness predicted by climate and high richness predicted by landscape (orange); intermediate richness predicted by climate and landscape (light green); low richness predicted by climate and high richness predicted by landscape (yellow); and low richness predicted by climate and intermediate richness predicted by landscape (light blue).

Figure 6. Frequency distribution of Atlantic Forest 1x1km² EcoLand cells in each category of species richness predictions: low climate and intermediate landscape richness (1 - light blue), intermediate climate and landscape richness (2 - light green), low climate and high landscape richness (3 - yellow), intermediate climate and high landscape richness (4 – orange), high climate and intermediate landscape richness (5 - dark green), and high climate and landscape richness (6 - red).

Figure 7. EcoLand colour scheme indicating different combinations between climate and landscape richness predictions and the recommended conservation and study approaches.

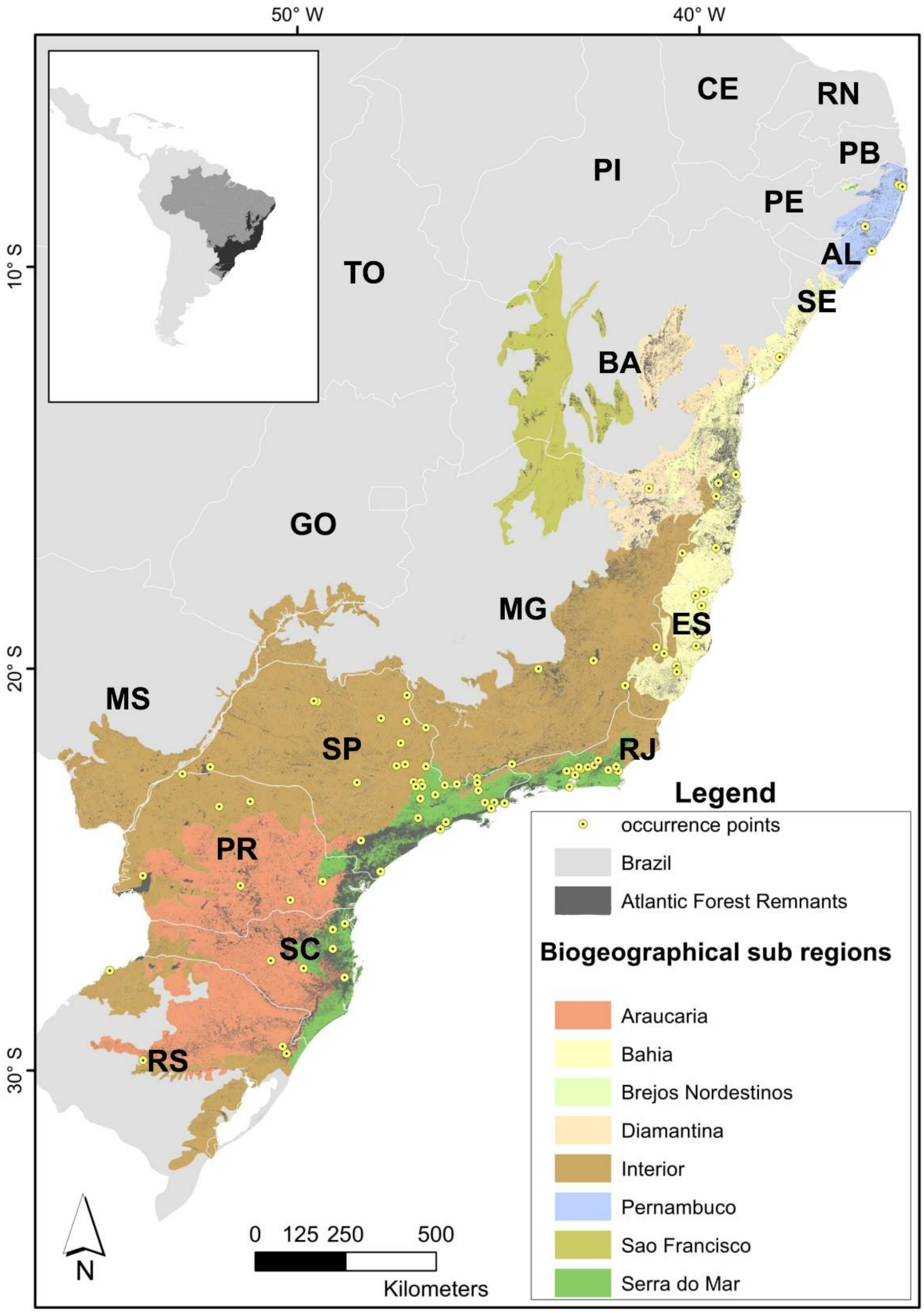
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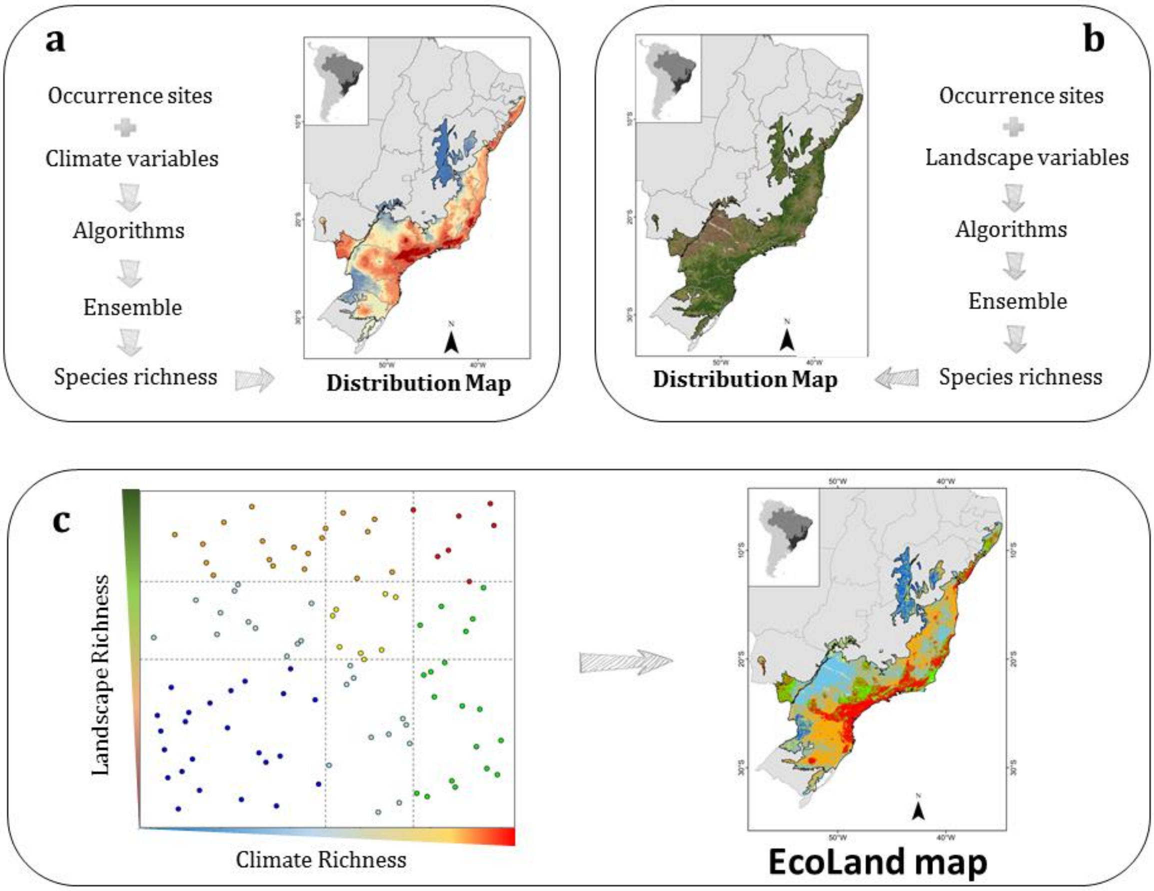
Figure 1.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Ensemble
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Distribution Map
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Figure 2.

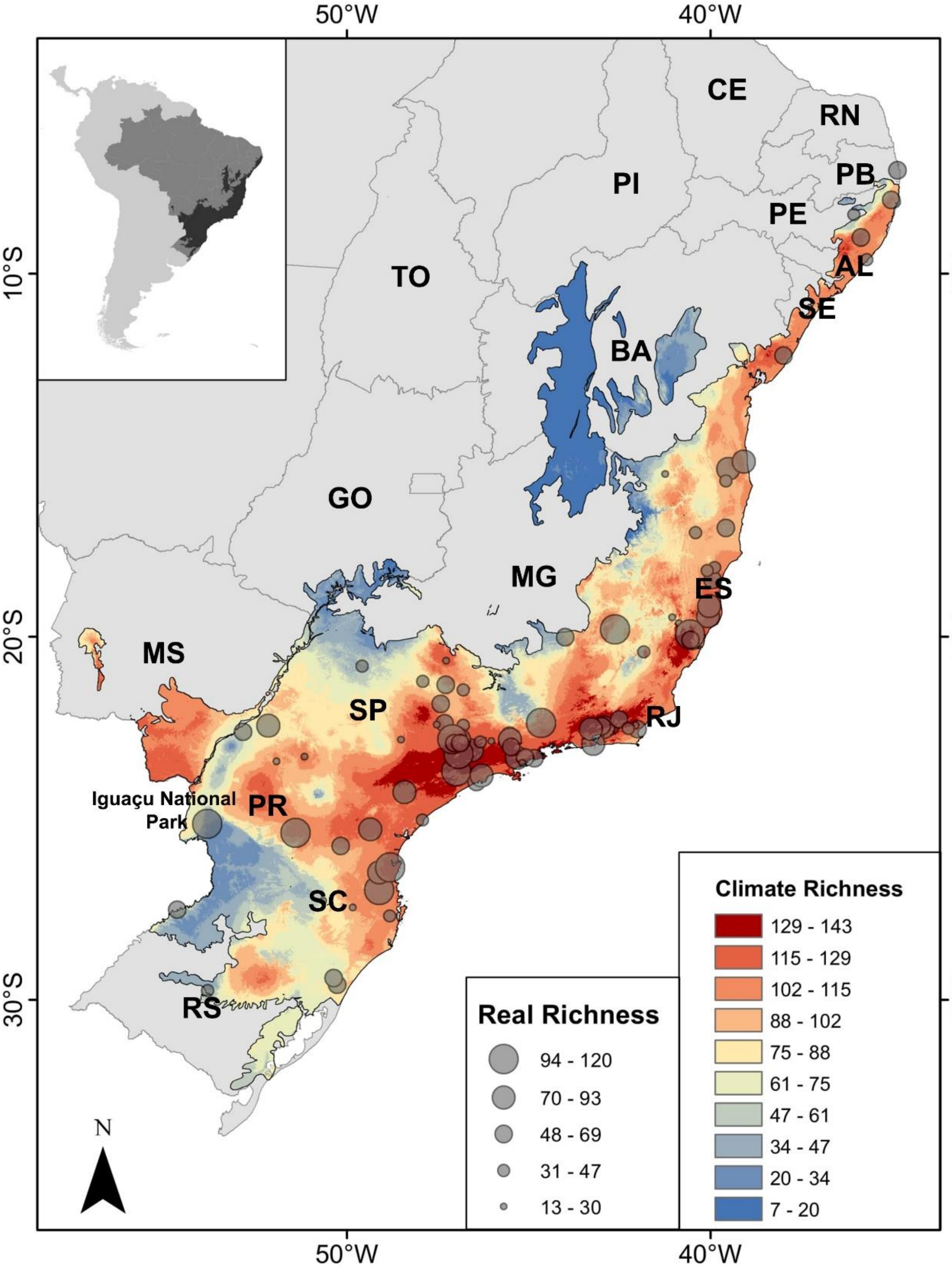
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Figure 3.

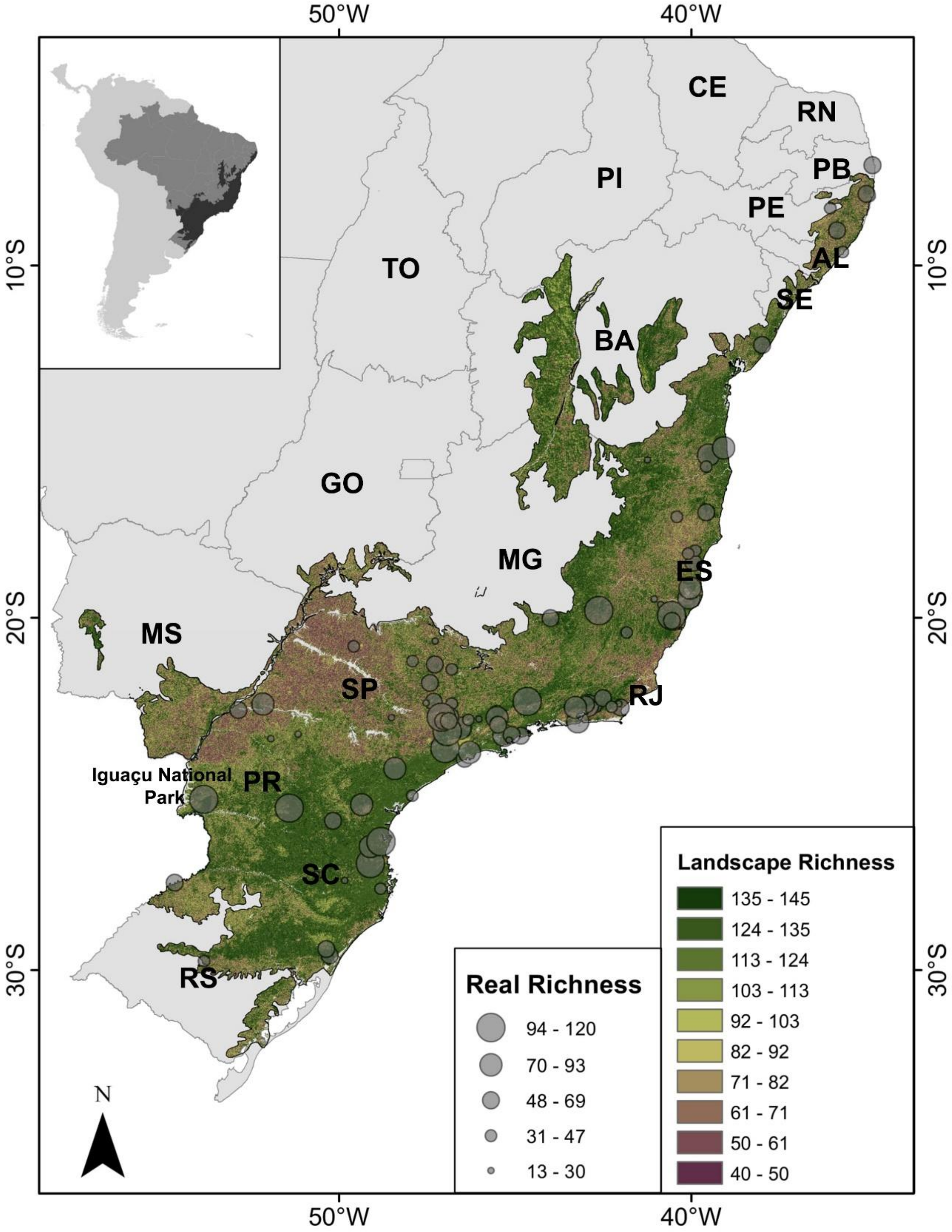
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Figure 4.

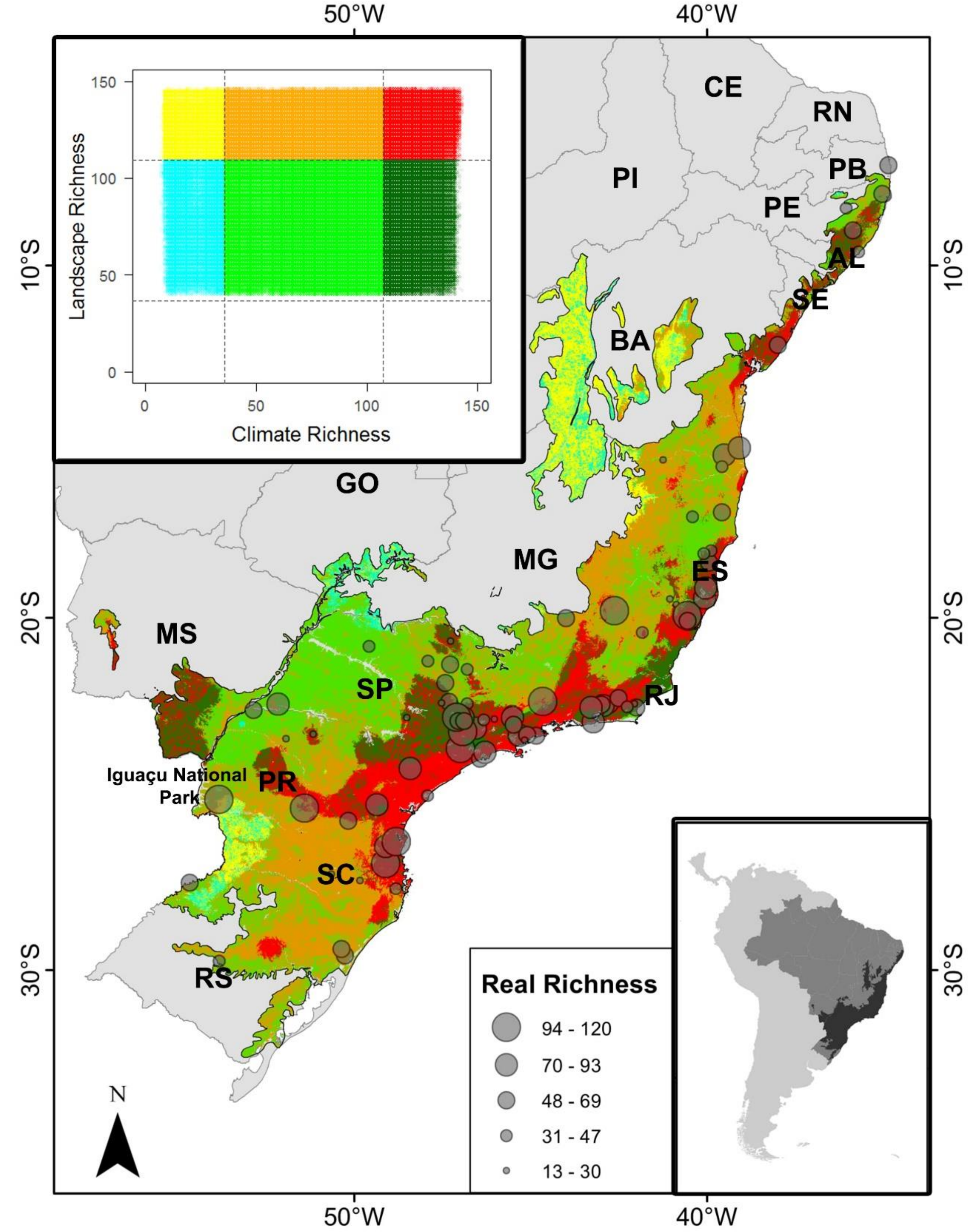
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Figure 5.

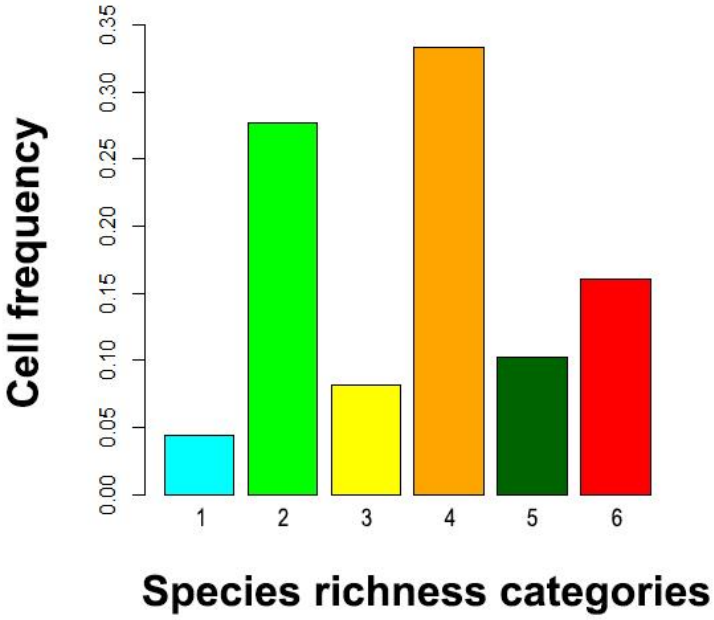

Figure 6.

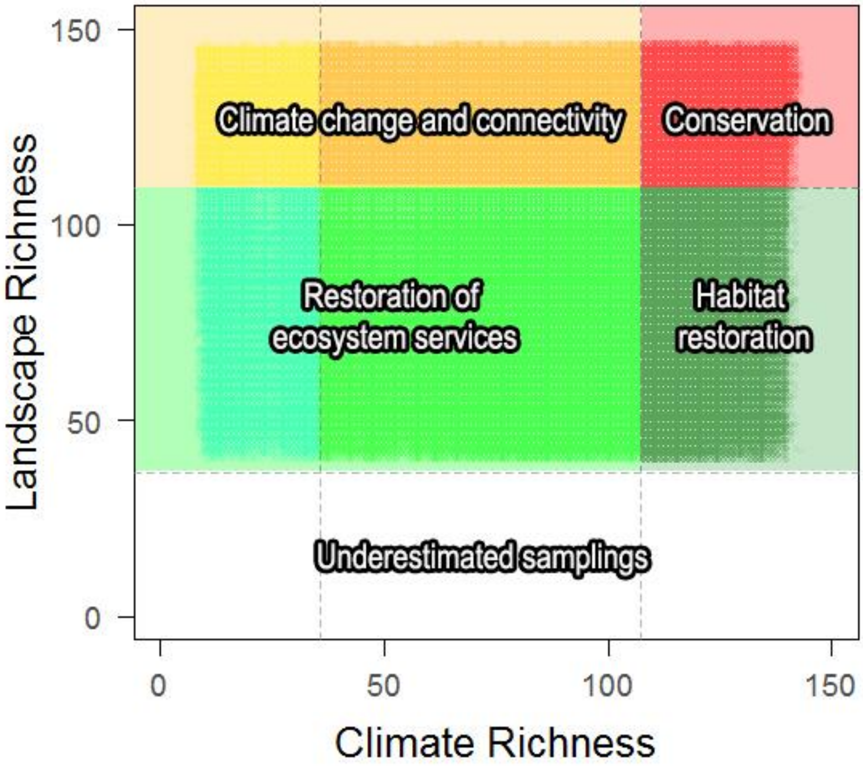

Figure 7.

Appendix 1. Butterfly surveys performed in Brazilian Atlantic Forest compiled from literature. The lists were ordered according to the respective Brazil state federation (First column), municipality, region or survey location (second column), and authors and year of publication (third column).

State Federation	**Location**	**Authors**
Rio Grande do Sul	Maquiné	Iserhard & Romanowski 2004, Santos et al 2011
Rio Grande do Sul	São Francisco de Paula (Floresta Nacional de São Francisco de Paula)	Santos et al 2011
Rio Grande do Sul	Santa Maria	Dessuy & Morais 2007, Spaniol & Morais 2015
Santa Catarina	Florianópolis (Parque Estadual da Serra do Tabuleiro)	Carneiro et al 2008, Corso & Hernández 2012
Paraná	Curitiba	Mielke 1994
Paraná	Guarapuava	Dolibaina et al 2011
Paraná	Jaguariaíva	Casagrande et al 2012
Paraná	Maringá	Almeida 1986
Paraná	Diamante do Norte (Estação Ecológica do Caiuá)	Garcia-Salik et al 2014
Paraná	Porto Mauá	Thiele et al 2014
Paraná	São Luiz do Purunã (Balsa Nova)	Beltrami et al 2014
Paraná	Foz do Iguaçu (Parque Nacional do Iguaçu)	Graciotim & Morais 2014, Greve et al 2015

Minas Gerais	Belo Horizonte	Brown & Mielke 1968, Soares et al 2012, Silva et al 2012
Minas Gerais	Vale do Rio Doce (Parque Estadual do Rio Doce)	Silva et al 2010
São Paulo	Baixada Santista	Francini et al 2011
São Paulo	Teodoro Sampaio (Parque Estadual do Morro do Diabo)	Mielke & Casagrande 1997
São Paulo	Campinas	Brown & Freitas 2002
São Paulo	Jundiaí (Serra do Japi)	Santos et al 2017
São Paulo	Caucaia do Alto (Reserva Estadual do Morro Grande)	Uehara-Prado et al 2007
São Paulo	São Luiz do Paraitinga	Ribeiro et al 2012
Rio de Janeiro	Guapimirim	Soares et al 2011
Rio de Janeiro	Cachoeiras de Macacu	Soares et al 2011
Rio de Janeiro	Teresópolis	Soares et al 2011
Rio de Janeiro	Nova Friburgo	Soares et al 2011
Pernambuco	Parque Nacional do Catimbau	Nobre et al 2008, 2012
Pernambuco	Caruaru (Parque Ecológico João Vasconcelos Sobrinho)	Paluch et al 2011
Alagoas	Maceió	Cardoso 1949

Considerações finais

Apesar de serem consideradas um grupo modelo em estudos de diversas áreas da ecologia, pouco se conhece acerca da diversidade de borboletas do Brasil. Essa lacuna do conhecimento se torna ainda maior se considerarmos toda a região Neotropical. Buscamos reunir o máximo de informação relativa a comunidades de borboletas frugívoras de Floresta Atlântica. A maior parte da informação é proveniente de dados históricos não publicados, e de localidades próximas aos grandes centros de pesquisa de Lepidoptera. Muitas localidades da Floresta Atlântica sequer foram inventariadas, o que gera uma preocupação devido ao avanço das pressões antrópicas sob esse bioma. Através da divulgação de uma base de dados para as comunidades de borboletas frugívoras esperamos chamar atenção para áreas que carecem de amostragem, bem como subsidiar análises de padrões de diversidade. Através de abordagens integrativas com outros grupos de pesquisa e múltiplos táxons, ações que visam a conservação da diversidade da Floresta Atlântica podem ser melhor embasadas.

Em uma escala local, os resultados de nosso trabalho indicam que a fragmentação florestal afeta a composição de espécies de borboletas frugívoras e os atributos funcionais das espécies desta guilda. A estrutura vertical de florestas afeta os padrões de forma semelhante em termos de composição de espécies e funcionalidade. Entretanto, não foi confirmada estruturação filogenética em ambos os casos. Esses resultados indicam que os processos de fragmentação e a estrutura vertical das florestas de Mata Atlântica geram padrões similares de resposta nas comunidades locais de borboletas, embora sejam considerados filtros ambientais que atuam em diferentes dimensões espaciais (horizontal e vertical respectivamente). Mesmo que os resultados não evidenciem estruturação filogenética nestes habitats, a diferenciação de atributos funcionais sugere a ação de filtros funcionais sob similar mecanismo de seleção. Uma vez que borboletas maiores estão mais relacionadas ao interior de ambientes florestais conservados, a perda e modificação da paisagem tende a causar maior impacto nestes grupos, levando a uma potencial redução na diversidade local das borboletas frugívoras.

Em uma escala mais ampla, os modelos preditos pelo EcoLand indicaram que as áreas com alta riqueza de espécies de borboletas frugívoras da Mata Atlântica coincidem com os centros de endemismo para diversos outros táxons, incluindo outros grupos de borboletas. Entretanto, os padrões de riqueza de espécies que foram preditos pelo clima e pela paisagem não são totalmente congruentes. Os modelos baseados em variáveis de paisagem estimaram maior riqueza que os modelos climáticos. Isso indica a importância de paisagem florestais na manutenção da riqueza de borboletas frugívoras na Mata Atlântica. Localidades que tiveram alta riqueza predita pelo clima, mas com baixa riqueza predita pela paisagem são em sua maior parte adjacentes aos hotspots de riqueza. Esse resultado reforça a importância da conservação dos remanescentes florestais, da implementação de restauração florestal e corredores ecológicos para auxiliar na manutenção da diversidade deste grupo e demais espécies indicadoras.

Os resultados obtidos demonstram que processos relacionados a qualidade e quantidade da paisagem são importantes fatores estruturadores das comunidades locais, mas também da manutenção da riqueza de espécies em escalas geográficas maiores. Muito embora possa existir uma hierarquia na forma com que os fatores geram os padrões ou gradientes de diversidade e de estrutura das comunidades, os mesmos fatores podem ser importantes componentes em diferentes escalas, sejam estas espaciais ou temporais. Os resultados apresentados são extremamente importantes nos tempos atuais em que se discute o efeito das atividades antrópicas na perda da diversidade, principalmente por confirmarem o impacto da perda e modificação de paisagens naturais em diferentes facetas da diversidade, e em escalas distintas.

Referências

Adler, P. B., White, E. P., Lauenroth, W. K., Kaufman D. M., Rassweiler, A., Rusak, J. A. 2005. Evidence for a general species-time-area relationship. Ecology, 86, 2032-2039.

Aguiar, A. P., Santos, B. F., Couri, M. S., Rafael, J. A., Costa, C., Ide, S., Duarte, M., Grazia, J., Schwertner, C. F., Freitas, A. V. L., Azevedo, C. O. 2009. Insecta. (R.M. Rocha & W. A. Boeger, eds.). Estado da arte e perspectivas para a zoologia no Brasil, Editora UFPR, p. 131-55.

Barlow, J., Overal, W. L., Araujo, I. S., Gardner, T. A., Peres, C. A. 2007. The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. Journal of Applied Ecology, 44 (5), 1001-1012.

Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, J., Fritz, S. A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A., Winter, M., Dormann, C. F. 2012. What's on the horizon for macroecology? Ecography, 35, 673-683.

Blackburn, T. M., Gaston, K. J. 2002. Scale in macroecology. Global Ecology and Biogeography, 11, 185-189.

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L. & Ehrlich, P. R. 2010. More than just indicators: a review of tropical butterfly ecology and conservation. Biological Conservation, 143, 1831-1841.

Bossart, J. L., Opuni-Frimpong, E. 2009. Distance from edge determines fruit-feeding butterfly community diversity in Afrotropical forest fragments. Environmental Entomology, 38 (1), 43-52.

Brown, J. H. 1995. Macroecology. The University Chicago Press, Chicago, 270 pp.

Brown, J. H. & Maurer, B. A. 1989. Macroecology: The division of food and space among species on continents. Science, 243, 1145-1150.

Brown, J. H. 2014. Why are there so many species in the tropics? Journal of Biogeography, 41, 8-22.

Brown, K. S. 1991. Conservation of neotropical environments: insects as indicators. In The Conservation of insects and their habitats, 15th Symposium of the Royal Entomological Society of London, pp. 350-404. New York: Academic Press.

Brown, K. S. 2005. Geologic, evolutionary, and ecological bases of the diversification of neotropical butterflies: implications for conservation. pp. 166-201. In: Bermingham, E.; Dick, C. W.; Moritz, G. (Eds.). Tropical rainforests: past, present, and future.

Brown, K. S. & Freitas, A. V. L. 1999. Lepidoptera (C.R.F. Brandão & E.M. Cancello, eds.). Biodiversidade do Estado de São Paulo, Brasil. São Paulo, FAPESP, p.225-245.

Brown, K. S. & Freitas, A. V. L. 2000. Atlantic forest butterflies: indicators for landscape conservation. Biotropica 32, 934-956.

Brown, K. S., Sheppard, P. M., Turner, J. R. G., 1974. Quaternary refugia in tropical America: evidence from race formation in Heliconius butterflies. Proceedings of the Royal Society of London Series B – Biological Sciences 187, 369–378.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters, 12, 693-715.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals maintained only in a non-equilibrium state. Science 199, 1302-10.

Cornell, H. V. Harrison, S. P. 2014. What are species pool and when are they important? Annual Review of Ecology, Evolution, and Systematics, 45, 45-67.

Costa-pereira, R., Roque, F. O., Constantino, P. A. L., Sabino, J.; UEHARA-PRADO, M. 2013. Monitoramento in situ da biodiversidade: Proposta para um sistema brasileiro de monitoramento da biodiversidade. ICMBio. Brasilia. Brazil. 61 p.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness.

The American Naturalist 137, 27-49.

DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history, Volume 1: Papilionidae, Pieridae, Nymphalidae. New Jersey: Princeton University Press, Princeton.

DeVries, P. J. & Walla, T. R. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. Biological Journal of Linnean Society, 74 (1), 1-15.

Diniz-Filho, J. A. F, Bini, L. M. & Rangel, T. F. L. V. B. 2006. Macroecologia: visão panorâmica de sistemas ecológicos complexos. Ciência Hoje, 38 (226), 64-67.

Fermon, H., Waltert, M., Larsen, T. B., Dall'asta, U., Mühlenberg, M. 2000. Effects of forest management on diversity and abundance of fruit-feeding nymphalid butterflies in southeastern Côte d'Ivoire. Journal of Insect Conservation, 4 (3), 173-188.

Freitas, A. V. L., Francini, R. B. & Brown, K. S. 2003. Insetos como indicadores ambientais (L. Cullen, R. Rudran & C. Valladares-Padua, eds). In Métodos de estudos em biologia da conservação e manejo da vida silvestre. Fundação O Boticário de Proteção à Natureza, Curitiba, p.125-151.

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

Gardner, T. A., Barlow, J., Parry, L. W., Peres, C. A. 2007. Predicting the uncertain future of tropical forests species in a data vacuum. Biotropica, 39(1), 25-30.

Hawkins, B. A. 2001. Ecology's oldest pattern? Trends in Ecology and Evolution, 16, 470.

Hawkins, B. A. & Porter, E. E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. The American Naturalist, 161, 40–49.

Hawkins, B. A. & DeVries, P. J. 2009. Tropical niche conservatism and the species richness gradient of North American butterflies. Journal of Biogeography, 36, 1698-1711.

Hawkins, B. A., Diniz-Filho, J. A. F., Jaramillo, C. A., Soeller, C. A. 2007. Climate, niche conservatism, and the global bird diversity gradient. The American Naturalist, 170, 16-27.

Heikkilä, M., Kaila, L., Mutanen, M., Peña, C., Wahlberg, N. 2012. Cretaceous origin and repeated tertiary diversification of the redefined butterflies. Proceedings of the Royal Society B, 279, 1093-1099.

Heikkilä, M., Mutanen, M., Wahlberg, N., Sihvonen, P., Kaila, L. 2015. Elusive ditrysian phylogeny: an account of combining systematized morphology with molecular data (Lepidoptera). BMC Evolutionary Biology, 15, 260.

Hill, J. K., Hamer, K. C., 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. Journal of Applied Ecology 41, 744-754.

Hill, J. K., Hamer, K. C., Lace, L. A. and Banham, W. M. T. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. Journal of Applied Ecology 32, 754-60.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. The American Naturalist, 163(2), 192-211.

Horner-Devine, M. C., Daily, G. C., Ehrlich, P. R., Boggs, C. L. 2003. Countryside biogeography of tropical butterflies. Conservation Biology 17, 168-177.

Hutchinson, E. 1953. The concept of pattern in Ecology. Proceedings of the Academy of Natural Sciences of Philadelphia, 105, pp 1-12.

Jablonski, D., Roy, K., Valentine, J. W. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science, 314, 102-106.

Jablonski, D., Belanger, C. L., Berke, S. K., Huang, S., Krug, A. Z., Roy, K., Tomasovych, A., Valentine, J. W. 2013. Out of tropics, but how? Fossils, bridge, species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. Proceedings of the National Academy of Sciences, 110(26), 10487-10494.

Jenkins, D. G., Ricklefs, R. E. 2011. Biogeography and ecology: two views of one world. Philosophical Transactions of the Royal Society B, 366, 2331-2335.

Kaufman, D. M. & Willig, M. R. 1998. Latitudinal patterns of mammalian species richness in the New World: the effects of sampling method and faunal group. Journal of Biogeography, 25, 795-805.

Kerr, J. T., Vincent, R., Currie, D. J. 1998. Lepidopteran richness patterns in North America. Écoscience, 5(4), 448-453.

Kerr, J. T., Southwood, T. R. E. & Cihlar, J. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. Proceedings of the National Academy of Sciences USA, 98, 11365-11370.

Koh, L. P., 2007. Impacts of land use change on Southeast Asian forest butterflies: a review. Journal of Applied Ecology 44, 703-713.

Kremen, C., Merelender, A. M. & Murphy, D. D. 1994. Ecological monitoring: a vital need for integrated conservation and development programs in the tropics. Conservation Biology, 8, 388-397.

Laurance, W. F. 2009. Conserving the hottest of the hotspots. Biological Conservation 142, 1137.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos, 84(2), 177-192.

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., Hodda, M., Holt, R. D., Larsen, T. B., Mawdsley, N. A., Stork, N. E., Srivastava, D. S., Watt, A. D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391, 72-76.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters, 7: 601-613.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology, 73(6), 1943-1967.

Looijen, R. C. 1998. Holism and reductionism in biology and ecology. The mutual dependence of higher and lower level research programmes. Thesis, Rijksuniversiteit Groningen.

Lyons, S. K., Willig, M. R. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. Oikos 79, 568-80.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Princeton University Press, 269 pages.

Morellato, L. P. C. & Haddad, C. F. B. 2000. Introduction: the Brazilian Atlantic Forest. Biotropica 32(4), 786-792.

New, T. R., Pyle, R. M., Thomas, J. A., Thomas, C. D., Hammond, P. C. 1995. Butterfly conservation management. Annual Review of Entomology 40, 57-83.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. The American Naturalist 100, 33-46.

Pozo, C., Luis, A. M., Llorente, J. B., Salas, N., Maya, A., Vargas, I. F. 2008. Seasonality and phenology of butterflies (Lepidoptera: Pieridae, Papilionidae, Nymphalidae, Lycaenidae and Hesperiidae) in Calakmul, biosphere reserve. Florida Entomologist, 91 (3), 407-422.

Rapoport, E. H. 1975. Areografia: Estrategias Geograficas de Especies. Mexico City, DF: Fundo Cult. Econ.

Ribeiro, D. B. & Freitas, A. V. L. 2012. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. Journal of Insect Conservation, 16, 733-744.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science, 235, 167-171.

Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters, 7, 1-15.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65, 514-27.

Rohde, K. 1996. Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. Biodiversity Letters 3, 10-13.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge, MA: Cambridge University Press.

Rosser, N., Phillimore, A. B., Huertas, B., Willmott, K. R., Mallet, J. 2012. Testing historical explanations for gradients in species richness in heliconiine butterflies of tropical America. Biological Journal of the Linnean Society, 105, 479-497.

Sant'anna, C. L., Ribeiro, D. B., Garcia, L. C., Freitas, A. V. L. 2014. Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. Restoration Ecology, 22 (4), 480-485.

Santos, J. P., Marini-Filho, O. J., Freitas, A. V. L. & Uehara-Prado, M. 2016. Monitoramento de borboletas: o papel de um indicador biológico na gestão de unidades de conservação. Biodiversidade Brasileira, 6, 87-99.

Saunders, D. A., Hobbs, R. J., Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5(1): 18-32.

Shahabuddin, G., Terborgh, J. W. 1999. Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and the effects of isolation. Journal of Tropical Ecology, 15 (6), 703-722.

Shields, O., 1989. World numbers of butterflies. Journal of the Lepidopterists' Society 43, 178-183.

Shurin, J. B. 2007. How is diversity related to species turnover through time? Oikos, 116: 957-965.

Simonson, S. E., Opler, P. A., Stohlgren, T. J. & Chong, G. W. 2001. Rapid assessment of a butterfly diversity in a montane landscape. Biodiversity and Conservation, London, 10, 1369-1386.

Soria-Carrasco, V., Castresana, J. 2012. Diversification rates and the latitudinal gradiente of diversity in mammals. Proceedings of the Royal Society B, 279, 4148-4155.

Spitzer, K., Novotny, V., Tonner, M., Leps, J. 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. Journal of Biogeography 20, 109-121.

Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., Peres, C. A. 2010. Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. Biological Conservation, 143(10), 2328-2340.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B: Biological Sciences 360, 339-357.

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

Turner, J. R. G., Gatehouse, M. C. & Charlotte, A. C. 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. Oikos, 48, 195-205.

Uehara_Prado, M., Brown, K. S. & Freitas, A. V. L. 2007. Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. Global Ecology and Biogeography, 16, 43-54.

Uehara-prado, M., Fernandes, J. O., Bello, A. M., Machado, G., Santos, A. J., Vaz-de-mello, F. Z., Freitas, A. V. L. 2009. Selecting terrestrial arthropods as indicators of small-scale disturbance: a first approach in the Brazilian Atlantic Forest. Biological Conservation, 142 (6), 1220-1228.

Whittaker, R. H. 1975. Communities and ecosystems, 2nd ed. - Macmillan, New York.

Whittaker, R. J., Willis, K. J., Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography, 28, 453-470.

Wiegert, R. G. 1988. Holism and reductionism in ecology: Hypotheses, scales and systems models. Oikos, 53(2), 267-269.

Wiens, J. J. & Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. Trends in Ecology and Evolution, 19, 639-644.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Davies, T. J., Grytnes, J., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., Stephens, P. R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters, 13, 1310-1324.

Willig, M. R., Gannon, M. R. 1997. Gradients of species density and turnover in marsupials: a hemispheric perspective. Journal of Mammalogy 78, 756-65.

Willig, M. R., Kaufman, D. M., Stevens, R. D. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics, 34, 273-309.

Willis, K. J., Whittaker, R. J. 2002. Species diversity: Scale Matters. Science, 29-5, 1245-1248.

Wood, B., Gillman, M. P. 1998. The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. Biodiversity and Conservation 7, 597-616.

Almeida, G. S. S., Souza, C. L., Marques, E. E. 1986. Levantamento preliminar das espécies de borboletas (Rhopalocera) de ocorrência em Maringá (PR): I. Papilionoidea. Revista Unimar, 8(1): 29-36.

Barbosa, E. P., Silva, A. K., Paluch, M., Azeredo-Espin, A. M., Freitas, A. V. L. 2015. Uncovering the hidden diversity of the Neotropical butterfly genus Yphthimoides Forster (Nymphalidae: Satyrinae): description of three new species based on morphological and molecular data. Organisms Diversity & Evolution 15, 577-589.

Barlow, J., Overal, W. L., Araujo, I. S., Gardner, T. A., Peres, C. A. 2007. The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. Journal of Applied Ecology 44, 1001-1012.

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidea. Transactions of the Linnean Society of London 23, 495-566.

Bellard, C., C. Leclerc, B. Leroy, M. Bakkenes, S. Veloz, W. Thuiller, and F. Courchamp. 2014. Vulnerability of biodiversity hotspots to global change. Global Ecology and Biogeography 23: 1376-1386.

Bellaver, J., Iserhard, C. A., Santos, J. P., Silva, A. K., Torres, M., Siewert, R. R., Moser, A., Romanowski, H. P. 2012. Borboletas (Lepidoptera: Papilionoidea e Hesperioidea) de Matas Paludosas e Matas de Restinga da Planicie Costeira da regiao sul do Brasil. Biota Neotropica 12(4): 181-190.

Beltrami, L. C. C., Mielke, O. H. H., Casagrande, M. M., Carneiro, E. 2014. The Hesperioidea and Papilionoidea (Lepidoptera) of São Luiz do Purunã, Balsa Nova, Paraná State, Brazil. Tropical Lepidoptera Research 24(1): 30-36.

Biezanko, M. C. 1949. Acraeidae, Heliconiidae et Nymphalidae de Pelotas e seus arredores (Contribuição ao conhecimento da fisiografia do Rio Grande do Sul). Pelotas, Livraria Globo. 16 pp.

Boggs, C. L., Watt, W. B., Ehrlich, P. R. 2003. Butterflies: Ecology and Evolution Taking Flight. University of Chicago Press, Chicago.

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L., Ehrlich, P. R. 2010. More than just indicators: A review of tropical ecology butterfly ecology and conservation. Biological Conservation, 143(8): 1831-1841.

Brito, M. M., Ribeiro, D. B., Raniero, M., Hasui, E., Ramos, F. N., Arab, A. 2014. Functional composition and phenology of fruit-feeding butterflies in a fragmented landscape: variation of seasonality between habitat specialists. Journal of Insect Conservation, 18(4): 547-560.

Brown, K. S. 1991. Conservation of Neotropical environments: insects as indicators. In Collins, N.M. & Thomas, J. A. (eds). The conservation of insects and their habitats. Royal Entomological Society Symposium XV, Academic Press, London. pp 349-404.

Brown, K. S. 1992. Borboletas da Serra do Japi: diversidade, habitats, recursos alimentares e variação temporal. In (L.P.C. Morellato org.), História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil, Editora da Unicamp, Campinas, p. 142- 187.

Brown, K. S. 2005. Geological, evolutionary and ecological bases of the diversification of Neotropical butterflies: implications for conservation, p. 166–201. In: E. Bermingham E.; C. W. Dick & C. Moritz (eds.). Tropical rainforests: Past, Present and Future. Chicago, University of Chicago Press, 672 p.

Brown, K. S. & Freitas, A. V. L. 2000. Atlantic Forest butterflies: Indicators for landscape conservation. Biotropica 32(4b): 934-956.

Brown, K. S. & Freitas, A. V. L. 2003. Butterfly communities of urban forest fragments in Campinas, São Paulo, Brazil: structure, instability, environmental correlates, and conservation. Journal of Insect Conservation, 6, 217-231.

Brown, K. S. and Mielke, O. H. H. 1968. Lepidoptera of the Central Brazil Plateau. III. Partial list for the Belo Horizonte area, showing the character of the south eastern “blend zone”. Journal of the Lepidopterists’ Society 22: 147-157.

Camargo F. 2006. Avaliação da fauna de borboletas de seis áreas verdes de Porto Alegre, RS. M. S. Thesis, Universidade Federal do Rio Grande do Sul.

Cardoso, A. 1949. Lepidópteros de Alagoas. Revista de Entomologia 20: 427-436.

Carreira, J. Y. O. 2015. Dinamica temporal e sazonalidade de borboletas frugivoras na Mata Atlantica. M. S. Thesis, Universidade Estadual de Campinas.

Carneiro, E., Mielke, O. H. H., Casagrande, M. M. 2008. Borboletas do sul da ilha de Santa Catarina, Brasil (Lepidoptera: Hesperioidea & Papilionoidea). SHILAP Revista de Lepidopterologia, 36(142): 261-271.

Castro, D. 2008. Diversidade de borboletas (Lepidoptera: Papilionoidea e Hesperioidea) em três morros graníticos de Porto Alegre, RS. M. S. Thesis, Universidade Federal do Rio Grande do Sul.

Corso, G. and Hernández, M. I. M. 2012. Borboletas frugívoras da Mata Atlântica no Parque Estadual da Serra do Tabuleiro, Santa Catarina, Brasil. Biotemas 25(4): 139-148.

Costa-Pereira, R., Roque, F. O., Constantino, P. A. L., Sabino, J. & Uehara-Prado, M. 2013. Monitoramento in situ da biodiversidade. Proposta para um sistema brasileiro de monitoramento da biodiversidade. ICMBio, 61p.

Dessuy, M. B., Morais, A. B. B. 2007. Diversidade de borboletas (Lepidoptera: Papilionoidea & Hesperioidea) em fragmentos de Floresta Estacional Decidual em Santa Maria, Rio Grande do Sul, Brasil. Revista Brasileira de Zoologia, 24(1): 108-120.

Devries, P. J. 1987. The butterflies of Costa Rica and their natural history, Volume 1: Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton. 327pp.

Devries, P. J., Walla, T. R. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. Biological Journal of the Linnean Society 74 (1), 1-15.

Dolibaina, D. R., Mielke, O. H. H., Casagrande, M. M. 2011. Borboletas de Guarapuava e arredores, Paraná, Brasil: um inventário com base em 63 anos de registros. Biota Neotropica 11(1): 341-354.

Ebert, H. 1969. On the frequency of butterflies in eastern Brazil, with a list of butterfly fauna of Poços de Caldas, Minas Gerais. J. Lepid. Soc. 23(suplem. 3):1-48.

Fermon, H., Waltert, M., Larsen, T. B., Dall'asta, U., Mühlenberg, M. 2000. Effects of forest management on diversity and abundance of fruit-feeding nymphalid butterflies in south-eastern Côte d'Ivoire. Journal of Insect Conservation 4 (3), 173-188.

Filgueiras, B. K. C. 2015. Resposta dos besouros escarabeineos (Scarabaeidae) e borboletas frugivoras (Nymphalidae) a modificação de habitat na floresta atlantica nordestina. PhD Thesis, Universidade Federal de Pernambuco.

Fisher, R. A., Corbet, S. A., Williams, C. B. 1943. The relation between number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12, 42-58.

Francini, R. B., Duarte, M., Mielke, O. H. H., Caldas, A., Freitas, A. V. L. 2011. Butterflies (Lepidoptera, Papilionoidea and Hesperioidea) of the "Baixada Santista" region, coastal São Paulo, southeastern Brazil. Revista Brasileira de Entomologia 55(1): 55-68.

Freitas, A. V. L. & Brown, K. S. 2004. Phylogeny of the Nymphalidae (Lepidoptera). Systematic Biology 53(3): 1-25.

Freitas, A. V. L., Kaminski, L. A., Iserhard, C. A., Magaldi, L. M., Wahlberg, N., Silva-Brandão, K. L., Marini-Filho, O. J. 2014. *Paulogramma hydarnis* (n. comb.) (Nymphalidae: Biblidinae): Distribution, systematic position, and conservation status of a rare and endangered butterfly. Neotropical Entomology 43(3): 218-226.

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

Freitas, A. V. L., Barbosa, E. P., Siewert, R. R., Mielke, O. H. H., Zacca, T., Azeredo-Espin, A. M. L., 2015. Four new species of Moneuptychia (Lepidoptera: Satyrinae: Euptychiina) from Brazil. Zootaxa 3981 (4): 521-541.

Freitas, A. V. L., Brown, K. S., Mielke, O. H. H., Santos, J. P., Vasconcellos-Neto, J. 2016. In: Rolim, Samir Gonçalves, Menezes, Luis Fernando Tavares de Srbek-Araujo, Ana Carolina. (Org.). Borboletas da Reserva Natural Vale, Linhares/ES. In Floresta Atlântica de Tabuleiro: Diversidade e Endemismos na Reserva Natural Vale. Editora Rupestre, pp 317-328.

Fucilini, L. L. 2014. Avaliação do Efeito de Diferentes Iscas na Captura de Borboletas Frugívoras e Diversidade da Assembleia de Borboletas Frugívoras do Parque Estadual de Itapuã, Viamão, Rio Grande do Sul, Brasil. M. S. Thesis, Universidade Federal do Rio Grande do Sul.

Garcia-Salik, L. M., Carneiro, E., Dolibaina, D. R., Dias, F. M. S., Ribeiro-Leite, L. A., Casagrande, M. M., Mielke, O. H. H. 2014. Borboletas da Estação Ecológica do Caiuá, Diamante do Norte, Paraná, Brasil (Lepidoptera: Hesperioidea & Papilionoidea). SHILAP Revista de Lepidopterologia 42(166): 265-280.

Gilbert, L. E., Singer, M. C. 1975. Butterfly ecology. Annual Review of Ecology and Systematics 6, 365-395.

Graciotim, C. and Morais, A. B. B. 2016. Borboletas frugívoras em Florestas de Mata Atlântica do Parque Nacional do Iguaçu, Paraná, Brasil (Lepidoptera: Nymphalidae). SHILAP Revista de Lepidopterologia 44(173): 115-128.

Grotan, V., Lande, R., Engen, S., Saether, B.-E., Devries, P. J. 2012. Seasonal cycles of species diversity and similarity in a tropical butterfly community. Journal of Animal Ecology 81 (3), 714-723.

Gueratto, P. E. 2018. Estradas dentro de florestas afetam as comunidades de borboletas frugivoras? M. S. Thesis. Universidade Estadual de Campinas.

(IBGE) Brazilian Institute of Geography and Statistics. 2017a. Download de dados geográficos (http://mapas.mma.gov.br/i3geo/datadownload.htm). IBGE, Rio de Janeiro, Brazil.

(IBGE) Brazilian Institute of Geography and Statistics. 2017b. Download de dados geográficos (http://www.mma.gov.br/biomas/mata-atlantica/mapa-da-area-de-aplicacao). IBGE, Rio de Janeiro, Brazil.

Iserhard, C. A. and Romanowski, H. P. 2004. Lista de espécies de borboletas (Lepidoptera: Papilionoidea & Hesperioidea) da região do vale do Rio Maquiné, Rio Grande do Sul, Brasil. Revista Brasileira de Zoologia 21(3): 649-662.

Iserhard, C. A., Quadros, M. T., Romanowski, H. P., Mendonça, M. S. 2010. Borboletas (Lepidoptera: Papilionoidea & Hesperioidea) ocorrentes em diferentes ambientes na Floresta Ombrófila Mista e nos Campos de Cima da Serra do Rio Grande do Sul, Brasil. Biota Neotropica 10(1): 309-320.

Joly, C. A., J. P. Metzger, and Tabarelli, M. 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytologist 204: 459-473.

Lamas, G. 2004. Checklist: Part 4A, Hesperioidea - Papilionoidea, (Lamas ed.). In: J.B. Heppner (ed.). Atlas of Neotropical Lepidoptera. Gainesville, Association for Tropical Lepidoptera, Scientific Publishers. 439pp.

Marchiori, M. O. O. 2012. Composição e variação da assembleia de borboletas (Lepidoptera: Papilionoidea, Hesperioidea) ao longo do dia em matas de restinga e matas de araucária, Rio Grande do Sul, Brasil.

Melo, D. H. A. 2014. Efeito da fragmentação de habitat sobre borboletas frugivoras (Lepidoptera: Nymphalidae) na floresta atlantica nordestina. M. S. Thesis, Universidade Federal de Pernambuco.

Mielke, C. G. C. 1994. Papilionoidea e Hesperioidea (Lepidoptera) de Curitiba e seus arredores, Paraná, Brasil, com notas taxonômicas sobre Hesperiidae. Revista Brasileira de Zoologia 11(4): 759-776.

Mielke, O. H. H. and Casagrande, M. M. 1997. Papilionoidea e Hesperioidea (Lepidoptera) do Parque Estadual do Morro do Diabo, Teodoro Sampaio, São Paulo, Brasil. Revista Brasileira de Zoologia 14(4): 967-1001.

Mittermeier, R. A., W. R. Turner, F. W. Larsen, T. M. Brooks, and C. Gascon. 2011. Global biodiversity conservation: the critical role of hotspots, pp. 2–22. In F. E. Zachos, and J. C. Habel (eds.), Biodiversity hotspots: distribution and protection of conservation priority areas. Springer-Verla, Heidelberg, Germany.

Morellato, L. P. C. & Haddad, C. F. B. 2000. Introduction: the Brazilian Atlantic Forest. Biotropica 32: 786-792.

Muylaert, R. L., M. H. Vancine, R. Bernardo, J. E. F. Oshima, T. Sobral-Souza, V. R. Tonett, B. B. S. Niebuhr, and M. C. Ribeiro. Limites territoriais inclusivos para estudos ecológicos e biogeográficos na Mata Atlântica. Oecologia Australis (in review).

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Neves, D. A. and Paluch, M. 2016. Estrutura da comunidade de borboletas frugívoras na Mata Atlântica do litoral sul da Bahia (Brasil) (Lepidoptera: Nymphalidae). SHILAP Revista de Lepidopterologia 44(176): 593-606.

van Nieukerken, E. J., Kaila, L., Kitching, I. J., Kristensen, N. P., Lees, D. C., Minet, J., Mitter, C., Mutanen, M., … 2011. Order Lepidoptera Linnaeus, 1758. In Z.-Q. Zhang (ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148, 23 Dec 2011: 212-221.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D’amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51: 933–938.

Ortiz-Acevedo, E., Bonfantti, D., Casagrande, M., Mielke, O. H. H., Espeland, M., Willmott, K. R. 2017. Using molecules and morphology to unravel the systematics of Neotropical

Preponine butterflies (Lepidoptera: Charaxinae: Preponini). Insect Systematics and Diversity, 1(1): 48-56.

Paluch, M., Mielke, O. H. H., Nobre, C. E. B., Casagrande, M. M., Melo, D. H. A., Freitas, A. V. L. 2011. Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of the Parque Ecológico João Vasconcelos Sobrinho, Caruaru, Pernambuco, Brazil. Biota Neotropica 11(4): 229-238.

Paluch, M., Mielke, O. H. H., Linhares, L. M., Silva, D. C. 2016. Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of the Private Reserve of Natural Heritage Fazenda Lontra/Saudade, Itanagra, Northern Coast of Bahia, Brazil. Biota Neotropica 16(1): e20140085.

Peña, C. & Wahlberg, N. 2008. Prehistorical climate change increased diversification of a group of butterflies. Biology Letters 4: 274-278.

Pozo, C., Luis, A. M., Llorente, J. B., Salas, N., Maya, A.; Vargas, I. F. 2008. Seasonality and phenology of butterflies (Lepidoptera: Pieridae, Papilionidae, Nymphalidae, Lycaenidae and Hesperiidae) in Calakmul, biosphere reserve. Florida Entomologist 91(3), 407-422.

Pyrcz, T. W., Freitas, A. V. L., Boyer, P., Dias, F. M. S., Dolibaina, D. R., Barbosa, E. P., Magaldi, L. M., Mielke, O. H. H., Casagrande, M. M., Lorenc-Brudecka, J. 2018. Uncovered diversity of a predominantly Andean butterfly clade in the Brazilian Atlantic Forest: a revision of the genus *Praepedaliodes* Forster (Lepidoptera: Nymphalidae, Satyrinae, Satyrini). Neotropical Entomology 47, 211-255.

Ribeiro, D. B. 2006. A guilda de borboletas frugívoras em uma paisagem fragmentada no Alto Paraíba, SP. M. S. Thesis, Universidade Estadual de Campinas, Campinas.

Ribeiro, D. B., Freitas, A. V. L. 2011. Large-sized insects show stronger seasonality than small-sized ones: a case study of fruitfeeding butterflies. Biological Journal of the Linnean Society 104 (4), 820-827.

Ribeiro, D. B. and Freitas, A. V. L. 2012. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. Journal of Insect Conservation 16: 733-744.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142: 1141–1153.

Ribeiro, M. C., A. C. Martensen, J. P. Metzger, M. Tabarelli, F. Scarano, and M. Fortin. 2011. The Brazilian Atlantic Forest: a shrinking biodiversity hotspot, pp. 405–434. In F. E. Zachos, and J. C. Habe (eds.), Biodiversity hotspots: distribution and protection of conservation priority areas. Springer-Verlag, Heidelberg, Alemanha.

Richter, A. 2018. Estratificação vertical em borboletas frugivoras: diversidade taxonomica combinada a abordagem funcional e filogenetica em uma regiao de Mata Atlantica. M. S. Thesis, Universidade Federal de Pelotas.

Santos, J. P. 2018. Padrões de diversidade das borboletas frugívoras (família Nymphalidae) em diferentes escalas macroecológicas. PhD Thesis, Universidade Estadual de Campinas.

Santos, J. P., Iserhard, C. A., Teixeira, M. O., Romanowski, H. P. 2011. Fruit-feeding butterflies guide of subtropical Atlantic Forest and Araucaria Moist Forest in State of Rio Grande do Sul, Brazil. Biota Neotropica, 11(3): 253-274.

Santos, J. P., Marini-Filho, O. J., Freitas, A. V. L. & Uehara-Prado, M. 2016. Monitoramento de borboletas: o papel de um indicador biológico na gestão de unidades de conservação. Biodiversidade Brasileira 6: 87-99.

Santos, J. P., Iserhard, C. A., Carreira, J. Y. O., Freitas, A. V. L. 2017. Monitoring fruit-feeding butterfly assemblages in two vertical strata in seasonal Atlantic Forest: temporal species turnover is lower in the canopy. Journal of Tropical Ecology, 33(5), 345-355.

Schantz, A. A. 2000. Levantamento da Diversidade de Borboletas (Lepidoptera; Rhopalocera), no Parque Estadual do Turvo, RS e no Parque Estadual de Itapuã, RS. M. S. Thesis, Universidade Federal do Rio Grande do Sul.

Seraphim N., Marín M. A., Freitas A. V. L. & Silva-Brandão K. L. 2014. Morphological and molecular marker contributions to disentangling the cryptic Hermeuptychia hermes species complex (Nymphalidae: Satyrinae: Euptychiina). Molecular Ecology Resources 14: 39-49.

Shields, O. 1989. World number of butterflies. Journal of the Lepidopterist's Society 43(3): 178-183.

Sigovini, M., Keppel, E., Tagliapietra, D. 2016. Open nomenclature in the biodiversity era. Methods in Ecology and Evolution, 7, 1217-1225.

Silva, A. R. M., Guimarães, M. P. M., Vitalino, R. F., Bagni, A. S., Martins, Y. E., Cordeiro, A. M., Oliveira, E. G. 2010. Borboletas frugívoras do Parque Estadual do Rio Doce/MG. MG.Biota, 3(4): 5-21.

Silva, A. R. M., Castro, C. O., Mafia, P. O., Mendonça, M. O. C., Alves, T. C. C., Beirão, M. V. 2012. Borboletas frugívoras (Lepidoptera: Nymphalidae) de uma área urbana (Área de Proteção Especial Manancial Cercadinho) em Belo Horizonte, Minas Gerais Brasil. Biota Neotropica 12(3): 292-297.

Soares, A., Bizarro, J. M. S., Bastos, C. B., Tangerini, N., Silva, N. A., Silva, A. S., Silva, G. B. 2011. Preliminary analysis of the diurnal Lepidoptera fauna of the Três Picos State Park, Rio de Janeiro, Brazil, with a note on Parides ascanius (Cramer 1775). Tropical Lepidoptera Research 21(2): 66-79.

Soares, G. R., Oliveira, A. A. P., Silva, A. R. M. 2012. Borboletas (Lepidoptera: Papilionoidea e Hesperioidea) de um parque urbano em Belo Horizonte, Minas Gerais, Brasil. Biota Neotropica 12 (4): 209-217.

Spaniol, R. L. and Morais, A. B. B. 2015. Borboletas frugívoras em área de transição ecológica do sul do Brasil (Lepidoptera: Nymphalidae). SHILAP Revista de Lepidopterologia 43: 27-40.

Tabarelli, M., L. P. Pinto, J. M. C. Silva, M. M. Hirota, L. C. Bedê. 2005. Desafios e oportunidades para a conservação da biodiversidade na Mata Atlântica brasileira. Megabiodiversidade 1: 132-138.

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

Teixeira, E. C. 2003. A diversidade de borboletas (Lepidoptera: Rhopalocera) como elemento de caracterização de diferentes ambientes do Parque Estadual de Itapuã, RS. M. S. Thesis, Universidade Federal do Rio Grande do Sul.

Teixeira, M. O. 2005. Diversidade de Borboletas em duas áreas da Reserva Biológica do Lami, Porto Alegre, RS. Trabalho de conclusao de curso, Universidade Federal do Rio Grande do Sul.

Thiele, S. C., Milcharek, O., Santos, F. L., Kaminski, L. A. 2014. Butterflies (Lepidoptera: Hesperioidea and Papilionoidea) of Porto Mauá, Upper Paraná Atlantic Forest Ecoregion, Rio Grande do Sul State, Brazil. Biota Neotropica 14(2): 1-10.

Thomas, J. A., 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions B, 360(1454): 339–357.

Uehara-Prado, M., Freitas, A. V. L., Francini, R. B., Brown, K. S. 2004. Guia das Borboletas Frugívoras da Reserva Estadual do Morro Grande e região de Caucaia do Alto, Cotia (São Paulo). Biota Neotropica 4:1-25.

Uehara-Prado, M., Brown, K. S. & Freitas, A. V. L. 2007. Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. Global Ecology and Biogeography 16: 43-54.

Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V. L. & Brower, A. V. Z. 2009. Nymphalid butter lies diversify following near demise at the Cretaceous/Tertiary boundary. Proceedings of the Royal Society B Biological Sciences 276: 4295-4302.

Wallace, A. R. 1865. On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan region. Transactions of the Linnean Society of London 25, 1-71.

Warren, A. D., Davis, K. J., Stangeland, E. M., Pelham, J. P., Willmott, K. R., Grishin, N. V. 2017. Illustrated Lists of American Butterflies (North and South America). Available in http://butterfliesofamerica.com/L/Neotropical.htm.

Zacca, T., Bravo, F., Araujo, M. X. 2011. Butterflies (Lepidoptera: Papilionoidea and Herperioidea) from Serra da Jiboia, Bahia State, Brazil. EntomoBrasilis 4(3): 139-143.

Zacca, T., Mielke, O. H. H., Pyrcz, T. W., Casagrande, M. M., Freitas, A. V. L., Boyer, P. 2013. Stegosatyrus, a new genus of Euptychiina from the grasslands of neotropical realm (Lepidoptera: Nymphalidae: Satyrinae). Zootaxa 3682(2): 331-350.

Allee, W. C. 1926. Measurement of environmental factors in the tropical rain-forest of Panama. Ecology 7(3): 273-302.

Ackerly, D. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs 74, 25–44.

Baker, S. C., Barmuta, L. C., McQuillan, P. B., Richardson, A. M. M. 2007. Estimating edge effects on ground-dwelling beetles at clearfelled non-riparian stand edges in Tasmanian wet eucalypt forest. Forest Ecology and Management 239: 92-101.

Basset, Y., Novotny, V., Miller, S. E., Kitching, R. L. 2003. Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, UK.

Beck, M. W. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. Journal of Experimental Marine Biology and Ecology 249: 29-49.

Benedick, S., Hill, J. K., Mustaffa, N., Chey, V. K., Maryati, M., Searle, J. B., Schilthuizen, M., Hamer, K. C. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. Journal of Applied Ecology 43: 967-977.

Blomberg, S. P. & Garland, T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology 15: 899-910.

Blomberg, S. P., Garland Jr, T. & Ives, A. R. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57(4): 717-745.

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L. & Ehrlich, P. R. 2010. More than just indicators: a review of tropical butterfly ecology and conservation. Biological Conservation 143:1831-1841.

Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C., Silva, J. N. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141: 1745-1757.

Brose, U., Martinez, N. D. & Williams, R. J. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. Ecology 84: 2364-2377.

Brown, K. S. & Freitas, A. V. L. 2000. Atlantic Forest butterflies: indicators for landscape conservation. Biotropica 32:934-956.

Cadotte, M. W. & Tucker, C. M. 2017. Should environmental filter be abandoned? Trends in Ecology and Evolution 32(6): 429-437.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., White, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20: 620-631.

Cavender-Bares, J., Ackerly, D. D., Baum, D. A., Bazzaz, F. A. 2004. Phylogenetic overdispersion in Floridian Oak communities. The American Naturalist, 163(6): 823-843.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12: 693-715.

Chai, P. 1990. Relationships between visual characteristics of rainforest butterflies and responses of a specialized insectivorous bird. In Adaptive Coloration in Invertebrates. Proceedings of Symposium Sponsored by American Society of Zoologists (ed. M. Wicksten), pp. 31–60. Galveston: Seagrant College Program, Texas A & M University.

Chai, P. & Srygley, R. B. 1990. Predation and the flight, morphology, and temperature of Neotropical Rain-forest butterflies. The American Naturalist 135(6): 748-765.

Chazot, N., Panara, S., Zilbermann, N., Blandin, P., Poul, Y. L., Cornette, R., Elias, M., Debat, V. 2016. Morpho morphometrics: Shared ancestry and selection drive the evolution of wing size and shape in Morpho butterflies. Evolution 70: 181-194.

Condit R., Pitman N., Leigh Jr. E. G., Chave J., Terborgh J., Foster R. B., Núñez P. V., Aguilar S., Valencia R., Villa G., Muller-Landau, H. C., Losos E., Hubbel S. P. 2002. Beta-Diversity in Tropical Forest Trees. Science, 295: 666-669.

Cramer, M. J. & Willig, M. R. 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sandshinnery-oak landscape. Journal of Mammology 83: 743-753.

Debastiani, V. J. & Pillar, V. D. 2012. SYNCSA-R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28(12): 2067-2068.

Debastiani, V. J. & Duarte, L. D. S. 2014. PCPS – an R-package for exploring phylogenetic eigenvectors across metacommunities. Frontiers of Biogeography 6: 144-148.

DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history, Volume 1: Papilionidae, Pieridae, Nymphalidae. New Jersey: Princeton University Press, Princeton.

DeVries, P. J. 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican forest. Journal of Research on Lepidoptera 26:98-108.

DeVries, P. J., Penz, C. M. & Hill, R. I. 2010. Vertical distribution, flight behaviour and evolution of wing morphology in Morpho butterflies. Journal of Animal Ecology 79:1077-1085.

Duarte, L. D. S. 2011. Phylogenetic habitat filtering influences forest nucleation in grasslands. Oikos 120: 208-215.

Duarte, L. D. S., Debastiani, V. J., Freitas, A. V. L., Pillar, V. D. 2016. Dissecting phylogenetic fuzzy weighting: theory and application in metacommunity phylogenetics. Methods in Ecology and Evolution 7: 937-946.

Duarte, L. D. S., Debastiani, V. J., Carlucci, M. B., Diniz-Filho, J. A. F. 2017. Analyzing community-weighted trait means across environmental gradients: should phylogeny stay or should it go? Ecology Accepted Author Manuscript. doi:10.1002/ecy.2081

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34: 487-515.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125: 1-15.

Fermon, H., Waltert, M., Vane-Wright, R. I. & Mühlenberg, M. 2005. Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. Biodiversity and Conservation 14:333-350.

Filgueiras, B. K. C., Iannuzzi, L., Leal, I. R. 2011. Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biological Conservation 2011: 362-369.

Filgueiras, B. K. C., Melo, D. H. A., Leal, I. R., Tabarelli, M., Freitas, A. V. L., Iannuzzi, L. 2016. Fruit-feeding butterflies in edge-dominated habitats: community structure, species persistence and cascade effect. Journal of Insect Conservation 20: 539-548.

Fordyce, J. A. & DeVries, P. J. 2016. A tale of two communities: Neotropical butterfly assemblages show higher beta diversity in the canopy compared to the understory. Oecologia 181: 235-243.

Freitas, A. V. L., Benson, W. W., Marini-Filho, O. J. & Carvalho, R. M. 1997. Territoriality by the dawn's early light: the Neotropical owl butterfly Caligo idomenaeus (Nymphalidae: Brassolinae). Journal of Research on Lepidoptera 34: 14-20.

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

Gotelli, N. J. & Ellison, A. M. 2004. A primer of ecological statistics. Sinauer Associates, Sunderland, Massachusetts.

Graça, M. B., Pequeno, P. A. C. L., Franklin E. & Morais J. W. 2017. Coevolution between flight morphology, vertical stratification and sexual dimorphism: What we can learn from tropical butterflies? Journal of Evolutionary Biology, DOI: 10.1111/jeb.13145.

Grimbacher, P. S. & Stork, N. E. 2007. Vertical stratification of feeding guilds and body size in beetle assemblages from an Australian tropical rainforest. Austral Ecology 32: 77-85.

Hamer, K. C., Hill, J. K., Benedick, S., Mustaffa, N., Sherratt, T. N., Maryati, M. & Chey, V. K. 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. Journal of Applied Ecology 40: 150-162.

Hammer, Ø, Harper, D. A. T. & Ryan, P. D. 2001. Past: paleontological statistics software package for education and data analysis. Version 2.02. http://folk.uio.no/ohammer/past.

Hill, J. K., Hamer, K. C., Tangah, J., Dawood, M. 2001. Ecology of Tropical Butterflies in Rainforest Gaps. Oecologia 128(2): 294-302.

King, D., Wright, S., & Connell, J. 2006. The Contribution of Interspecific Variation in Maximum Tree Height to Tropical and Temperate Diversity. Journal of Tropical Ecology 22(1): 11-24.

Laurance, W. F. & Williamson, G. B. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. Conservation Biology 15(6): 1529-1535.

Legendre P, Legendre L. 1998. Numerical ecology. Amsterdam: Elsevier Science.

McCoy E.D., Bell S.S. 1991. Habitat structure: The evolution and diversification of a complex topic. In: Bell S.S., McCoy E.D., Mushinsky H.R. (eds) Habitat Structure. Population and Community Biology Series, vol 8. Springer, Dordrecht.

McGill, B. J., Enquist, B. J., Weiher, E., Westoby, M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution, 21: 178-185.

Mittelbach G. G., Schemske D. W., Cornell H. V., Allen A. P., Brown J. M., Bush M. B., Harrison S. P., Hurlbert A. H., Knowlton N., Lessios H. A., McCain C. M., McCune A. R., McDade L. A., McPeek M. A., Near T. J., Price T. D., Ricklefs R. E., Roy K., Sax D. F., Schluter D., Sobel J. M., Turelli M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10: 315-331.

Moffett, M. W. 2013. Comparative canopy biology and the structure of ecossystems. – In: Lowman, M. et al. (eds), Treetops at risk challenges of global canopy ecology and conservation. Springer, pp. 13-54.

Molleman, F., Arjan, K., Brakefield, P. M., DeVries, P. J. & Zwaan, B. J. 2006. Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. Biodiversity and Conservation 15:107-121.

Montgomery, R. A. & Chazdon, R. L. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82: 2707–2718.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution, 10(2): 58-62.

Novotny V., Drozd P., Miller S. E., Kulfan M., Janda M., Basset Y., Weiblen G. D. 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313: 1115-1118.

Pavoine, S., Baguette, M., Stevens, V. M., Leibold, M. A., Turlure, C., Bonsall, M. B. 2014. Life history traits, but not phylogeny, drive compositional patterns in a butterfly metacommunity. Ecology 95(12): 3304-3313.

Peres-Neto, P. R., S. Dray, and C. J. F. t. Braak. 2017. Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. Ecography 40: 806-816.

Pillar, V. D. & Duarte, L. d. S. 2010. A framework for metacommunity analysis of phylogenetic structure. Ecology Letters 13: 587-596.

Revell, L. J. 2013. Two new methods for mapping trait evolution on phylogenies. Methods in Ecology and Evolution 4: 754-759.

Revell, L. J. 2017. Phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3: 217-223.

Ribeiro, D. B. & Freitas, A. V. L. 2010. Differences in thermal responses in a fragmented landscape: temperature affects the sampling of diurnal, but not nocturnal fruit-feeding Lepidoptera. Journal of Research on Lepidoptera 42:1-4.

Ribeiro, D. B. & Freitas, A. V. L. 2012. The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. Journal of Insect Conservation 16: 733-744.

Salmon, S., Ponge, J. F., Gachet, S., Deharveng, L., Lefebvre, N., Delabrosse, F. 2014. Linking species, traits and habitat characteristics of Collembola at European scale. Soil Biology & Biochemistry 75: 73-85.

Santos J. P., Marini-Filho O. J., Freitas A. V. L., Uehara-Prado M. 2016. Monitoramento de borboletas: o papel de um indicador biológico na gestão de unidades de conservação. Biodiversidade Brasileira 6: 87-99.

Schluter, D., Price, T., Mooers, A. Ø. & Ludwig, D. 1997. Likelihood of ancestor states in adaptive radiation. Evolution 51: 1699-1711.

Schulze C. H., Linsenmair K. E. & Fiedler K. 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. Plant Ecology 153:133-152.

Shahabuddin, G. & Ponte, C. A. 2005. Frugivorous butterflies species in tropical forest fragments: correlates of vulnerability to extinction. Biodiversity and Conservation 14: 1137-1152.

Shahabuddin, G. & Terborgh, J. W. 1999. Frugivorous butterflies in Venezuelan forest fragments: abundance, diversity and the effects of isolation. Journal of Tropical Ecology 15: 703–722.

Srygley, R. B. 1994. Shivering and its costs during reproductive behaviour in Neotropical owl butterflies, Caligo and Opsiphanes (Nymphalidae: Brassolinae). Animal Behaviour 47:23-32.

Turner, J. R. G., Gatehouse, C. M. & Corey, C. A. 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. Oikos 48:195-205.

Uehara-Prado, M., Brown, K. S. & Freitas, A. V. L. 2007. Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. Global Ecology and Biogeography 16: 43-54.

Vieira, E. M. & Monteiro-Filho, E. L. A. 2003. Vertical stratification of small mammals in the Atlantic rain forest of southeastern Brazil. Journal of Tropical Ecology 19: 501-507.

Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A. V. L. & Brower, A. V. Z. 2009. Nymphalidae butterflies diversify following near demise at the cretaceous/tertiary boundary. Proceedings of the Royal Society of London B 276: 4295-4302.

Walther, B. A. 2002. Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. Journal of Ornithology 143:64-81.

Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33: 475–505.

Williams-Linera, G., Dominguez–Gastelu, V., Garcia–Zurita, M. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. Conservation Biology, 12(5): 1091-1102.

Xing, S., Bonebrake, T. C., Tang, C. C., Pickett, E. J., Cheng, W., Greenspan, S. E., Williams, S. E. & Scheffers, B. R. 2016. Cool habitats support darker and bigger butterflies in Australian tropical forests. Ecology and Evolution 6:8062-8074.

Allouche, O., Tsoar, A., Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43, 1223-1232.

Araújo, M., and New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* 22(1), 42-47.

Barlow, J., Overal, W. L., Araujo, I. S., Gardner, T. A., Peres, C. A. (2007). The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *Journal of Applied Ecology*, 44(5), 1001–1012.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, L., Maher, S. P., Peterson, A. T., Soberón, J., Villalobos, F. (2011). The crucial role of the acessible área in ecological niche modelling and species distribution modelling. *Ecological Modelling* 222(11), 1810-1819.

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F. (2014). Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography,* 23, 1376-1386.

Bello, C., Galetti, M., Montan, D., Pizo, M. A., Mariguela, T. C., Culot, L., … Jordano, P. (2017). Atlantic-frugivory: A plant-frugivore interaction dataset for the Atlantic Forest. *Ecology*, 98: 1729. doi:10.1002/ecy.1818.

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L., Ehrlich, P. R. (2010). More than just indicators: A review of tropical ecology butterfly ecology and conservation. *Biological Conservation*, 143(8), 1831-1841.

Bovendorp, R. S., Villar, N., Abreu-Junior, A. F., Bello, C., Regolin, A. L., Percequillo, A. R., Galetti, M. (2017). Atlantic small-mammal: a dataset of communities of rodents and marsupials of the Atlantic forests of South America. *Ecology*, 98(8), 2226.

Brito, M. M., Ribeiro, D. B., Raniero, M., Hasui, E., Ramos, F. N., Arab, A. 2014. Functional composition and phenology of fruit-feeding butterflies in a fragmented landscape: variation of seasonality between habitat specialists. Journal Insect Conservation 18(4): 547-560.

Brown, K. S. Jr. (1979). Ecologia geográfica e evolução nas florestas neotropicais. UNICAMP, Campinas, 120p.

Brown, K. S. Jr. (1987). Biogeography and evolution of neotropical butterflies. In Whitmore, T. C. & Prance, G. T. (Eds). *Biogeography and quaternary history in Tropical America* (Pp 66-104). Oxford: Clarendon Press.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59-67.

Carnaval, A. C. & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic Forest. *Journal of Biogeography*, 35(7), 1187-1201.

Carnaval, A. C., Hickerson, M. J., Haddad, C. F. B., Rodrigues, M. T., Moritz C. M. (2009). Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. *Science* 323, 785-789.

Carpenter, G., Gillison, A. N., Winter, J. (1993). DOMAIN: a flexible modeling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation*, 2, 667-680.

Ceballos, G. & Erhlich, P. R. (2006). Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences*, 103(51)**,** 19374-19379.

Costa, E. P., Leite, Y. L. R., Fonseca, G. B., Fonseca, M. T. (2000). Biogeography of South American forest mammals: endemism and diversity in the Atlantic Forest. *Biotropica* 32(4b), 872-881.

Costa, G. C., Nogueira, C., Machado, R. B., Colli, G. R. (2010). Sampling bias and the use of ecological niche modeling in conservation planning: a field evaluation in a biodiversity hotspot. *Biodiversity and Conservation*, 19(3), 883-899.

da Silva, J. M. C., Souza, M. C., Castelletti, C. H. M. (2004). Areas of endemism for passerine birds in the Atlantic forest, South America. *Global Ecology and Biogeography*, 13, 85-92.

DeVries, P. J., Murray, D., Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of Linnean Society,* 62, 343-364.

Diniz-Filho, J. A. F., Bini, L. M., Rangel, T. F., Loyola, R. D., Hof, C., Nogués-Bravo, D., Araújo, M. B. (2009). Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography*, 32, 897-906.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. G. B., Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401-406.

Franklin J. (2009*). Mapping Species Distributions: Spatial Inference and Prediction.* Cambridge, UK: Cambridge Univ. Press.

Freitas, A. V. L., Iserhard, C. A., Santos, J. P., Carreira, J. Y. O., Ribeiro, D. B., Melo, D. H. A., … Uehara-Prado, M. (2014). Studies with butterfly bait traps: an overview. *Revista Colombiana de Entomologia*, 40(2), 209-218.

Graça, M. B., Souza, J. L. P., Franklin, E., Morais, J. W., Pequeno, P. A. C. L. (2017). Sampling effort and common species: Optimizing surveys of understorey fruit-feeding butterflies in the Central Amazon. *Ecological Indicators*, 73: 181-188.

Graham, C. H., Moritz, C. & Williams, S. E. (2006). Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences USA*, 103(3), 632–636.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1(2), e1500052.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965-1978.

Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J. (2015). Dismo: Species Distribution Modeling. R Package Version 1.0-12.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., … O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105-109.

Horner-Devine, M. C., Daily, G. C., Ehrlich, P. R., Boggs, C. L. (2003). Countryside biogeography of tropical butterflies. *Conservation Biology* 17, 168-177.

Jenkins, C. N., Pimm, S. L., Joppa, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences USA*, 110(28), E2602-E2610.

Jorge, M. L. S., Galetti, M., Ribeiro, M. C., Ferraz, K. M. P. (2013). Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot. *Biological Conservation* 163, 49-57.

Karatzoglou, A., Smola, A., Hornik, K., Zeileis, A. (2004). kernlab – an S4 package for kernel methods in R. *Journal of Statistical Software*, 11(9), 1-20.

Koh, L. P. (2007). Impacts of land use change on South-east Asian forest butterflies: a review. *Journal of Applied Ecology* 44, 703-713.

Lamas, G. (2004). Checklist: Part 4A. Hesperioidea – Papilionoidea. In J. B. Heppner (Ed). *Atlas of Neotropical Lepidoptera 5A*. Gainesville: Association for Tropical Lepidoptera.

Laurance, W. F. (2009). Conserving the hottest of the hotspots. *Biological Conservation* 142, 1137.

Liu, C., Newell, G., White, M. (2016). On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution* 6(1), 337-348.

Margules, C. R. & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, 405, 243-253.

Metzger, J. P. (2001). O que é ecologia de paisagens? *Biota Neotropica*, 1, 1-9.

Morellato, L. P. C. & Haddad, C. F. B. (2000) Introduction: the Brazilian Atlantic Forest. *Biotropica*, 32(4), 786-792.

Muylaert, R. L., Stevens, R. D., Esbérard, C. E. L., Mello, M. A. R., Garbino, G. S. T., Varzinczak, L. H., … Galetti, M. (2017). Atlantic bats: a dataset of bat communities from the Atlantic forests of South America. *Ecology*, Accepted Author Manuscript. doi:10.1002/ecy.2007.

Mittermeier, R. A., Gill, P. R., Hoffmann, M., Pilgrim, J., Brooks, J., Mittermeier, C. J.,

Lamourux, J., Fonseca, G. A. B. (2005). *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. Washington, DC: CEMEX.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Nix, H. A. (1986). A biogeographic analysis of Australian Elapid snakes. In Longmore, R. (ed.), *Atlas of Australian Elapid Snakes* (pp 4-15). Canberra: Australian Government Publishing Service

Nobrega, C. C., de Marco Jr, P. (2011). Unprotecting the rare species: a niche-based gap analysis for odonates in a core Cerrado area. *Diversity and Distributions*, 17(3), 491-505.

Pearson, R.G., Raxworthy, C. J., Nakamura, M., Peterson, A. T. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, 34, 102-117.

Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martinez-Meyer, E., Nakamura, M., Araújo, M. B. (2011). *Ecological Niches and Geographic Distributions.* Princeton: Princeton University Press.

Phillips, S. J. and Dudik, M. (2008). Modeling of Species Distributions with MaxEnt: New Extensions and a Comprehensive Evaluation. *Ecography*, 31, 161-175.

Ribeiro, D. B. & Freitas, A. V. L. (2012). The effect of reduced-impact logging on fruit-feeding butterflies in Central Amazon, Brazil. *Journal of Insect Conservation*, 16(5), 733-744.

Ribeiro, D. B., Batista, R., Prado, P. I., Brown Jr, K. S., Freitas, A. V. L. (2012). The importance of small scales to the fruit-feeding butterfly assemblages in a fragmented landscape. *Biodiversity and Conservation*, 21(3), 811-827.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142(6), 1141-1153.

Rossato, D. O., Kaminski, L. A., Iserhard, C. A., Duarte, L. 2018. More than colours: An Eco-evolutionary framework for wing shape diversity in butterflies. Advances in Insect Physiology. ttps://doi.org/10.1016/bs.aiip.2017.11.003

Santos, J. P., Marini-Filho, O. J., Freitas, A. V. L. & Uehara-Prado, M. (2016). Monitoramento de borboletas: o papel de um indicador biológico na gestão de unidades de conservação. *Biodiversidade Brasileira*, 6, 87-99.

Santos, J. P., Iserhard, C. A., Carreira, J. Y. O., Freitas, A. V. L. (2017). Monitoring fruit-feeding butterfly assemblages in two vertical strata in seasonal Atlantic Forest: temporal species turnover is lower in the canopy. *Journal of Tropical Ecology*, 33(5), 345-355.

Silva, J. M. C., & Casteleti, C. H. M. (2003). Status of the biodiversity of the Atlantic Forest of Brazil. In C. Galindo-Leal & I.G. Câmara (Eds.), *The Atlantic Forest of South America:*

biodiversity status, threats, and outlook (Pp 43-59). Washington, D.C.: CABS and Island Press.

Siqueira, M. F., Durigan, G., de Marco Jr, P., Peterson, A. T. (2009). Something from nothing: Using landscape similarity and ecological niche modeling to find rare plant species. *Journal for Nature Conservation*, 17(1), 25-32.

Soberón, J, Nakamura, M., (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, 106, 19644-19650.

Sobral-Souza, T., Francini, R. B., Lima-Ribeiro, M. S., (2015). Species extinction risk might increase out of reserves: allowances for conservation of threatened butterfly *Actinote quadra* (Lepidoptera: Nymphalidae) under global warming. *Natureza & Conservação* 13, 159–165.

Sobral-Souza, T., Lima-Ribeiro, M. S. (2017). De volta ao passado: Revisitando a história biogeográfica das florestas neotropicais úmidas. *Oecologia Australis* 21(2), 93-107.

Sobral-Souza, T., Lautenschlager, L., Morcatty, T. Q., Bello, C., Hansen, D., Galetti, M. (2017). Rewilding defaunated Atlantic Forests with tortoises to restore lost seed dispersal functions. *Perspectives in Ecology and Conservation,* in press, https://doi.org/10.1016/j.pecon.2017.08.005.

Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., Peres, C. A. (2010). Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. *Biological Conservation*, 143(10), 2328-2340.

Tambosi, L. R., Martensen, A. C., Ribeiro, M. C. and Metzger, J. P. (2014). A Framework to Optimize Biodiversity Restoration Efforts Based on Habitat Amount and Landscape Connectivity. *Restoration Ecology*, 22(2), 169-177.

Tax, D. M. J. and Duin, R. P. W. (2004). Support vector data description. Machine Learning, 54(1), 45-66.

Thompson, P. L., Rayfield, B., Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography,* 40, 98-108.

Tyler, H., Brown, K. S., Wilson, K. (1994). *Swallowtail butterflies of the Americas. A study in biological dynamics, ecological diversity, biosystematics and conservation.* Gainesville: Scientific Publishers.

Veach, V., Di Minin, E., Pouzols, F. M., Moilanen, A. (2017). Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. *Diversity and Distributions*, 23(7), 715-726.

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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha , intitulada "**Padrões de diversidade das borboletas frugívoras (Nymphalidae) em diferentes escalas macroecológicas**", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

Assinatura: Jessie Santos
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Data: **01 de Agosto de 2018**

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Tese de Doutorado, intitulada **Padrões de Diversidade das borboletas frugívoras (Nymphalidae) em diferentes escalas macroecológicas**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, **01 de Agosto de 2018**

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