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**EVOLUÇÃO, GRADIENTES AMBIENTAIS E NICHOS TRÓFICOS LARVAIS
COMO DETERMINANTES PARA PADRÕES DE DIVERSIDADE DE
BORBOLETAS FRUGÍVORAS NA AMAZÔNIA**

MÁRLON BRENO COSTA SANTOS DA GRAÇA

Manaus, Amazonas, Brasil

Dezembro, 2018

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COMO DETERMINANTES PARA PADRÕES DE DIVERSIDADE DE
BORBOLETAS FRUGÍVORAS NA AMAZÔNIA**

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Sinopse:

Estudamos os padrões espaciais de diversidade taxonômica e filogenética de borboletas frugívoras amazônicas em relação à gradientes ambientais e a flutuação de traços funcionais desde microhabitats até a escala regional. Foram usadas abordagens de biologia evolutiva e ecologia de comunidades para responder a essas questões, utilizando um banco de dados coletado em sete localidades da Amazônia brasileira.

Palavras-chave: Filtros ambientais, Multidimensionalidade da diversidade, Radiação adaptativa, Resposta ecológica, Sinal filogenético.

Ao trabalho árduo de meus pais, Márcia e Domingos
Ao espírito infinitamente presente de meu irmão Patrick

*If we long for our planet to be important,
there is something we can do about it.
We make our world significant
by the courage of our questions
and by the depth of our answers.*

(Carl Sagan, Cosmos)

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RESUMO

A ocupação espacial dos organismos nos ecossistemas terrestres é resultado de processos e eventos evolutivos e ecológicos. Essa distribuição reflete a adaptação de espécies, por mediação de suas características intrínsecas, às exigências fisiológicas internas e às dinâmicas biológicas e filtros do meio circundante. Para estudar esses padrões, a ecologia de comunidades tem passado a analisar o componente funcional e filogenético da biodiversidade, ao invés da tradicional abordagem com base nos nomes binomiais de espécies. Tal abordagem complementar é particularmente importante quando investigam-se ambientes e organismos diversos, como borboletas na Amazônia. Na presente tese, investigamos (1) a influência da evolução da morfologia associada ao voo na distribuição vertical e no dimorfismo sexual de borboletas frugívoras, (2) a variação espacial de padrões de diversidade taxonômica, funcional e filogenética em um mosaico de florestas na Amazônia setentrional e (3) o papel do nicho ecológico larval na ocorrência espacial de adultos ao longo de gradientes locais e regionais da Amazônia brasileira. As borboletas foram coletadas com armadilhas e iscas atrativas em sete localidades de três estados brasileiros. Para o primeiro capítulo, foram utilizados modelos de mínimo de quadrados generalizados filogenéticos, enquanto que nos demais dois capítulos foram conduzidas análises de regressão (II) e modelos lineares de efeitos mistos (III). No primeiro capítulo, verificamos que a variação na morfologia de voo de borboletas pode ser explicada pela estratificação vertical, e que tal relação é mais forte em fêmeas. Há, ainda, acentuado dimorfismo sexual quanto à capacidade de voo, especialmente entre espécies do sub-bosque. No segundo capítulo, evidenciamos que florestas de areia com muita luminosidade abrigam alta abundância, porém baixa riqueza de espécies, as quais tendem a ser maiores, terem maior capacidade de voo e larvas mais generalistas. Em florestas ombrófilas, por sua vez, a especialização larval é maior, possivelmente devido à maior quantidade de nichos ecológicos disponíveis. No terceiro capítulo, vimos que o nicho larval é determinante para a distribuição espacial de borboletas adultas, porém não atua como mediador na influência da vegetação, posição geográfica (latitude e longitude) e biogeografia sobre a diversidade taxonômica e filogenética da comunidade. Dessa forma, é possível concluir que a heterogeneidade da Amazônia desde microhabitats à paisagens regionais é determinante para a manutenção dos padrões de diversidade de borboletas. Na escala de microhabitat, a retirada da estratificação vertical implicará na perda de espécies

associadas a estratos particulares. Na escala local, as fisionomias da floresta de areia abrigam comunidades taxonomicamente e funcionalmente distintas, logo sendo imprescindíveis para a biodiversidade desse grupo de insetos. À nível regional, vimos que os padrões de diversidade podem ser determinados por eventos de dispersão, colonização histórica e biogeografia. Essas três escalas interagem entre si e configuram a distribuição espacial tal como vemos atualmente. Esperamos que os resultados apresentados aqui sirvam como base para o estabelecimento de planos de manejo de áreas, bem como para a seleção de paisagens alvo para conservação.

Palavras-chave: biologia comparativa, dimorfismo sexual, diversidade filogenética, gradiente de vegetação, nicho trófico larval, regiões biogeográficas, traços funcionais.

ABSTRACT

Organismal spatial occupancy in Earth ecosystems results from evolutionary and ecological events. Species distribution reflects adaptation, mediated by their intrinsic attributes, to internal physiological demands and filters imposed by the surrounding environment. To study such patterns, community ecology has been associating strictly taxonomic approaches to start incorporating information on functional traits and phylogenetic relatedness of species. This method is particularly important when studying diverse landscapes and organisms, such as the Amazon rainforest and butterflies. In this thesis, we investigated (1) the evolutionary correlation between flight morphology, vertical stratification and sexual dimorphism of fruit-feeding butterflies, (2) the spatial variation in taxonomic, functional and phylogenetic diversity patterns of butterflies across an Amazonian vegetation mosaic and (3) the role of juvenile trophic niche on the spatial occurrence of adult butterflies across local and regional Amazon gradients. We sampled butterflies with bait traps in seven localities across three Brazilian states. For the first chapter, we used Phylogenetic Generalized Least Squares models, whereas for the remaining two chapters we ran multiple regressions (II) and linear mixed effects models (III). In chapter one, we found that variation in flight morphology may be explained by vertical stratification and that such association is stronger in females. Additionally, there is a sharp sexual dimorphism in flight morphology, especially among understorey-dwelling species. In chapter two, we demonstrated that highly illuminated white-sand forests harbour higher abundance, but lower species richness of fruit-feeding butterflies. These species tended to be larger, stronger flying and more generalist during larval stage. In ombrophilous forests, larvae are more specialized, possibly due to a greater availability of ecological niches. In chapter three, we verified that larval dietary niche is determinant for the spatial occurrence of adult butterflies. It however does not act as mediator for the influence of vegetation complexity, geographic position and biogeography on taxonomic and phylogenetic diversity patterns. Therefore, we conclude that Amazonian heterogeneity from local microhabitats to regional landscapes is imperative for maintaining the diversity patterns of frugivorous butterflies. At the microhabitat scale, the removal of the vertical stratification will result in the loss of species associated with particular strata, whose flight morphology is intimately connected to environmental physical conditions. At the local scale, white-sand phytophysionomies harbour butterfly communities that are

taxonomically and functionally unique, thus being irreplaceable for maintaining the diversity of these insects. At the regional scale, we detected diversity patterns likely driven by dispersion, historical colonization and biogeographical events. These three scales interact, ultimately determining the spatial distribution of organisms as we currently see. We hope our results will help strengthen the establishment of appropriate land use planning and the selection of conservation priority areas.

Keywords: biogeographical regions, comparative biology, functional traits, larval trophic niche, phylogenetic diversity, sexual dimorphism, vegetation gradient.

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INTRODUÇÃO GERAL

Por que algumas espécies ocorrem em determinado local e outras não? Essa talvez seja uma das questões centrais e mais amplamente pesquisadas por disciplinas como ecologia, biologia evolutiva e biogeografia, uma vez que os mecanismos que determinam essa diferenciação espacial inerentemente proporcionam a variação na riqueza, abundância e composição de espécies entre locais, originando distintas assembleias ecológicas (Palmer 1994, Weiher & Keddy 1995). Não existe resposta única para essa questão, mas acredita-se que sua raiz esteja na junção de fatores como os mecanismos de coexistência (e exclusão) entre espécies, a variação das condições ambientais entre locais (MacArthur & Levins 1967, Palmer 1994, Loreau 2010), bem como os eventos históricos relacionados a dispersão de espécies, tempo de diversificação, taxas de mutações, tempo de gerações, extinções e biogeografia (Rhode 1992, Marin & Hedges 2016, Weber *et al.* 2017). Por esse motivo, ecologia e evolução são disciplinas intimamente ligadas, apesar de muitas vezes serem tratadas isoladamente (Holt 1995), principalmente devido ao desafio de analisar a sua ação combinada ao longo do tempo (Jablonski 2008, Weber *et al.* 2017).

Eventos que determinam mutações genéticas aleatórias e recombinações de material genético ocorrem em nível de indivíduo e, uma vez expresso, o caráter alterado passa a sofrer ação da seleção natural (Loreau 2010). A pressão seletiva filtra mutações de acordo com reguladores intrínsecos (e.g. trade-offs na história de vida e fisiologia) e extrínsecos (e.g. condições abióticas, dinâmica populacional, interações biológicas) complexamente interligados, de modo que os organismos que alcançam o sucesso reprodutivo e alta adaptabilidade (*fitness*) são selecionados (Stearns 2000). Assim, os indivíduos em si tem o papel central na seleção por serem os portadores da mutação gênica e por potencialmente passarem a alteração aos descendentes, enquanto o ambiente circundante direciona e regula a pressão exercida (Loreau 2010). Como consequência, espécies tendem a viver em ambientes compatíveis com suas características (Cavender-Bares *et al.* 2009; Arnan *et al.* 2013), o que afeta diretamente os padrões de distribuição que observamos desde microhábitats a escalas globais.

É sabido, então, que os padrões de distribuição espacial da biodiversidade no planeta são determinados por fatores atuais/históricos e locais/regionais (e.g. Higgins *et al.* 2011; Ribas *et al.* 2012; Blanchet *et al.* 2014). Entretanto, a biodiversidade como conhecemos é multifacetada e o conceito de diversidade da vida vai além dos

números de diversidade de espécies, perpassando genes, história evolutiva, comportamentos e funções ecossistêmicas (Loreau, 2010). Apesar de corriqueiramente a maioria dos estudos ecológicos analisarem apenas a diversidade de espécies (e.g. riqueza, abundância), esse talvez seja o componente que carrega menos informação biológica no sistema (Swenson 2014). Por isso, nas últimas décadas, uma explosão de estudos tem avaliado outros aspectos da biodiversidade, como o componente funcional (Díaz & Cabido 2001; Poff *et al.* 2010; Baccaro *et al.* 2013; Arnan *et al.* 2017; Nascimento *et al.* 2018) e filogenético (Swenson *et al.* 2012; Blanchet *et al.* 2014; Carneiro *et al.* 2014; Lamarre *et al.* 2016). O componente funcional avalia a importância dos traços funcionais: características morfológicas, fenológicas, fisiológicas, comportamentais e de história de vida que são determinantes para o desempenho ecológico (*performance*) das espécies (Violle *et al.* 2007). Já o componente filogenético investiga como o parentesco filogenético influencia a estrutura das comunidades, podendo gerar padrões de agrupamento (*clustering*), onde espécies próximas filogeneticamente tendem a coexistir, ou dispersão (*overdispersion*), onde espécies distantes coexistem (Webb *et al.* 2002). Com a inclusão das diversidades funcional e filogenética, os estudos ecológicos não só geram padrões mais gerais e aumentam seu poder preditivo, como também podem exibir *insights* evolutivos que afetam a ocorrência atual das espécies (Webb *et al.* 2002; McGill *et al.* 2006; Swenson 2013). Inclusive, considera-se que um estudo completo da diversidade de um certo grupo deve necessariamente compreender esses três componentes principais (Swenson 2011). Tal abordagem unificada deve ser particularmente importante para investigar padrões ecológicos em paisagens amplamente diversas, como as florestas tropicais.

A floresta Amazônica cobre uma área de seis milhões de km², estendendo-se por oito países sul-americanos e é reconhecida por abrigar a maior diversidade animal e vegetal no planeta (Boubli & Hrbek 2012). Contudo, as origens dessa diversidade enorme e de sua distribuição em largas escalas são menos conhecidas, de modo que “regras” gerais que regem a estrutura das comunidades amazônicas (caso elas existam) ainda não foram desvendadas. Por exemplo, há evidências que corroboram (Ribas *et al.* 2012) e refutam (Santorelli Jr. *et al.* 2018) a hipótese dos rios como barreiras (Wallace 1852), a qual expressa que os grandes corpos d’água da Amazônia funcionam como obstáculos que provocaram o isolamento genético entre táxons irmãos, tendo, portanto, fomentado a diversificação de espécies (revisão em Leite &

Rogers 2013). Assim, a Amazônia funciona como um enorme, megadiverso e interessante sistema para investigar as causas da segregação da biodiversidade.

Com base nisso, a presente tese tem como tema central discutir os fatores que afetam a distribuição espacial de um grupo bastante diversificado na Amazônia: a guilda das borboletas frugívoras. As borboletas frugívoras são um grupo não-monofilético de espécies que durante a fase adulta adquirem seus nutrientes de frutos em decomposição, exsudatos de plantas, e as vezes carcaças e fezes de animais (DeVries 1987). Tais espécies pertencem a Nymphalidae (Lepidoptera, Papilionoidea), nas subfamílias Biblidinae, Charaxinae, Nymphalinae e Satyrinae (DeVries 1987). Por se alimentarem de matéria em apodrecimento, essas borboletas são atraídas e capturadas por armadilhas contendo tais substratos que funcionam como iscas, o que permite amostragens padronizadas e simultâneas, além de possibilitar a coleta da fauna presente em camadas superiores da floresta (Freitas *et al.* 2014). A taxonomia relativamente bem conhecida de sua ampla diversidade tropical, as cores exuberantes e seu potencial como táxon substituto fazem ainda com que a guilda das frugívoras esteja entre os invertebrados mais pretendidos nos estudos de conservação (Schulze *et al.* 2004; Uehara-Prado *et al.* 2007). Além disso, as borboletas são excelente bioindicadores, estando intimamente ligadas aos habitats em todas as fases de vida (Freitas *et al.* 2003) e, portanto, características tanto dos adultos quanto das larvas devem ser importantes para predizer sua ocorrência no espaço. Por todas essas razões, consideramos que a guilda de borboletas frugívoras funciona como um excelente modelo eco-evolutivo. Para elucidar os padrões de distribuição espacial desse grupo de borboletas no bioma Amazônico, os capítulos que seguem utilizam abordagens de biologia evolutiva e ecologia de comunidades. No capítulo I, foi investigado o papel da ancestralidade na relação entre estratificação vertical, morfologia de voo e dimorfismo sexual, de modo a explicar a ocorrência de diferentes espécies entre dossel e sub-bosque de florestas tropicais. No capítulo II, foi estudada a distribuição espacial da guilda em um mosaico vegetacional amazônico, utilizando variáveis provenientes das diversidades taxonômica, funcional e filogenética. Por fim, no capítulo III, foi investigada a distribuição da guilda utilizando preditores locais e regionais, com ênfase no papel mediador que o nicho larval pode exercer na ocorrência espacial das formas adultas.

OBJETIVOS

Capítulo I

1. Detectar qual a magnitude do sinal filogenético no atributo razão asa-tórax (morfologia de voo) em borboletas frugívoras.
2. Elucidar se adaptação radiativa tem sido mais forte do que ancestralidade entre espécies na associação entre morfologia de voo e estratificação vertical.
3. Verificar a influência do dimorfismo sexual na morfologia do voo e estratificação vertical.

Capítulo II

1. Entender como o gradiente ambiental (composição vegetal, luminosidade e alagamento) entre florestas ombrófilas e florestas de areia amazônicas determina a distribuição espacial em escala local da diversidade taxonômica, funcional e filogenética de borboletas frugívoras.

Capítulo III

1. Investigar o papel mediador da diferenciação do nicho larval de borboletas frugívoras no filtro ambiental que determina a segregação espacial em escala regional da riqueza de espécies e diversidade filogenética dos adultos.
2. Verificar a influência da amplitude do nicho larval de borboletas frugívoras nas associações de gradientes ambientais com padrões de composição de espécies e composição filogenética de borboletas adultas.

MATERIAL E MÉTODOS

I. Áreas de estudo

As coletas foram realizadas em sete localidades nas regiões setentrional, central e sudoeste da Amazônia brasileira, abrangendo um total de 33,41 km² (Fig. 1). As parcelas setentrionais estão localizadas no (1) Parque Nacional de Viruá, cuja floresta localiza-se em um ecotone e é composta de um mosaico de florestas de areia e florestas ombrófilas abertas (Laranjeiras *et al.* 2014). As florestas de areia dominam a paisagem em Viruá, perpassando fisionomias lembrando savanas com árvores baixas esparsamente distribuídas e vegetação rasteira (campinas) até florestas com árvores de aspecto raquítico, porém que podem atingir até 18 m de altura (campinaranas) (ICMBio 2014) (Fig. 2A, 2B). Locais com floresta ombrófila aberta estão em menor quantidade, primordialmente localizados em morros de solo argiloso, e abrigam alta abundância de árvores altas, palmeiras, lianas lenhosas, epífitas e algumas árvores emergentes (Damasco *et al.* 2013; ICMBio 2014) (Fig. 2C). Durante a estação chuvosa (junho a outubro), as planícies são inundadas devido à precipitação, enquanto que na estação seca (novembro a maio), a umidade no solo das florestas de areia atinge seu nível mínimo (ICMBio 2014). A temperatura e precipitação anual média registrada no parque é de 26° C e 1.900 mm respectivamente, com < 50 mm de precipitação durante a estação seca (Damasco *et al.* 2013).

Os sítios de coleta da Amazônia Central estão distribuídos em cinco localidades. As estações (2) Dimona, (3) Porto Alegre e (4) Colosso, dentro de fazendas abandonadas na década de 1980 devido ao malogro da pecuária, contém atualmente vegetação em vários estágios de regeneração e fragmentos florestais de floresta ombrófila densa (Fig. 2D) com diferentes tamanhos e níveis de isolamento (PDBFF 2018). Nós realizamos coletas em cinco fragmentos florestais, sendo um de 1 ha, um de 100 ha, e três com 10 ha de área. Além dos fragmentos, a ARIE PDBFF conta ainda com a (5) Reserva do KM41, que também possui vegetação do tipo ombrófila densa, porém a mata é contínua ao invés de fragmentada. Estas áreas estão à margem norte do Rio Amazonas. O sítio final da Amazônia Central está localizado na floresta adjacente à BR-319 (Manaus – Porto Velho) na altura do quilômetro 100, no módulo de coleta conhecido como (6) Manaquiri. A floresta é do tipo ombrófila densa (Fig. 2E) de aproximadamente 7000 – 27000 anos, formada no interflúvio dos rios Purus e Madeira (Costa *et al.* 2001), com solo variando entre Laterita

Hidromórfica, Gleyzados e Aluviais Eutróficos ou Álicos (Quesada *et al.* 2011). Essa área está situada à margem sul do Rio Amazonas. Na região sudoeste da Amazônia, as amostragens foram realizadas no Parque Estadual Chandless, no Acre. A vegetação do parque compreende uma floresta ombrófila aberta, com manchas de mata dominada por bambus e palmeiras (PPBio 2018) (Fig. 2F). As seis últimas áreas estão localizadas no hemisfério sul e, por isso, a estação chuvosa se estende de Novembro a Maio.



Figura 1. Mapa de parte da região amazônica, evidenciando os sítios de coleta (números) de borboletas frugívoras. Territórios em branco são estados brasileiros; em cinza, outros países sul-americanos.

Em Viruá (Fig. 3), Manaquiri e Chandless, existem trilhas de amostragem em forma de grade contendo parcelas permanentes que permitem a coleta e comparação de dados de diferentes grupos biológicos e variáveis ambientais a curto, médio e longo prazo (método RAPELD, Magnusson *et al.* 2005, Costa & Magnusson 2010). Tais parcelas permanentes tem 250 m de extensão e seguem a curva de nível do solo, para minimizar a variação edáfica dentro de cada parcela. Esse método é aplicado nos estudos desenvolvidos dentro do Programa de Pesquisas em Biodiversidade (PPBio). As áreas do PBDFF não seguem esse método, logo as parcelas não seguiram a curva de nível do terreno, porém procuramos adaptar a amostragem para manter a mesma distância entre amostras que nas demais áreas.

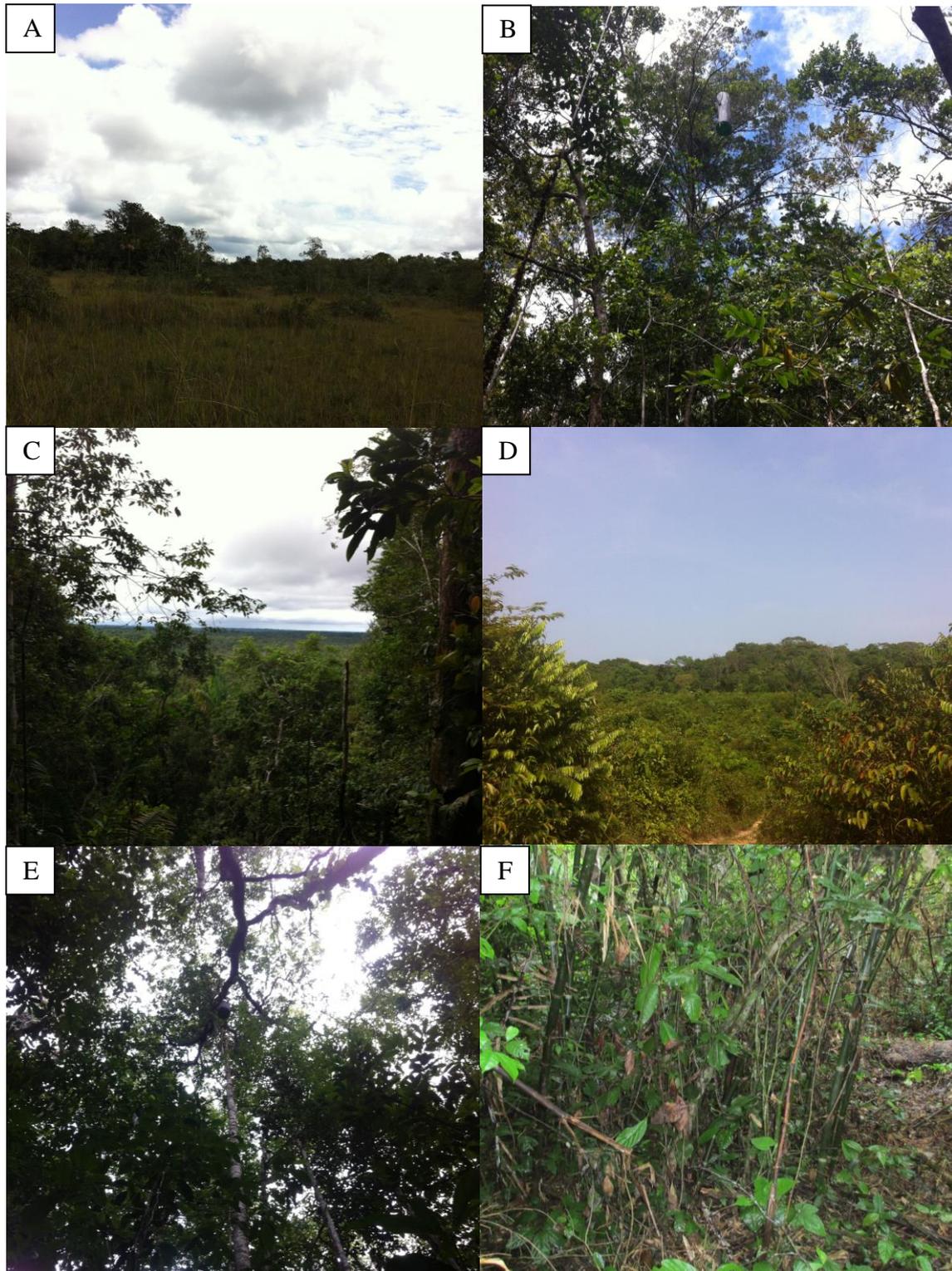


Figura 2. Paisagens estudadas. A. Campina; B. Campinarana; C. Dossel de floresta ombrófila aberta vista de um morro em Viruá, Roraima; D. Fragmento florestal de floresta ombrófila densa (ao fundo) cercado por capoeira na fazenda Porto Alegre, Amazonas; E. Floresta ombrófila densa no módulo Manaquiri, km 100 da BR-319, Amazonas; F. Trecho de floresta ombrófila aberta com predominância de bambus no Chandless, Acre. Imagens: M.B. Graça.

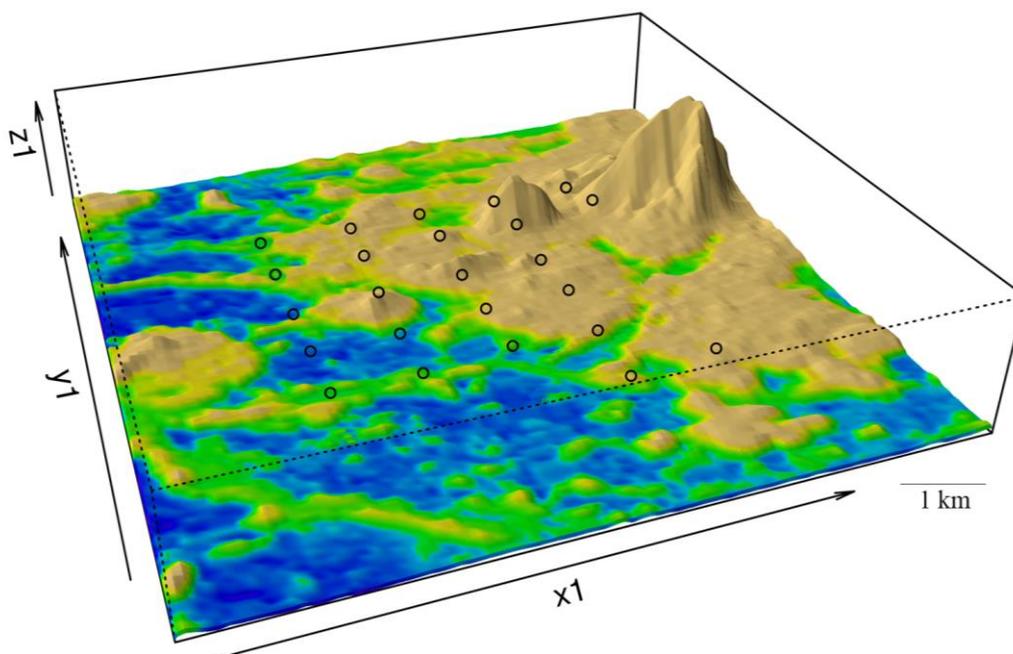


Figura 3. Exemplo da distribuição das parcelas (círculos pretos) de acordo com o método RAPELD em Viruá. As parcelas ficam a 1 km de distância entre si. Destacadas as 24 parcelas onde coletamos borboletas frugívoras. Imagem: C.S. Dambros.

II. Delineamento amostral

As borboletas foram coletadas no período de Maio de 2015 a Outubro de 2016, sendo que cada sítio foi visitado uma vez. Os pontos de amostragem estão localizados em parcelas de 250 m de extensão distantes entre si pelo menos 900 m e seguem a curva de nível do solo (exceto os pontos da ARIE PDBFF, que não seguem). Em cada parcela, instalamos seis armadilhas tipo Van Someren-Rydon, contendo uma mistura de caldo de cana e bananas pacovan bastante maduras (*Musa x paradisiaca*) fermentada por 48 h *a priori*, e mantendo a distância de 50 m entre si. As armadilhas foram penduradas em galhos de árvores disponíveis, sendo três no sub-bosque (1,5 – 2 m de altura) e três no dossel (≥ 15 m) (Fig. 4A, 4B). Pela falta de cobertura vegetal nas campinas de Viruá, foram instaladas seis armadilhas em árvores disponíveis, mas que não possuíam mais de 2 m de altura (Fig. 4C). As armadilhas eram visitadas a cada 24 h para coleta dos indivíduos capturados e reposição da isca, o que ocorreu

durante cinco dias seguidos.

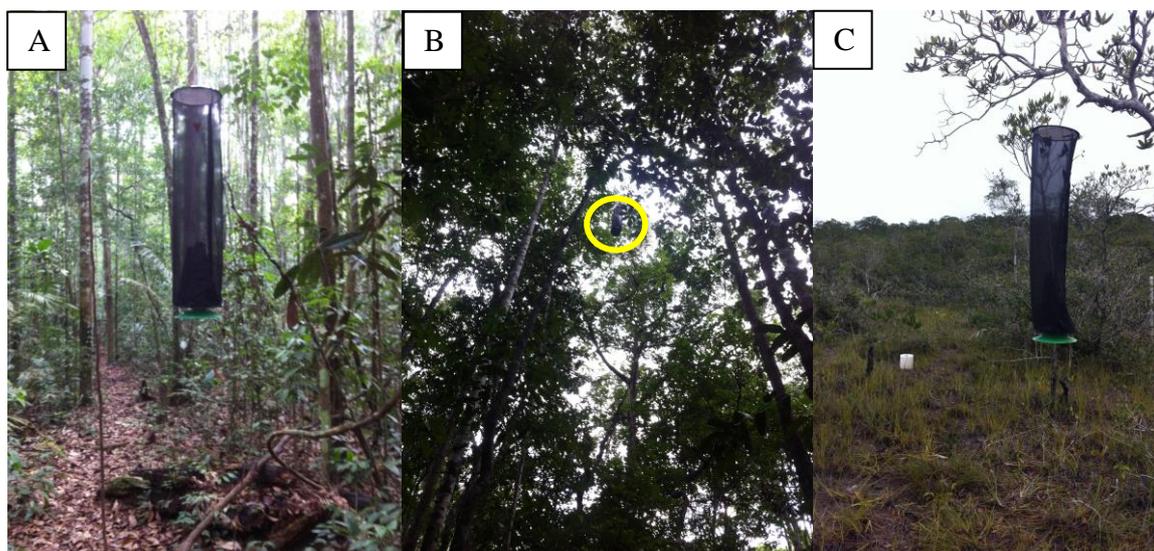


Figura 4. Armadilhas Van Someren-Rydon instaladas no sub-bosque (A), dossel (B) e campina (C). Imagens: M.B. Graça.

A maioria dos indivíduos foi trazido de campo (uma parte marcada e solta) e será depositada nas coleções de invertebrados do Instituto Nacional de Pesquisas da Amazônia e da Universidade do Estado do Pará. Outras informações referente ao tratamento dos dados, variáveis utilizadas e análise estatística particulares a cada capítulo estarão na respectiva sessão Material e Métodos.

Coevolution between flight morphology, vertical stratification and sexual dimorphism: what can we learn from tropical butterflies?

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Coevolution between flight morphology, vertical stratification and sexual dimorphism: what can we learn from tropical butterflies?

Abstract

Occurrence patterns are partly shaped by the affinity of species with habitat conditions. For winged organisms, flight-related attributes are vital for ecological performance. However, due to the different reproductive roles of each sex, we expect divergence in flight energy budget, and consequently different selection responses between sexes. We used tropical frugivorous butterflies as models to investigate coevolution between flight morphology, sex dimorphism and vertical stratification. We studied 94 species of Amazonian fruit-feeding butterflies sampled in seven sites across 3341 ha. We used wing-thorax ratio as a proxy for flight capacity and hierarchical Bayesian modeling to estimate stratum preference. We detected a strong phylogenetic signal in wing-thorax ratio in both sexes. Stout fast-flying species preferred the canopy, while more slender slow-flying species preferred the understorey. However, this relationship was stronger in females than in males, suggesting that female phenotype associates more intimately with habitat conditions. Within species, males were stouter than females and sexual dimorphism was sharper in understorey species. Because trait-habitat relationships were independent from phylogeny, the matching between flight morphology and stratum preference is more likely to reflect adaptive radiation than shared ancestry. This study sheds light on the impact of flight and sexual dimorphism on the evolution and ecological adaptation of flying organisms.

Key Words: Amazon rainforest; Fruit-feeding butterflies; Habitat preference; Phylogenetic signal; Physiological trade-off; Wing-thorax ratio

Introduction

Species traits and occurrence patterns result from a series of ecological and evolutionary processes (Ackerly, 2003; Thomas *et al.*, 2016). Among them, adaptive radiation and niche conservatism are acknowledged as the opposite ends of a spectrum (Ackerly, 2009). Whilst adaptive radiation suggests that successful diversification is due to changes in species attributes in response to ecological opportunities promoted by available niche space (e.g. colonization of new, vacant

areas), niche conservatism describes the tendency of closely related species to retain similar characteristics, thus minimizing evolutionary change (Harvey & Pagel, 1991; Ackerly, 2003, 2009). In part, niche conservatism reflects phylogenetic signal, i.e., the weight of phylogenetic relatedness on trait evolution. Although phylogenetic signal alone does not directly denote niche conservatism, it is a necessary evidence for its existence (Losos, 2008). For that reason, the estimation of the phylogenetic constraint in traits and in trait-habitat relationships helps understand the mechanisms of underlying evolutionary selection (Ackerly, 2009) and their impact on current ecological patterns.

Besides biotic interactions and stochastic processes, species are locally assembled by environmental pressures that select for traits fit to habitat conditions (Ricklefs, 2004; Cavender-Bares *et al.*, 2009). Thus, species tend to occur in habitats compatible with their functional traits (e.g. Arnan *et al.*, 2013; Graça *et al.*, 2015). For flying organisms, flight-related traits should be important in determining fitness, as the ability to take flight improved foraging, mate search and avoidance of unfavorable conditions (Norberg, 1990; Grimaldi & Engel, 2005). For instance, bats, birds and butterflies that forage near flat and smooth surfaces (forest floor, water surface) have modified body aerodynamics to glide in ground effect and enhance flight performance at lower costs (Rayner, 1991; Cespedes *et al.*, 2014; Kim *et al.*, 2014). In particular, the transition from understorey to canopy habitats generates gradients of sunlight availability, temperature, humidity, and habitat complexity (Richards, 1996; Ricklefs, 2004), and species are expected to be better adapted to a particular stratum depending on the performance of their attributes. This results in the common pattern of stratification of species richness, composition and traits from lower to higher strata in tropical forests (Basset *et al.*, 2001; Walther, 2002; Basset *et al.*, 2015; Giovanni *et al.*, 2015; Marques *et al.*, 2015). Given the essential role of flight for winged organisms, we may expect vertical stratification to reflect adaptation of flight-related traits. For *Morpho* butterflies, for example, wing shape changed at the evolutionary switch from understorey to canopy, suggesting that stratum preference is intimately related to flight behaviour, energy budget and mate location strategy (DeVries *et al.*, 2010). However, thoracic measurements may provide further insights on this matter, as thorax kinematics also plays a central role in flight behaviour (Dudley, 2000). Further, the difference in wing shape has only been observed in males (DeVries *et al.*,

2010), which suggests that sexual dimorphism may modulate such stratification patterns.

Males and females from the same species often differ in traits related to morphology, physiology and behaviour, and such disparities are thought to arise from the asynchrony of resource allocation (Lammers *et al.*, 2001; Isaac, 2005), especially regarding reproduction (Badyaev, 2002). Commonly, males will search and compete for females, while females will choose from competing males and generate the offspring (Petrie *et al.*, 1991; Miller, 2014). Such general background leads to disproportional investments in traits between sexes, with females investing relatively more in the reproductive apparatus and the brood in most cases (Thornhill & Alcock, 1983; Miller, 2014). There is a reported negative correlation between muscle and ovarian mass in flying dimorphic organisms, so that flightless females tend to invest more in ovary mass relative to muscle mass when compared to macropterous forms (Roff, 1986; Mole & Zera, 1993; Zera & Denno, 1997). Therefore, if flight and reproduction indeed compete over the resource share (e.g. Rankin & Burchsted, 1992; Wheeler, 1995), then sexual dimorphism per se should reflect this trade-off (Jervis *et al.*, 2005).

For this study, we elected tropical fruit-feeding butterflies as models to analyze the linkages between flight morphology, stratum preference and sex dimorphism. Frugivorous butterflies are useful because they display vertical stratification in tropical forests, which is relatively easy to assess using canopy and understorey bait traps (DeVries, 1988; DeVries & Walla, 2001; Fermon *et al.*, 2005). Although many studies have offered hypotheses about the causes and implications of this vertical pattern (e.g. Beccaloni, 1997; Schulze *et al.*, 2001), the evolutionary relationship between stratum preference and butterfly functional traits (e.g. DeVries *et al.*, 2010), as well as the mechanisms behind the canopy/understorey species segregation have received less attention (Fordyce & DeVries, 2016). Additionally, several morphological traits of butterflies are known to reflect flight performance, e.g. relative thorax mass, forewing area, wing loading, wing centroid position (Chai, 1990; Chai & Srygley, 1990; Dudley, 2000; Berwaerts *et al.*, 2002; DeVries *et al.*, 2010, Cespedes *et al.*, 2014). In particular, the allometry ratio between wing length and thorax volume (wing-thorax ratio) expresses flight power and speed (Chai, 1990; Hall & Willmott, 2000). While lower ratios indicate species with high-speed flights and relatively high wing beat frequencies, species with higher values are slow flying and

beat their wings at lower frequencies (Hall & Willmott, 2000). Finally, both male and female fruit-feeding species are able to fly, so that we can test for the effect of sexual dimorphism on relative investment in flight.

In this context, we formulated the four following questions: (i) What is the magnitude of the phylogenetic signal in the evolution of flight morphology (wing-thorax ratio)? (ii) Has adaptive radiation been stronger than phylogenetic relatedness in driving the matching between flight morphology and vertical stratification? If so, we expected this association to hold independently of phylogenetic signal in wing-thorax ratio and in vertical stratification (see Fordyce & DeVries, 2016). (iii) Is there sex dimorphism in flight morphology and in vertical stratification? (iv) Is sex dimorphism in flight morphology related to vertical stratification? These questions were addressed using an original, large dataset on morphological and ecological traits of frugivorous nymphalids obtained with standardized sampling at seven locations across the Amazon basin.

Material and Methods

Study sites and sampling

The core information on study sites and sampling is disclosed in the general Material and Methods section of this thesis (page 5). For this chapter, we used the data collected in 150 understory and 150 canopy traps from Viruá National Park, BDFFP areas, Manaquiri module and Chandless State Park. In particular, we excluded traps located in campinas (non-forested white-sand habitats), but included data from traps activated outside the PPBio grid plots.

Morphological traits and stratum preference

We measured 1092 individuals when fresh, i.e., prior to dehydration for mounting and within the first twelve hours of sampling. Also, the estimation of all morphological traits and habitat preference was done for each sex separately. We obtained three morphological measurements: forewing length, thorax length and thorax width. Using a millimeter ruler, we estimated forewing length as the linear distance between the base of the discal and the interception of vein R5 with the wing margin (Céspedes *et al.*, 2014) on the ventral surface. To calculate thoracic volume, we firstly measured thorax length, as the distance between the vertex and the thoracic-abdominal junction

in lateral view, and thorax width at its maximum distance in ventral view. Following Hill *et al.* (2001), thorax volume was given by:

$$tv = tl \times tw^2$$

where *tl* was thorax length and *tw* was thorax width. Further, we calculated wing-thorax ratio by dividing the squared forewing length by the thoracic volume to estimate body allometry. Lower values indicate stouter bodies and faster flights, while higher values indicate slenderer bodies and slower flights (Hall & Willmott, 2000).

To estimate the preference of adult butterflies for a particular stratum, we ran a hierarchical Bayesian model with 5000 Markov chain Monte Carlo permutations and a 1000 generations burn-in, using butterfly occurrence in either canopy or understorey as input (Fordyce & DeVries, 2016). Values close to 1 indicate high canopy fidelity, while those close to 0 indicate preference for the understorey. The analysis was conducted in R (R Development Core Team, 2017) using package *bayespref* 1.0 (Fordyce *et al.*, 2011) (data is available on doi: 10.5061/dryad.db827).

Phylogenetic signal in wing-thorax ratio

The phylogenetic relationships among sampled species (Fig. 5) were reconstructed based on the nymphalid generic topology proposed by Wahlberg *et al.* (2009), with further resolution whenever available, e.g., Ortiz-Acevedo & Willmott (2013) and Penz *et al.* (2013). Genera without a formal proposal for species relatedness (e.g., *Eunica*) were treated as polytomies. Because branch length data were not available for all studied lineages, they were standardized to 1 in all cases (García-Barros, 2015). We extracted the mean value of wing-thorax ratio for each species and tested for phylogenetic signal in both sexes using λ (Pagel, 1999). The analyses were performed in the statistical environment R (R Development Core Team, 2017).

Correlation between flight morphology and stratum preference

Before performing the analyses, wing-thorax ratio values were \log_{10} transformed. We assessed the association between WTR and stratum preference using Phylogenetic Generalized Least Squares models (PGLS; Grafen, 1989) in order to account for any phylogenetic autocorrelation in the residuals of this relationship. Our analysis assumed the Ornstein-Uhlenbeck model of trait evolution (Martins & Hansen, 1997), which posits that continuous characters tend to evolve around a certain value rather than randomly and, thus, is more realistic than the popular Brownian motion model

(Paradis, 2012). PGLS analyses were conducted separately for males and females. We also analyzed whether absolute thorax volume (regardless of wing size) correlated with stratum preference in parallel PGLS analyses.

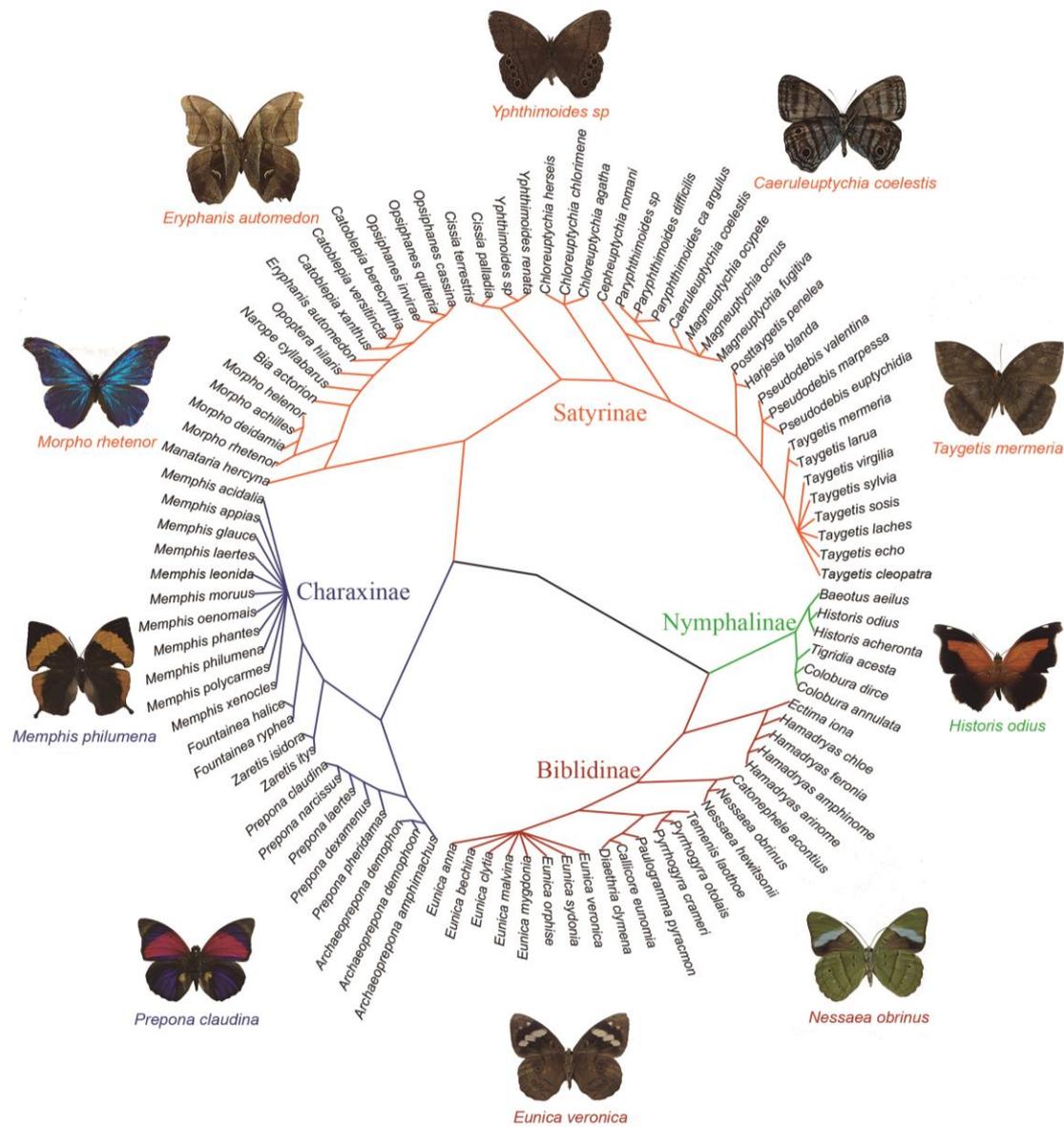


Figure 5. Phylogenetic tree reconstructed considering all 94 studied species.

Sexual dimorphism in morphology and stratum preference

We investigated whether males and females from the same species differed regarding wing-thorax ratio and stratum preference. We firstly selected the 40 species for which we had sampled both sexes, calculated the wing-thorax ratio of each individual butterfly, and then extracted the mean value per species per sex. For each species, we

then calculated the difference between male and female mean values. This difference thus represented sexual dimorphism in wing-thorax allometry.

For the same 40 species, we accessed sexual dimorphism in stratum preference by estimating the difference in the mean canopy fidelity of males and females. Finally, we used the average value of canopy fidelity between males and females to score the species overall stratum preference.

To determine whether sexual dimorphism was greater than expected by chance (i.e. mean difference between sexes = 0) in both wing-thorax ratio and stratum preference, we performed PGLS analysis. We further tested whether sexual dimorphism correlated with stratum preference by running PGLS and assuming the Ornstein-Uhlenbeck model of trait evolution, as before. Because we were interested in quantifying dimorphism per se (and not whether males were stouter or slenderer than females), we used absolute differences in wing-thorax ratio.

Results

Overall, we studied 94 species of Amazonian fruit-feeding butterflies, from which we had 73 males and 61 females (Table 1). For males, wing-thorax ratio ranged from 1.31 in *Prepona narcissus* to 21.76 in *Chloreuptychia agatha*, whereas for females, it ranged from 2.63 in *Historis odius* to 24.40 in *Chloreuptychia herseis*.

Table 1. List of the 94 species of fruit-feeding nymphalids studied, with their respective sex, wing-thorax ratio (WTR), thorax volume (TV) and stratum preference (CF = canopy fidelity, 0 = understorey only, 1 = canopy only).

| Species | Sex | WTR | TV | CF |
|----------------------------------------------|-----|------|--------|------|
| Biblidinae | | | | |
| <i>Callicore eunomia</i> (Hewitson, 1853) | M | 4.73 | 127.50 | 0.91 |
| <i>Catonephele acontius</i> (Linnaeus, 1771) | M | 3.22 | 262.48 | 0.09 |
| | F | 6.30 | 203.28 | 0.05 |
| <i>Diaethria clymena</i> (Cramer, 1775) | M | 7.55 | 64.09 | 0.90 |
| <i>Ectima iona</i> E. Doubleday, [1848] | M | 9.62 | 37.50 | 0.90 |
| | F | 9.55 | 60.29 | 0.80 |
| <i>Eunica anna</i> (Cramer, 1780) | M | 5.00 | 168.02 | 0.85 |
| <i>Eunica bechina</i> (Hewitson, 1852) | M | 3.76 | 223.27 | 0.84 |
| | F | 6.05 | 129.56 | 0.80 |
| <i>Eunica clytia</i> (Hewitson, 1852) | M | 6.21 | 64.40 | 0.91 |
| <i>Eunica malvina</i> H. Bates, 1864 | F | 8.45 | 113.63 | 0.80 |

| | | | | |
|---------------------------------------------------------|---|-------|---------|------|
| <i>Eunica mygdonia</i> (Godart, [1824]) | M | 4.61 | 193.52 | 0.97 |
| | F | 5.27 | 164.43 | 0.93 |
| <i>Eunica orphise</i> (Cramer, 1775) | F | 6.07 | 102.91 | 0.87 |
| <i>Eunica sydonia</i> (Godart, [1824]) | M | 7.21 | 169.69 | 0.84 |
| <i>Eunica veronica</i> H. Bates, 1864 | F | 6.44 | 130.45 | 0.80 |
| <i>Hamadryas amphinome</i> (Linnaeus, 1767) | M | 3.55 | 364.89 | 0.97 |
| | F | 3.99 | 352.07 | 0.88 |
| <i>Hamadryas arinome</i> (Lucas, 1853) | M | 3.19 | 416.63 | 0.06 |
| | F | 4.32 | 325.21 | 0.50 |
| <i>Hamadryas chloe</i> (Stoll, 1787) | M | 7.08 | 95.40 | 0.37 |
| <i>Hamadryas feronia</i> (Linnaeus, 1758) | M | 4.15 | 303.41 | 0.91 |
| | F | 5.08 | 286.03 | 0.85 |
| <i>Nessaea hewitsonii</i> (C. Felder & R. Felder, 1859) | F | 6.87 | 144.27 | 0.12 |
| <i>Nessaea obrinus</i> (Linnaeus, 1758) | M | 4.32 | 270.73 | 0.90 |
| | F | 6.13 | 227.20 | 0.04 |
| <i>Paulogramma pyracmon</i> (Godart, [1824]) | M | 3.28 | 134.38 | 0.91 |
| <i>Pyrrhogyra crameri</i> Aurivillius, 1882 | M | 11.75 | 44.99 | 0.06 |
| <i>Pyrrhogyra otolais</i> H. Bates, 1864 | M | 9.83 | 58.58 | 0.06 |
| <i>Temenis laothoe</i> (Cramer, 1777) | M | 4.39 | 182.49 | 0.96 |
| | F | 6.51 | 111.91 | 0.93 |
| Charaxinae | | | | |
| <i>Archaeoprepona amphemachus</i> (Fabricius, 1775) | M | 2.54 | 906.45 | 0.12 |
| <i>Archaeoprepona demophon</i> (Linnaeus, 1758) | M | 2.53 | 967.73 | 0.08 |
| | F | 3.36 | 894.79 | 0.12 |
| <i>Archaeoprepona demophoon</i> (Hübner, [1814]) | M | 1.79 | 1408.76 | 0.68 |
| | F | 3.10 | 1009.15 | 0.80 |
| <i>Fountainea halice</i> (Godart, [1824]) | F | 4.62 | 175.73 | 0.93 |
| <i>Fountainea ryphea</i> (Cramer, 1775) | M | 3.17 | 235.02 | 0.93 |
| | F | 5.17 | 185.54 | 0.88 |
| <i>Memphis acidalia</i> (Hübner, [1819]) | M | 2.93 | 293.44 | 0.93 |
| | F | 4.25 | 220.71 | 0.91 |
| <i>Memphis appias</i> (Hübner, [1825]) | F | 4.63 | 181.41 | 0.87 |
| <i>Memphis glauce</i> (C. Felder & R. Felder, 1862) | M | 3.67 | 228.80 | 0.95 |
| <i>Memphis laertes</i> (Cramer, 1775) | F | 5.29 | 214.14 | 0.91 |
| <i>Memphis leonida</i> (Stoll, 1782) | M | 4.71 | 132.47 | 0.95 |
| | F | 4.66 | 193.06 | 0.87 |
| <i>Memphis moruus</i> (Fabricius, 1775) | M | 2.83 | 296.38 | 0.91 |
| | F | 3.12 | 302.68 | 0.93 |
| <i>Memphis oenomais</i> (Boisduval, 1870) | M | 3.46 | 195.05 | 0.91 |
| <i>Memphis phantes</i> (Hopffer, 1874) | F | 3.31 | 435.92 | 0.87 |
| <i>Memphis philumena</i> (E. Doubleday, [1849]) | F | 4.41 | 269.51 | 0.93 |
| <i>Memphis polycarmes</i> (Fabricius, 1775) | M | 2.58 | 296.41 | 0.93 |
| | F | 4.75 | 189.19 | 0.80 |

| | | | | |
|----------------------------------------------------------------|---|-------|---------|------|
| <i>Memphis xenocles</i> (Westwood, 1850) | M | 4.19 | 161.32 | 0.90 |
| <i>Mesoprepona pheridamas</i> (Cramer, 1777) | M | 3.72 | 520.14 | 0.12 |
| <i>Prepona claudina</i> (Godart, [1824]) | M | 1.69 | 896.24 | 0.97 |
| | F | 2.64 | 731.93 | 0.88 |
| <i>Prepona dexamenus</i> Hopffer, 1874 | M | 2.07 | 808.43 | 0.91 |
| | F | 2.97 | 758.39 | 0.87 |
| <i>Prepona laertes</i> (Hübner, [1811]) | M | 2.16 | 960.08 | 0.95 |
| | F | 2.92 | 889.28 | 0.91 |
| <i>Prepona narcissus</i> (Staudinger, [1885]) | M | 1.31 | 1174.23 | 0.65 |
| <i>Zaretis isidora</i> (Cramer, 1779) | M | 3.67 | 270.26 | 0.95 |
| | F | 5.33 | 216.56 | 0.87 |
| <i>Zaretis itys</i> (Cramer, 1777) | M | 3.33 | 252.17 | 0.79 |
| Nymphalinae | | | | |
| <i>Baeotus aeilus</i> (Stoll, 1870) | F | 3.89 | 489.37 | 0.95 |
| <i>Colobura annulata</i> Willmott, Constantino & J. Hall, 2001 | F | 4.69 | 307.28 | 0.13 |
| <i>Colobura dirce</i> (Linnaeus, 1758) | M | 4.88 | 187.33 | 0.35 |
| | F | 4.94 | 207.23 | 0.20 |
| <i>Historis acheronta</i> (Fabricius, 1775) | M | 3.84 | 337.47 | 0.90 |
| | F | 4.34 | 354.88 | 0.85 |
| <i>Historis odius</i> (Fabricius, 1775) | M | 2.18 | 1193.03 | 0.86 |
| | F | 2.63 | 1364.09 | 0.80 |
| <i>Tigridia acesta</i> (Linnaeus, 1758) | M | 9.53 | 62.07 | 0.02 |
| | F | 11.17 | 46.75 | 0.27 |
| Satyrinae | | | | |
| <i>Bia actorion</i> (Linnaeus, 1763) | M | 9.72 | 59.22 | 0.12 |
| | F | 13.85 | 52.61 | 0.12 |
| <i>Caeruleptychia coelestis</i> (A. Butler, 1867) | F | 14.39 | 33.62 | 0.26 |
| <i>Caeruleptychia romani</i> (Aurivillius, 1929) | F | 13.42 | 24.13 | 0.18 |
| <i>Catoblepia berecynthia</i> (Cramer, 1777) | M | 5.22 | 405.12 | 0.21 |
| | F | 7.78 | 308.29 | 0.07 |
| <i>Catoblepia versitincta</i> Stichel, 1901 | M | 6.85 | 257.21 | 0.07 |
| <i>Catoblepia xanthus</i> (Linnaeus, 1758) | M | 8.94 | 266.41 | 0.02 |
| | F | 7.60 | 288.51 | 0.18 |
| <i>Chloreuptychia agatha</i> (A. Butler, 1867) | M | 21.76 | 24.31 | 0.12 |
| <i>Chloreuptychia chlorimene</i> (Hübner, [1819]) | F | 23.51 | 14.29 | 0.08 |
| <i>Chloreuptychia herseis</i> (Godart, [1824]) | M | 19.80 | 16.36 | 0.12 |
| | F | 24.40 | 15.31 | 0.09 |
| <i>Cissia palladia</i> (A. Butler, 1867) | M | 14.33 | 17.86 | 0.84 |
| <i>Cissia terrestris</i> (A. Butler, 1867) | M | 16.28 | 18.44 | 0.50 |
| | F | 19.36 | 14.25 | 0.16 |

| | | | | |
|-------------------------------------------------------|---|-------|--------|------|
| <i>Eryphanis automedon</i> (Cramer, 1775) | F | 8.80 | 556.64 | 0.20 |
| <i>Harjesia blanda</i> (Möschler, 1877) | M | 9.35 | 83.78 | 0.12 |
| <i>Magneuptychia fugitiva</i> Lamas, [1997] | F | 16.31 | 15.69 | 0.20 |
| <i>Magneuptychia ocnus</i> (A. Butler, 1867) | M | 13.93 | 34.74 | 0.85 |
| <i>Magneuptychia ocypete</i> (Fabricius, 1776) | M | 12.39 | 37.85 | 0.52 |
| | F | 11.48 | 39.60 | 0.36 |
| <i>Manataria hercyna</i> (Hübner, [1821]) | F | 7.67 | 275.58 | 0.93 |
| <i>Morpho achilles</i> (Linnaeus, 1758) | M | 10.01 | 434.81 | 0.05 |
| <i>Morpho deidamia</i> (Hübner, [1819]) | F | 7.12 | 768.50 | 0.12 |
| <i>Morpho helenor</i> (Cramer, 1776) | F | 8.17 | 625.18 | 0.06 |
| <i>Morpho rhetenor</i> (Cramer, 1775) | M | 13.49 | 416.82 | 0.79 |
| | F | 13.60 | 349.99 | 0.80 |
| <i>Narope cyllabarus</i> Westwood, 1851 | M | 2.70 | 332.40 | 0.90 |
| <i>Opoptera hilaris</i> Stichel, 1901 | M | 5.08 | 254.63 | 0.91 |
| <i>Opsiphanes cassina</i> C. Felder & R. Felder, 1862 | M | 2.05 | 739.15 | 0.91 |
| <i>Opsiphanes invirae</i> (Hübner, [1808]) | M | 2.40 | 563.78 | 0.66 |
| | F | 3.96 | 421.62 | 0.52 |
| <i>Opsiphanes quiteria</i> (Stoll, 1780) | M | 2.39 | 808.30 | 0.31 |
| | F | 3.47 | 747.56 | 0.50 |
| <i>Paryphthimoides ca argulus</i> | M | 12.96 | 30.85 | 0.06 |
| | F | 14.34 | 25.16 | 0.21 |
| <i>Paryphthimoides difficilis</i> Forster, 1964 | M | 10.22 | 49.49 | 0.95 |
| <i>Paryphthimoides</i> sp. | M | 10.36 | 38.61 | 0.14 |
| | F | 12.38 | 29.14 | 0.60 |
| <i>Posttaygetis penelea</i> (Cramer, 1777) | F | 12.53 | 58.14 | 0.12 |
| <i>Pseudodebis euptychidia</i> (A. Butler, 1868) | M | 8.34 | 120.78 | 0.03 |
| | F | 11.16 | 89.41 | 0.20 |
| <i>Pseudodebis marpessa</i> (Hewitson, 1862) | M | 11.59 | 77.99 | 0.65 |
| <i>Pseudodebis valentina</i> (Cramer, 1779) | M | 9.50 | 107.76 | 0.08 |
| | F | 11.49 | 94.74 | 0.12 |
| <i>Taygetis cleopatra</i> C. Felder & R. Felder, 1867 | M | 7.99 | 143.77 | 0.03 |
| | F | 9.91 | 130.75 | 0.04 |
| <i>Taygetis echo</i> (Cramer, 1775) | M | 9.40 | 118.09 | 0.08 |
| <i>Taygetis laches</i> Fabricius, 1793 | F | 9.77 | 127.96 | 0.09 |
| <i>Taygetis larua</i> C. Felder & R. Felder, 1867 | M | 7.39 | 273.90 | 0.12 |
| <i>Taygetis mermeria</i> (Cramer, 1776) | M | 7.34 | 294.41 | 0.06 |
| | F | 6.08 | 394.88 | 0.12 |
| <i>Taygetis sosis</i> Hopffer, 1874 | M | 8.46 | 143.05 | 0.05 |
| <i>Taygetis sylvia</i> H. Bates, 1866 | M | 8.81 | 119.04 | 0.09 |
| <i>Taygetis virgilia</i> (Cramer, 1776) | M | 7.56 | 190.98 | 0.06 |
| | F | 8.21 | 197.96 | 0.18 |
| <i>Yphthimoides renata</i> (Stoll, 1780) | M | 14.72 | 51.96 | 0.36 |
| <i>Yphthimoides</i> sp. | M | 9.89 | 48.91 | 0.21 |

We detected a strong evidence for phylogenetic signal in the wing-thorax ratio of both males ($\lambda = 0.99$, $P < 0.001$, Fig. 6) and females ($\lambda = 0.99$, $P < 0.001$, Fig. 7), thus wing-thorax ratio covariance among species is stronger than expected under no phylogenetic autocorrelation.

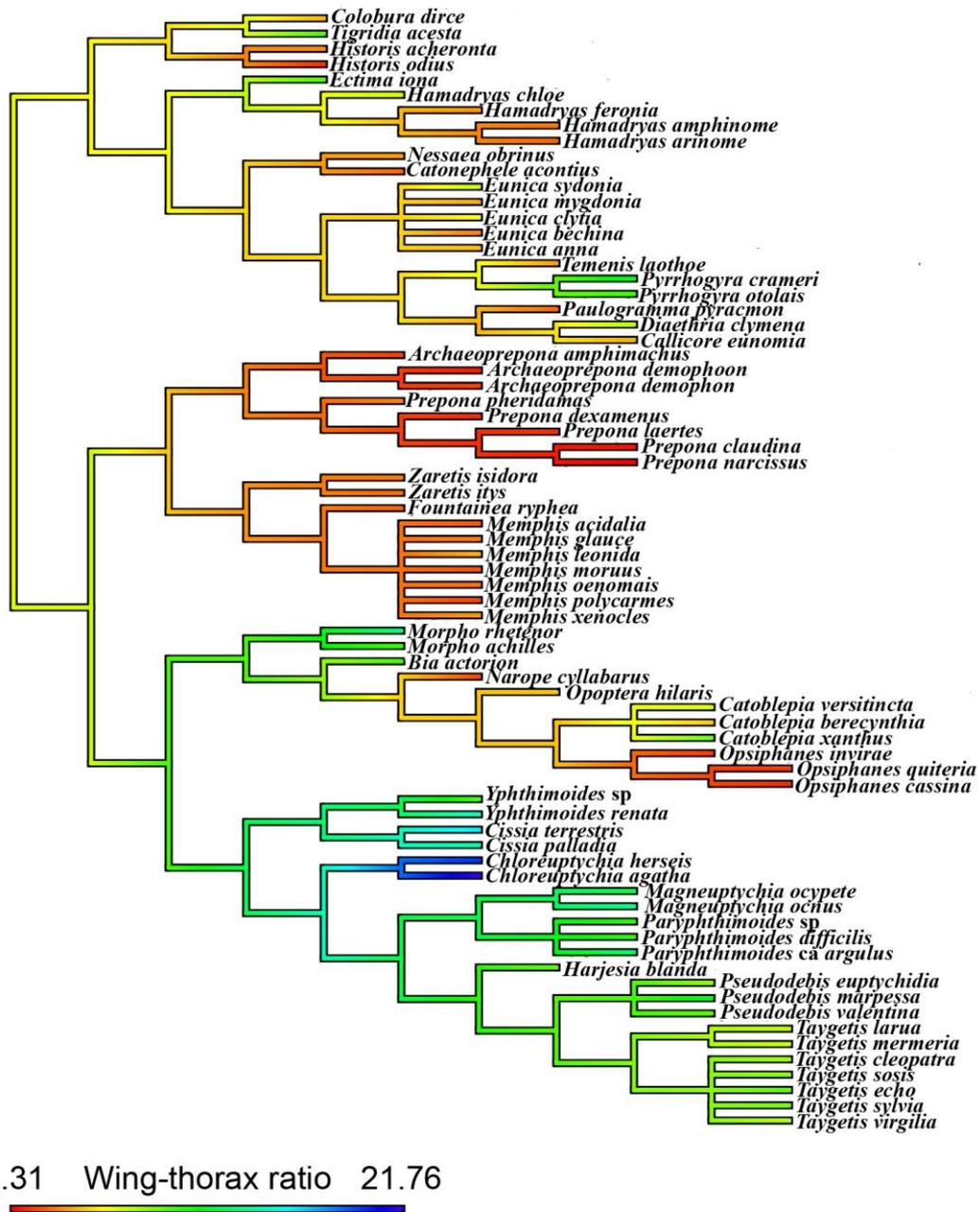


Figure 6. Diversification of wing-thorax ratio of males among butterfly lineages showing strong phylogenetic signal. Similar color shades represent similar values for WTR.

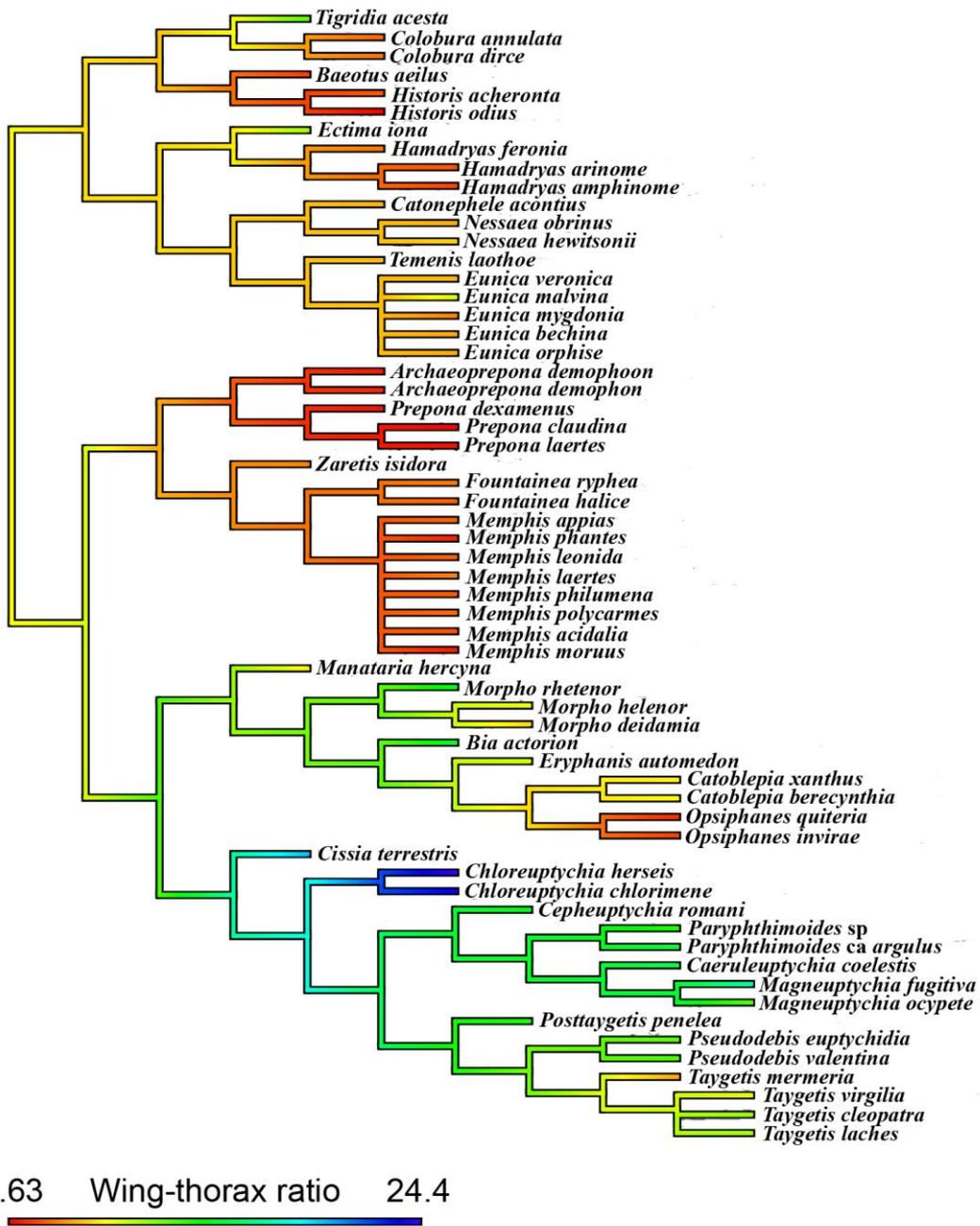


Figure 7. Diversification of wing-thorax ratio of females among butterfly lineages showing strong phylogenetic signal. Similar color shades represent similar values for WTR.

Our PGLS models retrieved negative relationships between butterfly wing-thorax ratio and canopy fidelity (Fig. 8). For both males ($t_{2, 71} = -2.740$, $R^2 = 0.20$, $P = 0.007$) and females ($t_{2, 59} = -2.138$, $R^2 = 0.35$, $P = 0.036$), stouter species tended to associate with the canopy and became more slender towards the understorey, although this relationship was stronger in females (as judged from R^2). Most species indeed showed a preference for either canopy (canopy fidelity > 0.8) or understorey (< 0.2),

while a minority showed transitional values, not exhibiting a clear preference (Fig. 7). The parallel PGLS test revealed that absolute thorax volume (Fig. 9, males: $t_{2, 71} = 1.374$, $P = 0.17$; females: $t_{2, 59} = 1.592$, $P = 0.11$) did not correlate with canopy fidelity.

Regarding between-sex differences, we found that females were significantly more slender than males of the same species ($t_{1, 39} = 6.820$, $\mu = 1.33$, $P < 0.001$), but did not differ from conspecific males in stratum preference ($t_{1, 39} = -0.414$, $\mu = -0.01$, $P = 0.681$) (Fig. 10). Additionally, sexual dimorphism in wing-thorax ratio decreased as canopy fidelity increased (Fig. 11, $t_{2, 38} = -3.054$, $R^2 = 0.21$, $P = 0.004$), thus indicating that in canopy species, males and females had more similar flight morphology than in those associated with the understorey.

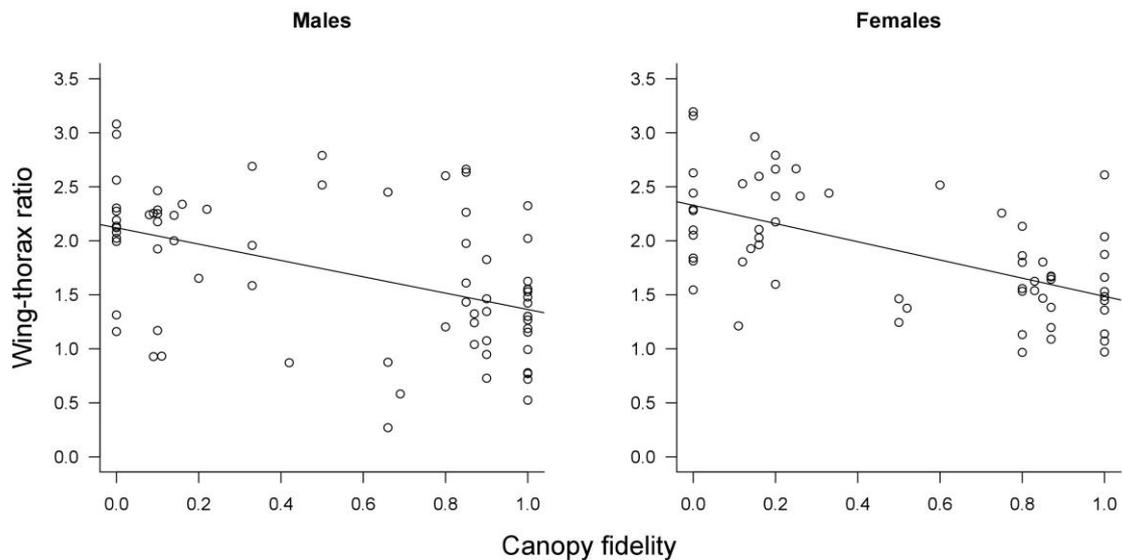


Figure 8. PGLS models for the relationship between canopy fidelity (0 = understorey only; 1 = canopy only) and wing-thorax ratio (log-transformed). Each dot represents a species (males, $n = 73$; females, $n = 61$).

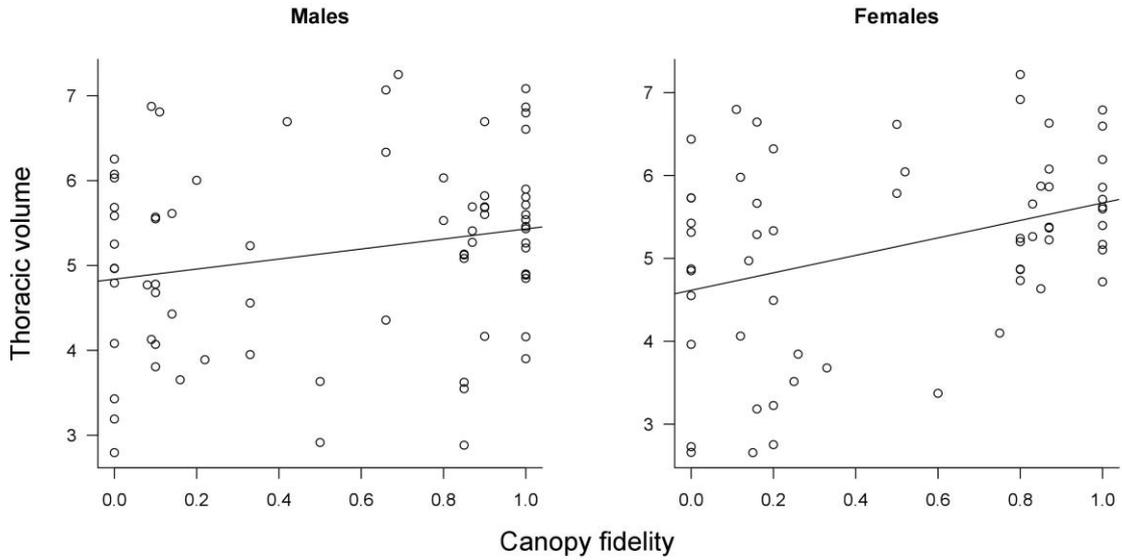


Figure 9. PGLS models for the relationship between canopy fidelity (0 = understorey only; 1 = canopy only) and absolute thorax mass (log-transformed). Each dot represents a species (males, n = 73; females, n = 61).

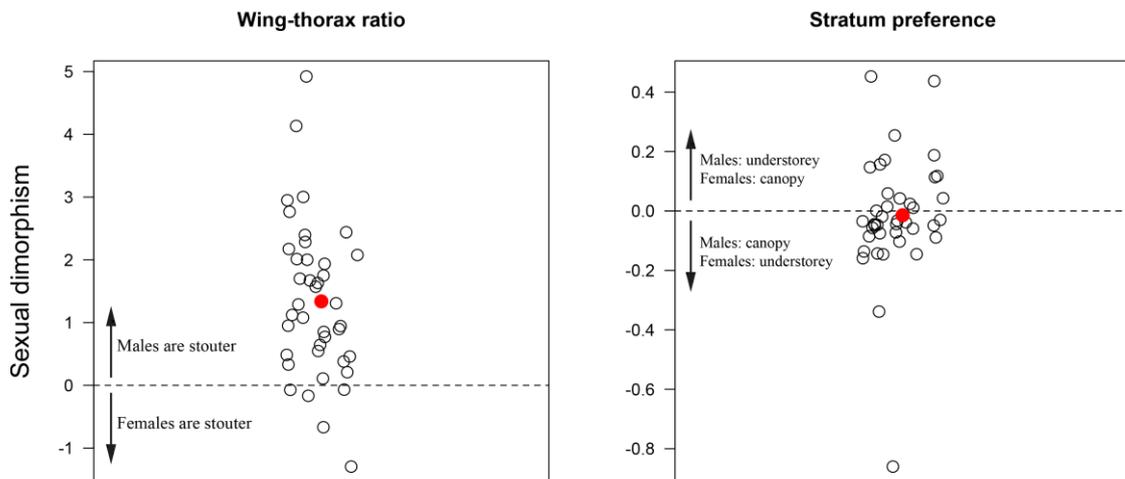


Figure 10. Sexual dimorphism regarding wing-thorax ratio and stratum preference. The dashed line represents the mean difference expected under the null hypothesis. The filled red dots represent the observed mean difference. Each empty dot represents a species (n = 40).

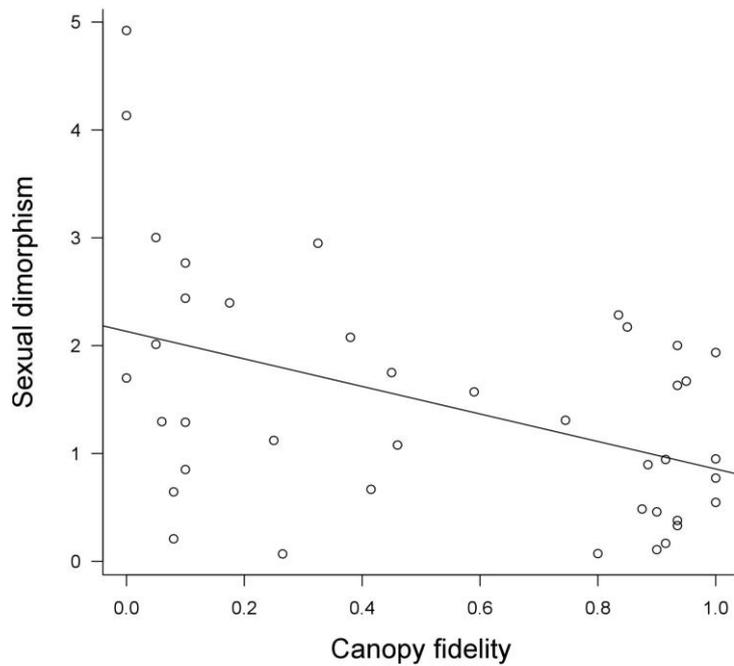


Figure 11. PGLS model for the relationship between intraspecific sexual dimorphism in wing-thorax ratio and canopy fidelity (0 = understorey only; 1 = canopy only). Each dot represents a species (n = 40).

Discussion

This study represents an endeavor to address the evolutionary processes underlying the disruption of species diversity and composition between understorey and canopy layers in tropical forests, while attempting to elucidate whether and how sexual dimorphism interferes in habitat preference. We tackled flight morphology as a key factor for ecological performance and evolutionary success of a diverse group of butterflies (fruit-feeding guild).

Our results suggest that flight mechanisms have been evolving under the strong constraint of species relatedness. Thorax and wing kinematics are determinants of flight characteristics of butterflies (Dudley, 2000; DeVries *et al.*, 2010; Cespedes *et al.*, 2014). Therefore, an evolutionary constraint on these morphological features should affect directly occurrence patterns, as butterflies rely largely on flight when adults. Similar to other winged organisms, flight represents a milestone in the evolution of butterflies for enhancing their aptitudes in mating, foraging and survival (Srygley, 1994; Srygley, 2004; Grimaldi & Engel, 2005). Accordingly, slightest phenotypic changes in flight-related attributes may produce deleterious outcomes, and

evolutionary pressures may be in play to maintain wing-thorax ratio evolving close to specific values in each clade. This results in closely related species being more similar to each other than expected from random sampling the phylogenetic tree (Blomberg & Garland, 2002). The robust phylogenetic signal in wing-thorax ratio of both sexes may also be the initial evidence that flight morphology is undergoing niche conservatism (Wiens & Graham, 2005; Losos, 2008). By estimating the rates of trait evolution, one could gain insights into whether flight-related attributes have been kept from diverging among closely related species and how this could have impacted the evolution of flying organisms.

Although several ecological studies have observed and quantified the vertical stratification in tropical forests (DeVries, 1988; Walther, 2002; Krömer *et al.*, 2007; Basset *et al.*, 2015), the evolutionary causes of this pattern are much less known (e.g. Fordyce & DeVries, 2016). For butterflies in particular, some hypotheses for the understorey/canopy segregation involve the difference in sunlight levels (DeVries, 1988) and host plant vertical distribution (Beccaloni, 1997). Here, we found that the association between flight morphology and stratum preference holds independently from phylogenetic relatedness among species, and independently from the phylogenetic signal in vertical stratification (Fordyce & DeVries, 2016) and in wing-thorax ratio. We hypothesize that stouter species (powerful and high-speed flying) benefit from the higher temperature of canopies to sustain flight power and speed. Considering that habitat complexity and aerial-hawking predation pressure increases towards upper forest layers (Schulze *et al.*, 2001; Ricklefs, 2004), high-speed flying butterflies may use higher canopy temperature to boost their flight muscles, thus facilitating navigation and escape from predation. In contrast, the flight morphology of slenderer species fits better the understorey conditions, where they are seemingly more successful. Due to the average low amount of light reaching the understorey in tropical forests (< 15% on average, Montgomery & Chazdon, 2001), the supply of environmental heat needed by ectotherms to activate their metabolism is more limited at lower forest strata, and costly high-speed flights could be unfavorable. We further theorized that species in the understorey might rely more on thermoregulation (e.g. shivering, Srygley, 1994), since external energy is restricted. So, we also tested whether thorax mass alone, a surrogate for potential to generate heat from muscles, was associated with vertical stratification in phylogenetically controlled analysis. The non-significant relationships in males and the marginally significant increase in

thorax mass towards the canopy in females contested our expectations though. However, we believe this subject still needs proper investigation, especially through direct measures of thermoregulation and under experimental perspectives.

Interestingly, the correlation between wing-thorax ratio and forest stratum was stronger in females ($R^2 = 0.35$) than in males ($R^2 = 0.22$), thus indicating that female phenotype varies more between strata than that of males. Regardless of sex, flying is essential for butterfly routine activities, such as searching for food, escaping predation and dispersal (Kingsolver, 1983; Srygley, 2004; Niitepõld *et al.*, 2011). Nevertheless, males and females differ in reproduction: while males may perch or patrol territories for mating encounters, females are engaged in finding suitable hosts for larvae (Lederhouse *et al.*, 1992; Wiklund, 2003; Bergman *et al.*, 2007). Because females face additional extrinsic limitations to successfully complete the reproductive cycle, i.e. host plant distribution, female phenotype should associate more strongly with environmental gradients, such as vertical stratification. This intricate matching between flight morphology, optimal conditions for flight and host occurrence may help explain some reported divergence between female and host stratification. For instance, some stout-bodied species that inhabit the canopy and descend to the understorey for oviposition (e.g., *Temenis laothoe* and *Zaretis itys*) are associated with plants growing in areas that resemble canopy conditions of light, temperature and moisture, such as understorey gaps and forest edge (Muysshondt, 1973; DeVries, 1987). This further supports the argument that sunlight and its correlates are important in determining vertical diversity patterns (DeVries, 1988).

The sexual dimorphism analyses showed that males did not differ from females regarding stratum preference, meaning that, on average, both sexes fly either in the understorey or the canopy. Conversely, females were significantly slenderer than males from the same species independently from phylogeny (Fig. 9). This was somewhat expected, especially considering the reported trade-off between flight and reproduction (oogenesis-flight syndrome hypothesis, Johnson, 1963; Jervis *et al.* 2005; Gibbs & Van Dyck, 2010) and that different reproductive roles likely drive morphological divergence between sexes (Badyaev, 2002). Females prioritize abdominal mass in their energy budget because of reproductive duties (Thornhill & Alcock, 1983; Marden & Chai, 1991). As a consequence, they possess a smaller quantity of flight muscles per body mass unit (Berwaerts *et al.*, 2002) and may fly most of the time near maximum energy output (Berrigan, 1991). Males, on the other

hand, are able to invest more in flight power, which is advantageous because flight performance often determines the winner in male-male mating contests (Thornhill & Alcock, 1983). Further, in perching species, higher thoracic capacity may enable the constant energetic outbursts that males need for taking off to intercept potential mates and competing males (Van Dyck *et al.*, 1997; Dudley, 2000; Berwaerts & Van Dyck, 2004). Thus, our results support the assumption that flight and reproduction may indeed compete for resources (Wheeler, 1995).

Vertical stratification had also an effect on flight sexual dimorphism, as our PGLS model indicated that males and females of understorey species differed more strongly in wing-thorax ratio compared to canopy inhabitants (Fig. 10). Because upper layers have more complex forest structure and a higher predation pressure (Schulze *et al.*, 2001; Ricklefs, 2004), females may have evolved bodies as robust as those of their conspecific males, so that they could benefit from the optimal conditions for high-speed flight as well. After seeing our results, we believe that female phenotype is driving the sex dimorphism in vertical stratification, because their flight morphology varies more strongly between strata than that of males (Fig. 7).

In summary, our study revealed that (i) wing-thorax ratio has a strong phylogenetic signal, (ii) flight morphology explains in part the vertical stratification of tropical fruit-feeding nymphalids, (iii) females are significantly more slender than males, which possibly reflect less investment in flight to redirect resources for reproduction, and (iv) sexual dimorphism is more accentuated in understorey species. As these conclusions were independent of phylogenetic relatedness, we conclude that evolutionary processes related to adaptive radiation have been stronger than phylogenetic constraint in the matching between flight morphology and stratum preference. Nonetheless, the three-way association of stratum preference, flight morphology and sexual dimorphism revealed much unexplained variation, suggesting that other factors are important in driving habitat stratification among species. Our findings shed light on the background of the coevolution of flight morphology, habitat preference and sexual dimorphism in winged organisms.

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**Taxonomic, functional and phylogenetic perspectives
on butterfly spatial assembly in northern Amazonia**

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Taxonomic, functional and phylogenetic perspectives on butterfly spatial assembly in northern Amazonia

Abstract 1. Understanding the causes for the spatial variation of biodiversity is an important goal in community ecology. We investigated the response of fruit-feeding butterfly assemblages to environmental gradients resulting from the transition from ombrophilous forests to white-sand forests in northern Brazil by assessing taxonomic, functional and phylogenetic descriptors of community structure.

2. Butterflies were sampled with bait traps in the Brazilian Amazon, while their traits and phylogenetic relatedness were either measured directly or gathered from the literature. Then, we tested for the effect of plant species turnover, light intensity and flood risk on butterfly community patterns.

3. Butterfly abundance increased with light intensity in non-forested white-sand habitats, whereas ombrophilous forests harboured higher species richness. We observed a trade-off between richness and abundance across the gradient. Plant turnover strongly drove shifts in butterfly species composition. In white-sand habitats, butterflies had higher dispersal capacity, faster flights and generalist larvae, whereas in periodically flooded plots the functional diversity of flight-related traits was higher. We detected no phylogenetic response to environmental gradients.

4. These results exposed the complexity of community structure across a mosaic landscape and how analyzing more than one dimension of biodiversity may reveal underlying relationships unapparent under isolated approaches. Caution is required when using phylogeny as a proxy for functional similarity, as the responses were not congruent in our study. The ecological patterns revealed here, aligned with further regional-scale studies, can provide complementary perspectives on butterfly spatial distribution and ensure that appropriate conservation policies are developed.

Keywords. Amazon floodplain, functional diversity, Nymphalidae, ombrophilous forests, phylogenetic diversity, white-sand forests.

Introduction

Community ecology is challenged with incorporating the multidimensional aspect of biodiversity into distributional studies in order to broaden the understanding of the current species occurrence and predict the future patterns (McGill *et al.*, 2006;

Swenson, 2013). There has been a trend towards abandoning strictly taxonomic approaches, and linking species diversity with functional and phylogenetic components (Blanchet *et al.*, 2014; Arnan *et al.*, 2016; Graça *et al.*, 2016). This tendency finds support on the notion that nomenclatural perspectives are little informative on carrying functional and evolutionary signals (Swenson, 2014). In turn, trait distribution and phylogenetic relatedness can furnish evidence for processes affecting contemporary assembly patterns (Webb *et al.*, 2002). Additionally, the combination of approaches may enhance the detectability of ecological patterns (McGill *et al.*, 2006), because the diversity components may capture different variations in the community. For instance, Graça *et al.* (2016) found that the association between tropical butterflies and birds was evident when analyzing variation in butterfly body size (functional component), but was undetected when looking at butterfly species composition (taxonomic component). Therefore, the linkage among approaches can be advantageous when studying diverse assemblages, such as those found in the Amazon tropical rainforest.

Throughout the Amazon Basin, ombrophilous forests meet with white-sand vegetation to form extensive and diverse landscape mosaics (Fine *et al.*, 2010; Ter Steege *et al.*, 2013). In general, white-sand forests have lower plant species diversity (Fine *et al.*, 2010; Guevara *et al.*, 2016), nutrient-poor soils and are under the influence of periodic flooding due to rainfall (Do Vale *et al.*, 2015), contrasting with plant- and nutrient-rich non-flooded ombrophilous forests. As a result, sharp environmental gradients of herbivore resources (host plants, plant juices) and abiotic factors (light intensity, flood regime) are created (Coomes & Grubb, 1996; Baraloto *et al.*, 2011). For primary producers, white-sand soils are strong diversity constraints (Fine & Kembel, 2011), but there is little evidence of how the transition from low-resource white-sand forests to high-resource ombrophilous forests affects communities in higher trophic levels, such as herbivores (see Lamarre *et al.*, 2016).

Among insect herbivores, fruit-feeding butterflies in the Nymphalidae are preferred ecological models because they can be sampled with standardized methods (DeVries *et al.*, 2016) and species-level identification is not an issue for most groups. Additionally, for butterflies in general, many functional traits have been studied. For instance, wing length is considered a key element in butterfly dispersal capacity (Tufto *et al.*, 2012) and should play a role in avian predation avoidance (Chai & Srygley, 1990). Similarly, wing and thorax architecture may indicate adult habitat

preference (Hill *et al.*, 2001; Pardonnet *et al.*, 2013), as well as influence flight characteristics (Chai, 1990; DeVries *et al.*, 2010). The diet specialization of larvae is reported to be a limiting factor and shape butterfly distributional patterns (Curtis *et al.*, 2015; Graça *et al.*, 2016), even though adults may be mobile and forage across extensive areas (Marchant *et al.*, 2015). These differences in life history traits are likely to be important attributes of the ecological performance of butterflies and should be affected by environmental gradients, such as the transition from ombrophilous to white-sand Amazonian forests. Furthermore, the phylogeny of nymphalids (e.g. Wahlberg *et al.*, 2009) helps merge systematics with ecology to estimate unmeasured traits of potential ecological importance, under the assumption that closely related species are more ecologically similar (Webb, 2000).

In this light, we aimed at disentangling the effect of resources and abiotic gradients on the taxonomic diversity, life history traits and phylogenetic diversity of fruit-feeding butterfly communities across a heterogeneous Amazon landscape. With this complementary approach, we intended to understand the distribution of butterfly assemblages, while spotting evolutionary and functional signals that underlie such patterns and enhancing the ecological predictive power (McGill *et al.*, 2006; Swenson, 2014). Accordingly, we formulated the following hypotheses:

1. Butterfly abundance should increase with light intensity in non-forested white-sand habitats for two reasons: in tropical forests, plant productivity increases with light availability, thus decreasing the food limitation for herbivores (Richards & Coley, 2007) and enabling their populations to grow; the environmental heat may benefit the ectothermic nature of butterfly metabolism (Wickman, 2009) and facilitate the foraging in non-forested white-sand habitats.

2. Ombrophilous forests should harbour higher butterfly species richness, as they combine higher plant species richness (niche space for larval butterflies) and less stressful abiotic conditions (Baraloto *et al.*, 2011; Guevara *et al.*, 2016).

3. The spatial turnover in plant species composition results in changes of host availability. Because the occurrence patterns of larval hosts impact on adult butterflies (Curtis *et al.*, 2015), we expect plant and butterfly species turnover to correlate.

4. Habitats with high light intensity and flood risk should harbour large-winged and powerful flying butterflies, because their enhanced flight capacity may help exploit unstable and temporary habitats (Hill *et al.*, 2001), which in turn should result in lower functional diversity of these traits.

5. Because plants of white-sand forests have stronger anti-herbivory assets (e.g. sclerophylly, Fortunel *et al.*, 2014), we expect a higher level of diet specialization in the butterfly communities of these habitats (Pellissier *et al.*, 2012).

6. Assuming that phylogenetically close butterflies tend to display larval diet similarity (Pellissier *et al.*, 2013) and lower resources may intensify competitive exclusion among closely related species, we expect higher functional (diet breadth) and phylogenetic diversity in resource-poor white-sand forests.

Methods

Study site and sampling

Our survey was conducted in 24 sampling plots at Viruá National Park. Refer to the Material and Methods section on page 5 for more details on the study area and sampling design.

Functional traits

Dispersal capacity represents a key attribute for living organisms, and records of individual movements can convey significant insights into the ecological performance of insects (Tufto *et al.*, 2012). Here dispersal relates to any butterfly movement, random or pre-determined (e.g. search for a specific host plant), seasonal or aseasonal, at the individual level. The association between wingspan and dispersal capacity has been debated among lepidopteran studies, with mixed results (Sekar, 2012, and references therein). However, models of dispersal rates under Brownian motion for fruit-feeding butterflies indicated that wing length accounted for most of the interspecific variation in dispersal rate ($r = 0.81$), while the unexplained variance could be linked to mating behaviour and sex of particular species (Tufto *et al.*, 2012). We measured the linear distance between the base of the discal cell and the intersection of vein R5 with the wing margin (Cespedes *et al.*, 2015) as a proxy for adult dispersal capacity. We measured forewing length on the ventral surface using a millimeter ruler within 24 hours after sampling.

We calculated the ratio of wing area per thorax volume (WTR) to estimate flight power and speed (Hall & Willmott, 2000; Hill *et al.*, 2001). Thorax mass and width have been positively correlated with investment in flight (Chai & Srygley, 1990; Srygley & Chai, 1990), but controlling for the allometry between wing and thorax is important to render measurements less biased (Dudley, 1990; Hall &

Willmott, 2000). This means that a species may have a large thorax (allocation of flight muscles) to support equally large wings, or may have developed a robust thorax to empower stronger flights, even if the wings are shorter than expected. WTR dimensionless values were obtained as:

$$WTR = \frac{w^2}{tv}$$

where w is forewing length and tv is thorax volume (length x width²; Hill *et al.*, 2001). All individuals were measured in the field with a digital millimeter caliper prior to drying to avoid errors due to shrinking. Lower values of WTR indicate stout-bodied butterflies that perform speeding aerial movements, while higher values indicate slender-bodied butterflies with slower flights and low wing beat frequencies (Chai, 1990).

Larval diet breadth was used to estimate the feeding specialization of species. Host plant records were gathered from online databases and published sources (see the full list on supplementary material). The diet of species not mentioned in any sources (~32% of the overall richness) was estimated from a congener, and when possible based on phylogenetic relatedness. For instance, hosts for *Taygetis echo* (Cramer) were estimated from *Taygetis thamyra* (Cramer) due to their close relatedness (*sensu* Matos-Maraví *et al.*, 2013). We followed Graça *et al.*, (2016) to score larval diet breadth: feeds on (1) one plant species (2) more than one species from the same genus (3) more than one genus from the same family (4) more than one family from the same order (5) more than one order from the same clade and (6) more than one clade. The classification is according to the updated systematic review of the flowering plants (APG III, 2009).

Community phylogenetic structure

In order to incorporate phylogenetic relatedness information into the analyses, we constructed a phylogenetic supertree containing all sampled species as terminal taxa (Fig. 12). The supertree backbone was based on the Wahlberg *et al.*, (2009) topology for nymphalid genera, and complemented with resolutions within genera whenever available (e.g., Ortiz-Acevedo & Willmott 2013; Penz *et al.*, 2013). Genera without a formal proposition for species relatedness (e.g., *Memphis*) were left as polytomies and all branch lengths were standardized to equal length (1.00) (García-Barros, 2015) for

lack of information on all lineages, and because results with weighted and non-weighted branches differ very little (Rezende & Diniz-Filho, 2012).

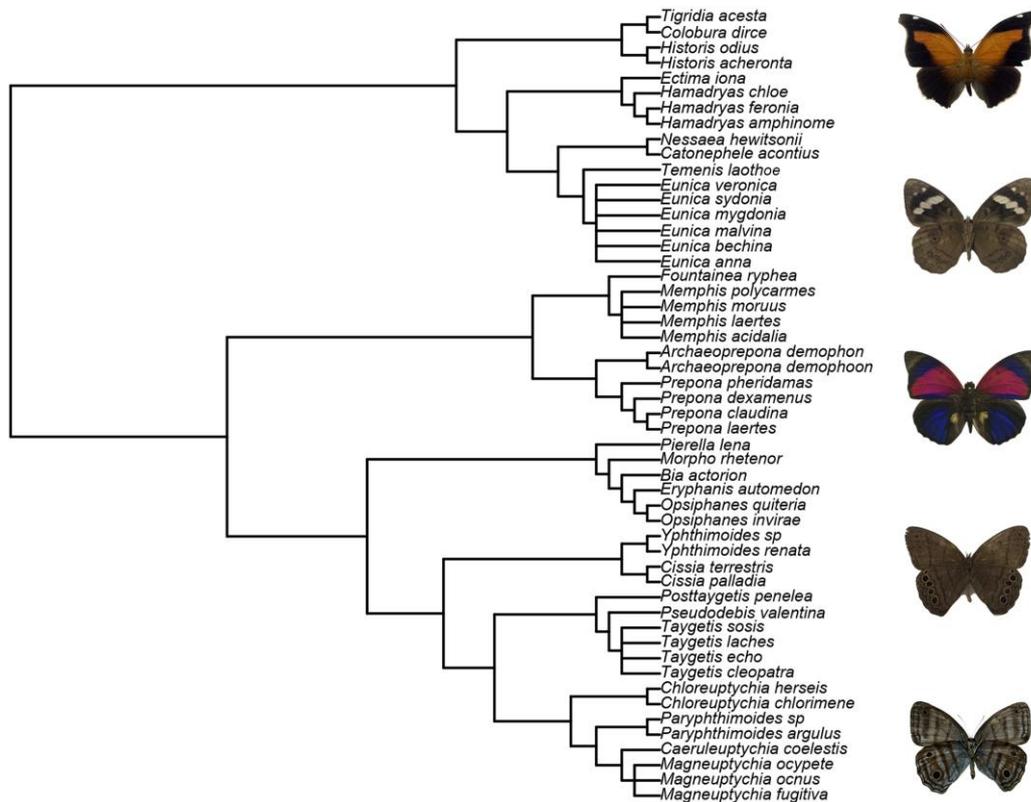


Figure 12. Phylogenetic tree used to obtain metrics of phylogenetic diversity (MPD and MNTD) of the butterfly community in Viruá National Park.

Environmental gradients

The three environmental variables used were plant spatial turnover, light intensity and flood. Data on the spatial distribution of plant species was obtained from previous surveys conducted in Viruá (see Damasco *et al.*, 2013 for plants sampling details) and standardized by species occurrence. The plant species data matrix was submitted to Non-metric Multidimensional Scaling (NMDS) to converge into an ordination axis that scored the plots according to their dissimilarity in plant species composition. We used the first NMDS axis to represent the plant spatial turnover. Lower scores values in the plant NMDS axis 1 tend to represent ombrophilous forests, intermediate values are forested white-sand habitats and higher values correspond to non-forested white-sand habitats.

Light intensity was accessed by directly measuring the diffuse light in low forest stratum of the sampling plots. We used a digital lux meter (Minipa MLM-1011) to obtain six measures of light intensity in each of the 24 sampling plots. For standardization, the measures were taken at a 1-m height, every 50 m, between 9:00 and 10:00 a.m., and in days with cloudy weather conditions. For each sampling plot, we extracted the mean luminosity value.

Data on flood regime in Viruá were obtained from the Brazilian Biodiversity Research Program (PPBio) database (Do Vale *et al.*, 2015 for methods). We sampled butterflies in 12 plots periodically flooded and 12 plots free from flooding effects. Hence, the periodical flood was coded as a binary variable in our following statistical models.

Statistical analyses

For each approach, we had different response variables - (1) taxonomic approach: abundance, species richness and species turnover; (2) functional approach: median wing length, median wing/thorax ratio, median diet breadth, and functional diversity (MPD) and (3) phylogenetic approach: phylogenetic diversity (MPD and MNTD).

Taxonomic response variables: alongside abundance and richness, we estimated the spatial turnover in butterfly species composition. For that, we ran NMDS ordinations with butterfly relative abundance standardized by samples standardization to equal totals (Faith *et al.*, 1987), which controls for the discrepancy between abundant and rare species. The first NMDS ordination axis captures the highest variation in butterfly species turnover and therefore was used as the response variable in subsequent analyses.

Functional response variables: we calculated the median value of the traits in each of the 24 plots according to the co-occurring species. In addition, to estimate the functional diversity of each plot, we calculated the mean pairwise distance (MPD) of co-occurring species traits. With MPD, we can discuss functional diversity, as lower values indicate plots with similar species traits (low functional diversity), while higher values indicate plots with different species traits (high functional diversity). In order to eliminate the correlation between functional diversity and species richness, we ran null models (Swenson, 2014) for both median and MPD. Let us assume that any species can colonize any plot in our area. In the data set, plot number 1 had three species. The null model will randomly draft three species from the total species pool,

thus creating a random species composition for this plot, and calculate the random trait value according to the three species randomly drafted. This procedure was done 999 times, which generated 999 null values of trait distribution for the 24 plots. During randomizations, species were weighted by their prevalence across all 24 plots to mimic their natural chance of occurrence at any plot within the studied area. Then, we standardized the median and MPD metrics by calculating the standardized effect sizes (SES), which consists in subtracting the mean null value from the real value, then dividing by the standard deviation of the null values (Swenson, 2014).

Phylogenetic response variables: we calculated the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD) of the co-occurring species in the 24 butterfly communities. Similarly, we ran null models to account for the effect of species richness by randomizing the phylogenetic tree tips 999 times, thus generating 999 random values of phylogenetic diversity for each of the 24 plots. Both MPD and MNTD underwent the aforementioned SES procedure.

Predictor variables and regression models: firstly, we tested for the pairwise interaction among plant turnover, light intensity and flood in regression models, and since no significant interaction was encountered, we removed the interaction term. All relationships were investigated using multiple regressions with the three predictor variables used simultaneously to control for the autocorrelation among them and test for their independent effect (Harrell, 2015). We used generalized linear models with Poisson error distribution corrected for overdispersion (quasipoisson) to detect the environmental influence on butterfly abundance and richness (count variables). For the remaining variables (butterfly species turnover, functional and phylogenetic variables), we used traditional linear models.

All analyses were performed in the statistical environment R version 3.3.3 (R Development Core Team, 2017). We used packages *vegan* 2.3-5 (Oksanen *et al.*, 2016) for running the ordinations procedures, *picante* 1.6-2 (Kembel *et al.*, 2014) for estimating MPD and MNTD, *car* 2.1-2 (Fox *et al.*, 2016) for plotting the regression charts, and *ape* 3.5 (Paradis *et al.*, 2016) for writing and plotting the phylogenetic tree.

Results

We collected 626 individual butterflies belonging to 52 species, and allocated in all four fruit-feeding subfamilies of Nymphalidae (Table 2). The most abundant species was *Historis acheronta*, accounting for around 60% of total abundance, but

Opsiphanes invirae was the most widespread, occurring in 15 out of 24 plots. Singletons and doubletons were represented by 30 species (~58%). In ombrophilous forests we captured 119 individuals from 33 species, while in white-sand forests we sampled 507 individuals also from 33 species.

Table 2. Fifty-two species of fruit-feeding butterflies collected in 24 sampling plots in Viruá National Park, state of Roraima, Brazil, with their respective abundance and averaged values for morphological measurements and specialization rank. FWL = Average forewing length (mm), WTR = Average wing/thorax ratio, LDB = Larval diet breadth.

| Species | Abundance | FWL | WTR | LDB |
|---------------------------------------------------|-----------|------|------|-----|
| Biblidinae | | | | |
| <i>Catonephele acontius</i> (L., 1771) | 3 | 30.6 | 4.14 | 6 |
| <i>Ectima iona</i> E. Doubleday, [1848] | 1 | 21.5 | 9.58 | 2 |
| <i>Eunica anna</i> (Cramer, 1780) | 1 | 29.0 | 5.00 | 1 |
| <i>Eunica bechina</i> (Hewitson, 1852) | 2 | 28.5 | 4.90 | 1 |
| <i>Eunica malvina</i> H. Bates, 1864 | 1 | 31.0 | 8.45 | 1 |
| <i>Eunica mygdonia</i> (Godart, [1824]) | 14 | 29.8 | 4.95 | 1 |
| <i>Eunica sydonia</i> (Godart, [1824]) | 1 | 35.0 | 7.21 | 1 |
| <i>Eunica veronica</i> H. Bates, 1864 | 1 | 29.0 | 6.44 | 1 |
| <i>Hamadryas amphinome</i> (L., 1767) | 7 | 37.0 | 3.76 | 3 |
| <i>Hamadryas chloe</i> (Stoll, 1787) | 1 | 28.0 | 6.09 | 6 |
| <i>Hamadryas feronia</i> (L., 1758) | 10 | 37.6 | 4.92 | 6 |
| <i>Nessaea hewitsonii</i> (Felder & Felder, 1859) | 2 | 31.5 | 6.87 | 3 |
| <i>Temenis laothoe</i> (Cramer, 1777) | 2 | 28.4 | 5.47 | 3 |
| Charaxinae | | | | |
| <i>Archaeoprepona demophon</i> (L., 1758) | 3 | 51.5 | 3.02 | 6 |
| <i>Archaeoprepona demophoon</i> (Hübner, [1814]) | 4 | 50.6 | 1.94 | 5 |
| <i>Fountainea ryphea</i> (Cramer, 1775) | 5 | 28.2 | 3.67 | 2 |
| <i>Memphis acidalia</i> (Hübner, [1819]) | 2 | 30.2 | 4.11 | 2 |
| <i>Memphis laertes</i> (Cramer, 1775) | 1 | 33.5 | 5.33 | 2 |
| <i>Memphis moruus</i> (Fabricius, 1775) | 4 | 31.0 | 3.31 | 6 |
| <i>Memphis polycarmes</i> (Fabricius, 1775) | 2 | 28.6 | 3.29 | 5 |
| <i>Mesoprepona pheridamas</i> (Cramer, 1777) | 2 | 44.0 | 3.72 | 6 |
| <i>Prepona claudina</i> (Godart, [1824]) | 1 | 40.2 | 1.87 | 6 |
| <i>Prepona dexamenus</i> Hopffer, 1874 | 2 | 45.3 | 2.67 | 6 |
| <i>Prepona laertes</i> (Hübner, [1811]) | 4 | 49.8 | 2.64 | 6 |
| Nymphalinae | | | | |
| <i>Colobura dirce</i> (L., 1758) | 1 | 32.0 | 4.94 | 6 |
| <i>Historis acheronta</i> (Fabricius, 1775) | 425 | 37.4 | 4.15 | 6 |

| | | | | |
|---------------------------------------------------|----|------|-------|---|
| <i>Historis odius</i> (Fabricius, 1775) | 2 | 55.5 | 2.40 | 6 |
| <i>Tigridia acesta</i> (L., 1758) | 1 | 23.0 | 11.03 | 3 |
| Satyrinae | | | | |
| <i>Bia actorion</i> (L., 1763) | 3 | 26.0 | 12.48 | 3 |
| <i>Caeruleptychia coelestis</i> (A. Butler, 1867) | 4 | 23.5 | 13.31 | 4 |
| <i>Chloreuptychia chlorimene</i> (Hübner, [1819]) | 1 | 18.0 | 22.71 | 5 |
| <i>Chloreuptychia herseis</i> (Godart, [1824]) | 1 | 19.0 | 22.19 | 5 |
| <i>Cissia palladia</i> (A. Butler, 1867) | 1 | 16.0 | 14.33 | 3 |
| <i>Cissia terrestris</i> (A. Butler, 1867) | 19 | 16.8 | 18.65 | 3 |
| <i>Eryphanis automedon</i> (Cramer, 1775) | 1 | 70.0 | 8.80 | 1 |
| <i>Magneuptychia fugitiva</i> Lamas, [1997] | 1 | 16.0 | 16.30 | 4 |
| <i>Magneuptychia ocnus</i> (A. Butler, 1867) | 1 | 22.0 | 13.92 | 4 |
| <i>Magneuptychia ocypte</i> (Fabricius, 1776) | 6 | 21.5 | 12.03 | 4 |
| <i>Morpho rhetenor</i> (Cramer, 1775) | 2 | 72.0 | 13.54 | 6 |
| <i>Opsiphanes invirae</i> (Hübner, [1808]) | 32 | 37.9 | 3.01 | 5 |
| <i>Opsiphanes quiteria</i> (Stoll, 1780) | 4 | 46.3 | 2.64 | 3 |
| <i>Paryphthimoides ca. argulus</i> | 7 | 19.5 | 12.95 | 3 |
| <i>Paryphthimoides</i> sp1 | 8 | 19.6 | 12.44 | 3 |
| <i>Pierella lena</i> (L., 1767) | 2 | 37.0 | 16.30 | 3 |
| <i>Posttaygetis penelea</i> (Cramer, 1777) | 2 | 27.0 | 12.52 | 1 |
| <i>Pseudodebis valentina</i> (Cramer, 1779) | 1 | 32.0 | 9.12 | 3 |
| <i>Taygetis cleopatra</i> Felder & Felder, 1867 | 11 | 34.1 | 8.74 | 3 |
| <i>Taygetis echo</i> (Cramer, 1775) | 1 | 32.0 | 8.10 | 4 |
| <i>Taygetis laches</i> Fabricius, 1793 | 3 | 35.3 | 9.82 | 5 |
| <i>Taygetis sosis</i> Hopffer, 1874 | 5 | 34.7 | 8.38 | 3 |
| <i>Yphthimoides renata</i> (Stoll, 1780) | 3 | 27.0 | 14.09 | 3 |
| <i>Yphthimoides</i> sp1 | 1 | 22.0 | 9.89 | 3 |

In the taxonomic dimension (Table 3), abundance of butterflies significantly increased with light intensity (Fig. 13a) ($F_{3, 20} = 6.257$, $r^2 = 0.49$, $P = 0.003$). In this instance, there was a leverage of the points at the right-hand side of the plot, so after square root transforming the data, we observed that the association with light became weaker ($P = 0.084$). Butterfly species richness was significantly higher in ombrophilous forests (Fig. 13b) ($F_{3, 20} = 3.917$, $r^2 = 0.36$, $P = 0.023$) and species composition strongly associated with plant species turnover (Fig. 14) ($F_{3, 20} = 5.912$, $r^2 = 0.47$, $P = 0.004$).

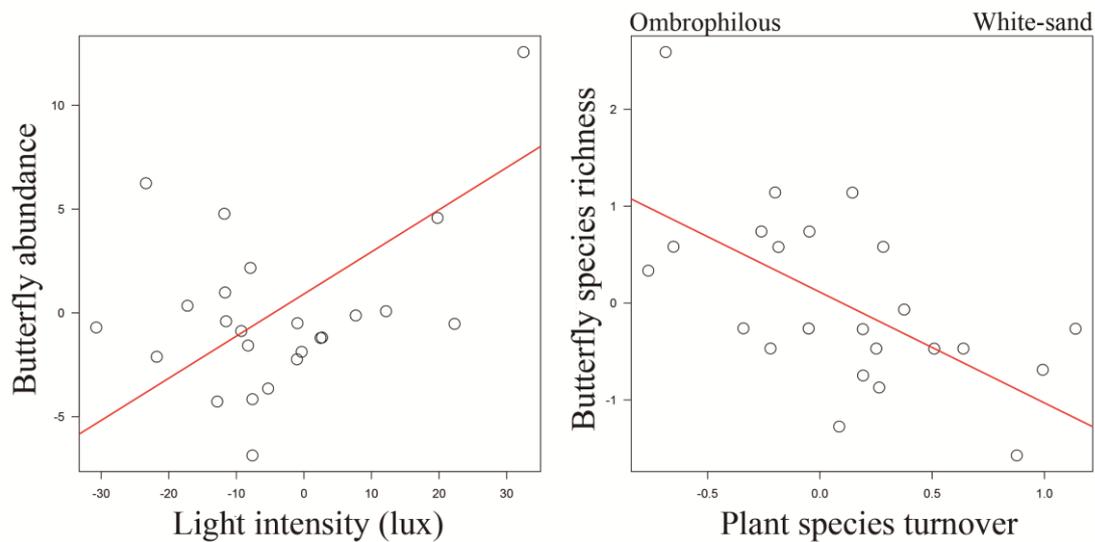


Figure 13. Taxonomic approach: influence of light intensity on the abundance of fruit-feeding butterflies (a) and influence of plant species turnover on butterfly species richness (b). Negative notations indicate residual values resulting from multivariate regressions.

According to the functional dimension (Table 3), forewing length was higher in white-sand forests (Fig. 15a) ($F_{3, 20} = 4.117$, $r^2 = 0.38$, $P = 0.019$). Wing/thorax ratio was lower in butterfly communities of white-sand forests (Fig. 15b) and non-flooded plots (Fig. 15c) ($F_{3, 20} = 3.925$, $r^2 = 0.37$, $P = 0.022$). Generalist communities occurred in white-sand forests (Fig. 15d), while specialized butterfly assemblages were associated with high light intensity and periodical flood ($F_{3, 20} = 3.309$, $r^2 = 0.34$, $P = 0.037$). We did not detect significant influence from the gradients on functional diversity of forewing length ($P = 0.245$). Regarding wing/thorax ratio however, functional diversity was lower in non-forested white-sand habitats (Fig. 16a), but higher in plots under flood risk (Fig. 16b) ($F_{3, 20} = 3.875$, $r^2 = 0.39$, $P = 0.018$). As for larval diet breadth, in non-forested white-sand habitats, butterfly communities had higher functional diversity (Fig. 16c), whereas plots under flood influence harboured

communities with lower functional diversity (Fig. 16d) ($F_{3, 20} = 11.7$, $r^2 = 0.63$, $P < 0.001$).

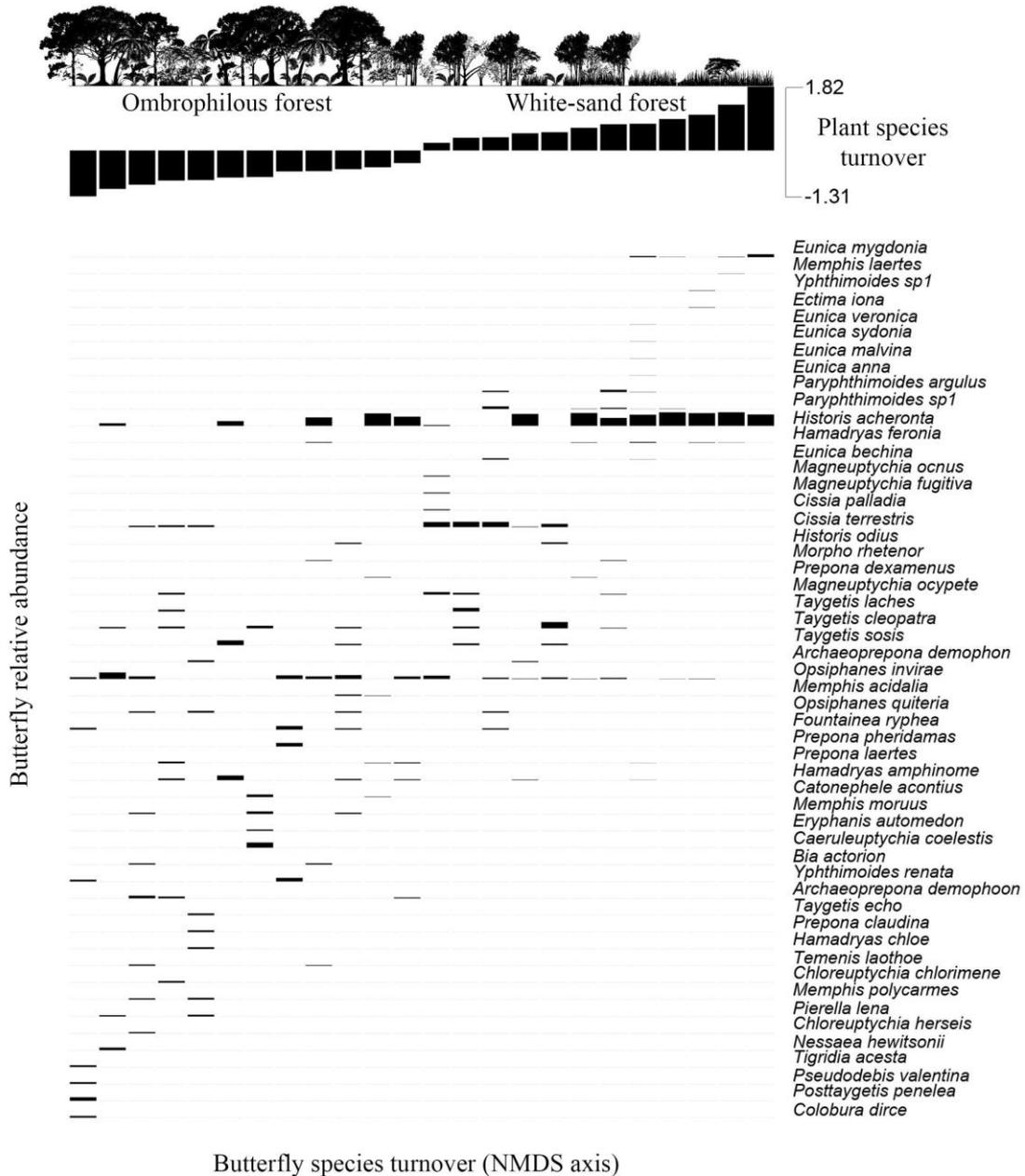


Figure 14. Taxonomic approach: association of butterfly species turnover (NMDS Axis 1) with the gradient of plant species composition (NMDS Axis 1).

Finally, neither MPD ($P = 0.137$) nor MNTD ($P = 0.681$) regression models showed significant relationships between phylogenetic diversity and environmental gradients (Table 3).

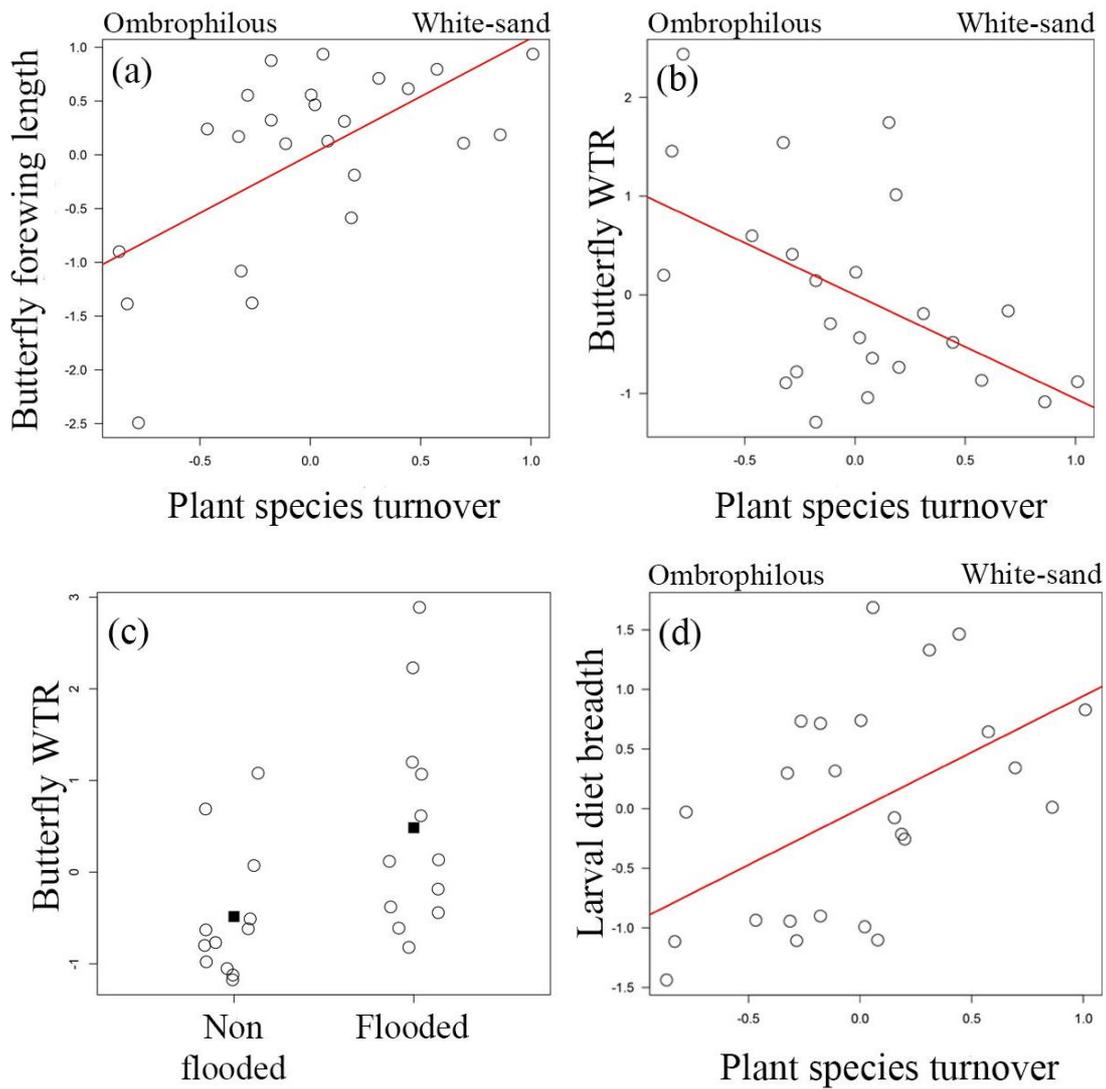


Figure 15. Functional approach: median species traits per plot. The effect of plant species turnover on butterfly forewing length (a), the influence of plant species turnover (b) and flood (c) on butterfly wing/thorax ratio, and the effect of plant species turnover on butterfly larval diet breadth (d). Negative notations indicate residual values resulting from multivariate regressions.

Table 3. Summary of the partial results of multiple regressions regarding taxonomic, functional and phylogenetic spatial patterns of the butterfly communities in Viruá. \tilde{x} = median, MPD = mean pairwise distance, MNTD = mean nearest taxon distance. In all models, d.f. = 20.

| Approach | Response variable | Plant composition | | Light intensity | | Flood | | r^2 |
|-------------------|-----------------------------------|------------------------------|--------------|-----------------|--------------|--------|--------------|-------|
| | | t | P | t | P | t | P | |
| Taxonomic | Abundance | -0.512 | 0.614 | 2.229 | 0.037 | 1.456 | 0.161 | 0.49 |
| | Richness | -3.327 | 0.003 | 2.018 | 0.057 | 2.169 | 0.042 | 0.36 |
| | Species composition | 2.961 | 0.007 | 0.076 | 0.938 | -1.950 | 0.065 | 0.47 |
| Functional | Wing length (\tilde{x}) | 3.448 | 0.002 | -2.009 | 0.051 | -3.210 | 0.003 | 0.38 |
| | Wing/thorax ratio (\tilde{x}) | -2.699 | 0.014 | 0.161 | 0.932 | 3.219 | 0.004 | 0.37 |
| | Diet breadth (\tilde{x}) | 2.589 | 0.015 | -2.696 | 0.014 | -2.278 | 0.032 | 0.34 |
| | Wing length (MPD) | 1.003 | 0.341 | -2.051 | 0.063 | -0.419 | 0.658 | NS |
| | Wing/thorax ratio (MPD) | -2.190 | 0.024 | -0.759 | 0.691 | 2.255 | 0.018 | 0.39 |
| | Diet breadth (MPD) | 2.526 | 0.017 | 2.495 | 0.023 | -2.633 | 0.013 | 0.63 |
| | Phylogenetic | Phylogenetic diversity (MPD) | 1.611 | 0.129 | -1.901 | 0.063 | -1.338 | 0.206 |
| | Phylogenetic diversity (MNTD) | 0.927 | 0.342 | -1.124 | 0.245 | -0.766 | 0.438 | NS |

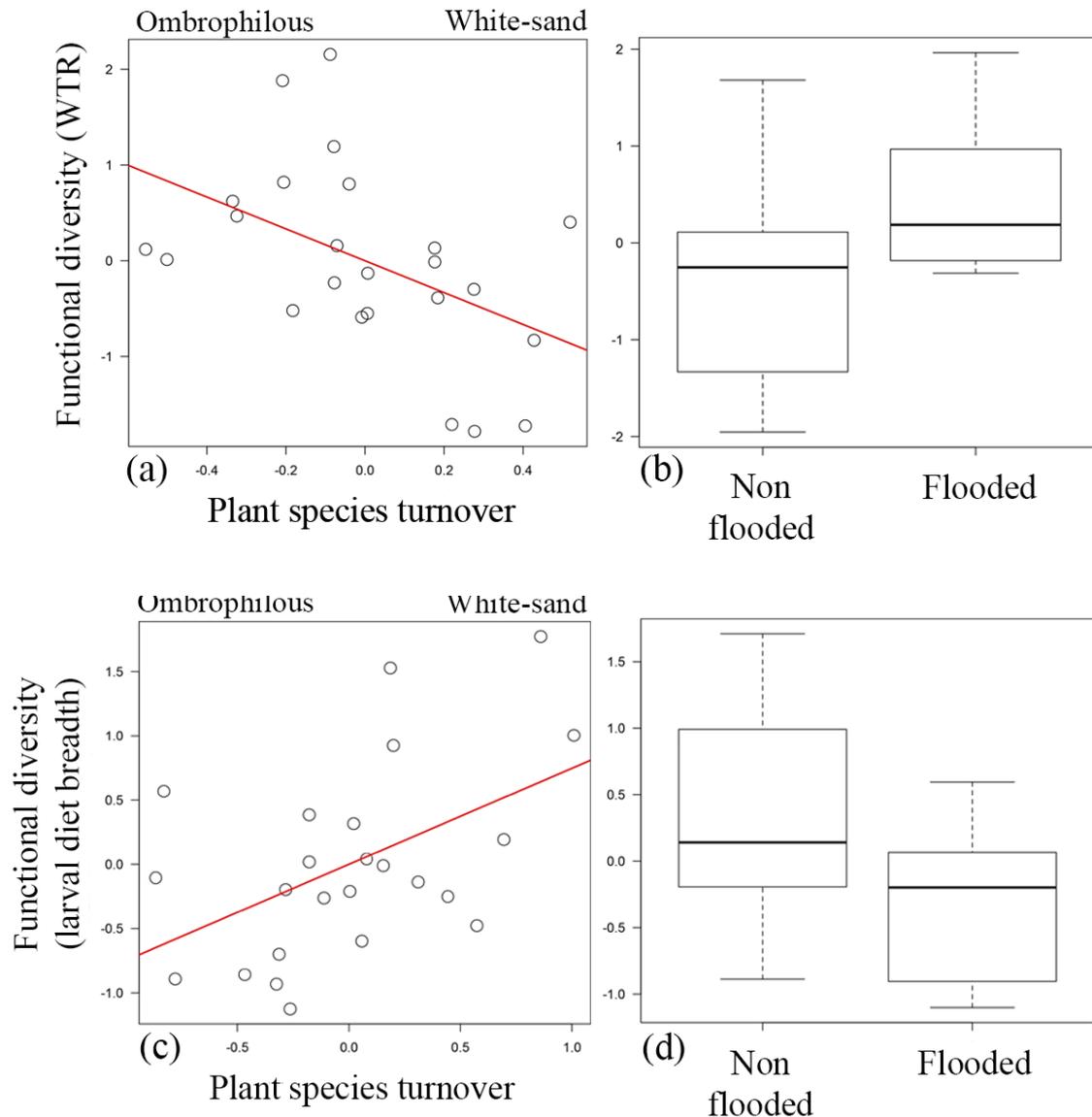


Figure 16. Functional approach: mean pairwise distance (MPD) of species traits per plot. The influence of plant species turnover and flood on the functional diversity of wing/thorax ratio (a, b) and larval diet breadth (c, d). Negative notations indicate residual values resulting from multivariate regression.

Discussion

Taxonomic approach

Our results showed that butterfly abundance increased with light intensity, and therefore, was higher in non-forested white-sand habitats. Such plots were dominated by light-loving *Historis acheronta*, the most abundant species in our study. This pattern may reflect the benefit of higher plant productivity habitats for herbivore populations (Richards & Coley, 2007) and that sun-loving ectotherms may be favored

by both biotic (resources) and abiotic (heat) conditions of these habitats. This relationship is more likely observed when the light gradient is wide, as the variation in butterfly abundance was slight under low to moderate light intensity.

In opposition, ombrophilous forests supported higher butterfly richness. Ombrophilous forests exhibit less stressful conditions, such as non-extreme droughts and higher diversity of plants (Baraloto *et al.*, 2011; Guevara *et al.*, 2016), which may have resulted in wider available niche space for butterflies to occupy, and thus less interspecific competitive exclusion. It is often expected that abundance and richness increase together (e.g., More Individuals Hypothesis, Wright, 1983), but we identified a trade-off in Viruá: while large populations of *H. acheronta* dominated non-forested white-sand habitats (average richness = 3 and abundance = 69), ombrophilous forests harboured higher species richness but smaller populations (average richness = 7 and abundance = 11). Studies have demonstrated that in both vertebrate and invertebrate communities such trade-off may be more usual than expected (Buckley & Jetz, 2010; Nimmo *et al.*, 2011), notably in habitats with high light intensity (agricultural landscapes in the Amazon, Barlow *et al.*, 2007; semi-arid habitats in southeastern Australia, Nimmo *et al.*, 2011). An experimental essay suggested that adult competition for resources might be a central driver of skewed abundance patterns in butterflies (Kunte, 2008). The community structure found in Viruá may be congruent with this inference, as juveniles of species in sunnier plots display little niche overlap to compete strongly: *Historis* feeds mainly on Urticaceae, *Memphis* primarily on Piperaceae, *Eunica* on Euphorbiaceae and *Paryphthimoides* on Poaceae (DeVries, 1987; Janzen & Hallwachs, 2009).

As we hypothesized, the turnover in plant species composition significantly drove the patterns in butterfly composition. We detected that some genera displayed preference for a particular habitat, while other congeneric species tended to partition their occurrence along the whole vegetation gradient. For instance, all *Chloreuptychia* species preferred ombrophilous forests, but *Hamadryas feronia* preferred non-forested white-sand habitats, *H. amphinome* tended to fly in forested white-sand habitats, and *H. chloe* only occurred in ombrophilous forests. Similar patterns of congeneric substitution in fruit-feeding species are reported along less heterogeneous forests (for *Magneuptychia* species, Graça *et al.*, 2016), and could reflect intrageneric competition for hosts.

Functional approach

Amazonian white-sand forests encompass peculiar vegetation structure and soil properties (Baraloto *et al.*, 2011; Damasco *et al.*, 2013; Ter Steege *et al.*, 2013; Do Vale *et al.*, 2015). In the dry season, the high temperature and the minimum moisture levels challenge water supply and maintenance, whereas in the rainy season the open vegetation provides few refuges from heavy rain, wind and inundation. Our results showed that species might benefit from having large wings and high mobility to forage across white-sand forests, which is consistent with the hypothesis that local instability and temporality of habitats demand high dispersal capacity from butterflies (Hill *et al.*, 2001; Pardonnet *et al.*, 2013). Similarly, wing/thorax ratio was lower in white-sand forests and in non-flooded plots. This supports the assumptions that insects exploiting patchy habitats tend to invest more in flight (Berwaerts *et al.*, 1998), and that speeding flights are advantageous for escaping avian predation (Chai, 1990), especially considering that non-flooded plots harbour higher bird diversity than flooded plots in Viruá (Laranjeiras *et al.*, 2014).

We detected lower larval specialization in white-sand forests, which goes contrary to our assumption that plants with enhanced development of physical and chemical defenses (Fine *et al.*, 2006; Fortunel *et al.*, 2014) would have driven herbivore larval specialization (Pellissier *et al.*, 2012). Knowing that the diversification of plants likely intensified the specialization levels of herbivores (Coley & Aide, 1991), the specialist strategy may be manifested more strongly in current plant-richer habitats, such as ombrophilous forests, rather than plant-poorer white-sand forests. This increase in herbivore specialization towards plant-diverse habitats has also been reported along plant richness gradients within ombrophilous forests (Graça *et al.*, 2016). Further, in ombrophilous forests, butterfly communities had low functional diversity of diet breadth, i.e., the communities are mostly composed of specialist species. These results suggest that the evolutionary linkage between specialist herbivores and plant-richer habitats could be stronger than the constraints imposed by white-sand vegetation.

Assemblages in ombrophilous forests tended to display high functional diversity of wing/thorax ratio. Compared with white-sand habitats, ombrophilous forests present a wider array of microhabitats to foster the irradiation of flight morphology. For example, ombrophilous forests have a clear distinction between canopy and understory, and we can observe a mosaic of shaded and open areas, which

are substantial factors for butterfly diversity patterns (DeVries & Walla, 2001; Pardonnet *et al.*, 2013). Similarly, the radiation of flight morphology in flooded plots suggests that many flight styles (gliding, flapping and speeding) are in play to help endure or escape heavy rains and consequent flood. For example, species with higher flight capacity and speeding flights may flee for other habitats during rain, and those with gliding flights may benefit from ground effect when flying near water surface during the flood period (see Cespedes *et al.* 2015). In any case, morphology seems to match the habitat to enhance species performance.

In this approach, the effect of light intensity on butterfly wing/thorax ratio was not significant, and thus our hypothesis was not corroborated. Nonetheless, we suppose this happened because our method of measuring light was limited to the detection of radiation visible to human eye. Part of the spectrum of radiant energy responsible for heat waves (*e.g.* infra-red) was not encompassed. This may also explain the weak influence of light in the taxonomic approach. Therefore, future studies using larger light spectrum would be required to properly address the influence of environmental heat on the spatial distribution of butterfly life traits.

Phylogenetic approach

Variation in phylogenetic diversity of the fruit-feeding butterfly assemblages across Viruá was not related to shifts in spatial gradients. Lamarre *et al.* (2016) detected a significant phylogenetic overdispersion of Lepidoptera communities in white-sand forests, but the different taxonomic scale of their study may have influenced the divergent outcomes. Indeed, the authors included three families of butterflies and moths on their phylogenetic tree (Nymphalidae, Saturniidae and Sphingidae), whereas we focused exclusively on nymphalid butterflies. It might be that the restrictions of white-sand forests are seemingly important in determining phylogenetic assembly among distantly related Lepidoptera groups, but not at the finer scale of Nymphalidae species. Moreover, the conflicting results between the phylogenetic and the functional approaches reinforce that the use of species relatedness to estimate functional attributes must be exerted with caution, as phylogenetic metrics summarize several species traits, which are ultimately impossible to disentangle (Swenson, 2013). Rather, the estimation of specific functional traits is essential for ecologists to understand more fully the environmental frameworks (Mayfield & Levine, 2010;

Blanchet *et al.*, 2014), and studies integrating taxonomic, functional and phylogenetic dimensions are more informative.

Implications of a holistic approach for biodiversity surveys and conservation

Our three-dimensional approach evidenced the complexity of the butterfly community structure in mosaic forests and highlighted the importance of simultaneously analyzing different dimensions of biodiversity for spotting the differences in community assembly (McGill *et al.*, 2006; Swenson, 2014). The taxonomic component revealed a trade-off between richness and abundance in the transition from white-sand habitats to ombrophilous forests. The compilation of results using the functional approach evidenced that we may find relationships by investigating species functional traits that are not discernible under strictly taxonomic or phylogenetic approaches, and provided more general patterns by taking into account species attributes rather than looking particularly at species composition. In addition, the functional turnover from ombrophilous forests to white-sand forests reflects the importance of Amazonian mosaic landscapes and the necessity to preserve habitat heterogeneity in order to maintain the beta diversity of ecosystems. The lack of an evident phylogenetic response emphasizes that relatedness should be considered a complement, not a complete surrogate for functional traits (Pavoine *et al.*, 2014), and surveys with purely phylogenetic standpoints may increase type II errors. We hope these findings encourage the merging of phylogenetics with functional ecology.

Finally, this study was carried out at a subregional scale, so that mainly local patterns were susceptible of detection. Future studies aiming at regional patterns are desired to complement these findings by addressing historical events that may have shaped current butterfly distribution, such as biogeographical barriers and evolutionary divergence (e.g. Arnan *et al.*, 2016 for ants). This should provide decision-makers with concrete knowledge for developing present and future rational environmental policies at both local and regional scales.

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**The role of caterpillar dietary niche in broad scale
diversity patterns of adult butterflies across
Amazonian landscapes**

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Formatting follows *Journal of Animal Ecology* guidelines



The role of caterpillar dietary niche in broad scale diversity patterns of adult butterflies across Amazonian landscapes

Abstract

1. Ecological niche is a major force in structuring biological assemblages. In animals, the juvenile dietary affects development, growth and survival of individuals, thus directly affecting species fitness. Thus, it is intuitive to expect that the adults' choices for habitats and ecological patterns reflect in part the niche requirements of immature forms, which should eventually determine the community structure across space.

2. We investigated the extent to which larval trophic niche mediated the effect of forest complexity, landscape type, geographic position and biogeographic region on taxonomic and phylogenetic diversity patterns of adult fruit-feeding butterflies. We also analyzed whether these environmental predictors influenced butterfly spatial patterns independently from trophic niche.

3. We sampled the butterflies with bait traps in 50, 250-m-long transects across 33.41 km² and 10 latitudinal degrees in the Amazon basin, which encompassed four main forest types. We fitted taxonomic and phylogenetic metrics to community-wide measures of larval trophic niche (differentiation and breadth) and environmental gradients in separate mixed effects models.

4. Phylogenetic diversity increased with larval niche differentiation across transects, but did not correlate with measured vegetation and geographic variables. We observed no influence of the environment on niche differentiation. Taxonomic and phylogenetic composition did not correlate with larval niche breadth, but correlated with vegetation, geographic position and biogeographic region. In parallel, trophically specialized communities were associated with contrasting vegetation complexity: open white-sand forests and dense ombrophilous forests.

5. Our study sheds light on how juvenile niche may account for the structure of biological assemblages. Juvenile trophic niche did not act as a mediator of the community-environment relationships investigated, but was itself an important factor underlying adult spatial distribution. This should be helpful in elucidating the causes for the observed distribution of the paramount rainforest biodiversity. We hope to encourage further investigations on how juvenile traits affect species assembly, as this life stage certainly plays a role in ecological adaptation and fitness of species.

Keywords

Biogeographical regions, diet breadth, forest complexity, fruit-feeding butterflies, niche differentiation, phylogenetic diversity.

1. INTRODUCTION

The ecological niche has numerous concepts and interpretations, but can be summarized as the particular extrinsic conditions (e.g. resources, natural enemies) in which species live, their ability to modify such conditions as well as their own traits (e.g. behaviour, physiology) in response, and the eventual function they play in biological communities (Schoener, 2009; Pocheville, 2015). Species that consume similar resources are classically expected to exclude one another, leading ultimately to the local elimination of one of them (“Competitive Exclusion Principle”, Hardin, 1960). Thus, niche differentiation among species is an accredited regulator of coexistence (Chase & Leibold, 2003) and should shape at least partly community and ecosystem dynamics (Leibold & McPeck, 2006). The counterpart for this niche assumption is the neutral perspective, in which species are equivalent to each other and factors involving niche-related attributes and species-species relationships have no significance in shaping diversity patterns; instead, stochastic processes such as ecological drift and dispersal would be important (Hubbell, 2001; Chave, 2004; Tang & Zhou, 2011). Yet, in factual communities, both niche and neutral processes are likely to occur, thus raising the question of the extent to which each process accounts for community structure (Li et al., 2015; Liao et al., 2016).

Besides differentiation, niche breadth may also influence coexistence (e.g. Ashton et al., 2010). Specialized herbivores are often assumed to overcome plant defenses, manipulate hosts and avoid natural enemies more efficiently (Whittaker & Feeny, 1971; Cornell & Hawkins, 2003; Ali & Agrawal, 2012), rendering them better competitors. On the other hand, generalist herbivores may be less susceptible to novel plant compounds, but plant defenses in their usual host spectrum are more toxic than they are to specialists (Ali & Agrawal, 2012). Generalists are also regarded as relatively inefficient resource users (Kunte, 2007) and might thus display lower competitive capacity. Aligned with that, there is evidence that generalists are able to coexist by occupying unique nutritional niches even if they explore the same food source (e.g. grasshoppers, Behmer & Joern, 2008), thus loosening further competitive pressures. Such interactions between specialist and generalist species and bottom-up

controls imposed by plants are likely to affect herbivore community assembly (Price, 2002).

For animals, the dietary of juveniles is crucial for appropriate growth rates, survival and development (Telang & Wells, 2004; Hahn, 2005; Tigreros, 2013; Johnson et al., 2014; Cecere et al., 2016; Mendez-Martínez et al., 2016), and much of the energy necessary for building adult tissues stems from immature nutrient acquirement. In a few cases, juvenile diet may account for nearly the entire energy supply for mating and reproduction in species with non-feeding adults (e.g. Ruszczyk & Carvalho Jr., 1993). Not surprisingly, young dietary niche is reported to associate with ecological spatial patterns. For instance, butterflies with specialized larvae tend to occur in plant-richer environments within (Graça et al., 2016) and between forest types (Graça et al., 2017), whereas larval diet generality increases with altitude (Pellissier et al., 2012). Therefore, the use of diet traits may shed light on patterns of community structure and broad-scale historical processes.

In species-rich tropical forests, habitat and geographic effects are important in modeling biological communities at large-scales (Hoorn et al., 2010; Lamarre et al., 2016). At the habitat level, variables related to vegetation are possibly the most important factors affecting herbivore diversity patterns. Particularly for butterflies, associations with plant species composition (Graça et al. 2016, 2017), vegetation type (Carneiro et al., 2014), forest phenology (Barlow et al., 2007), fragmentation (Ramos, 2000; Uehara-Prado et al., 2007) and land use (Fermon et al., 2005; Martins et al., 2017) have been demonstrated. Geographic distance may also account for differences in species occurrence independently from environmental gradients, and this may result from geographic isolation per se (Dambros et al., 2017) or divergence in the historical origin (Lamarre et al., 2016), e.g. due to major rivers acting as physical barriers for terrestrial organisms (Wallace, 1852; Ribas et al. 2012, but see Santorelli Jr. et al., 2018). However, while many studies have investigated the relative importance of niche processes in driving large-scale diversity patterns in tropical forests, the extent to which resulting patterns are mediated by species traits is not clear.

In this context, our study aims at determining the importance of larval niche differentiation and breadth as mediators of the influence of environmental variables (forest complexity, landscape type, latitude, longitude and biogeographic region) on diversity patterns of adult butterflies in the Amazon rainforest (Fig. 17). Particularly,

we expected that niche differentiation would allow for the occurrence of higher species richness, assuming interspecific competition pressures would be loosened, eventually permitting higher species coexistence (Hardin, 1960; Holt, 2001; Tang & Zhou, 2011). Considering that phylogenetically close species share and feed on closely related host plants (Pellissier et al., 2013), we tested for phylogenetic signal in larval host plant composition and expected increasing niche differentiation among coexisting species to drive phylogenetic overdispersion. Additionally, we tested whether changes in mean niche breadth (specialization vs generalization) of coexisting species would drive shifts in taxonomic and phylogenetic composition. Finally, we verified the influence of environmental variables on both larval trophic niche and diversity measures.

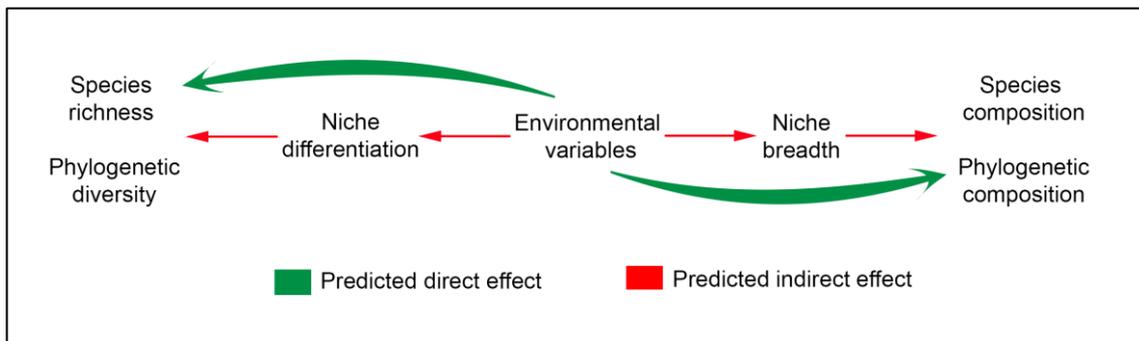


Figure 17. Flow chart indicating the relationships tested to investigate the effect of Amazon environmental variables on butterfly taxonomic and phylogenetic patterns.

2. METHODS

2.1. Study sites

We carried out the study in 50 sampling plots across Viruá National Park (24), BDFFP areas (8), Manaquiri module (10) and Chandless State Park (8). For area descriptions, please refer to page 7.

2.2. Sampling design

Sampling schemes are described on page 10.

2.3. Larval feeding niche and phylogenetic signal

We characterized species trophic niche according to the identity of host plants used by larval butterflies. The information on diet breadth was used to estimate species larval diet breadth, which summarizes the extent of specialization/generalization of species

diet, and interspecific niche differentiation, which indicates the dissimilarity in host use among species. We gathered records of larval hosts from online databases and published sources (Table 4). For butterfly species without records on hosts (~35% of sampled species), we estimated their diet from a congeneric species.

We ranked larval diet breadth taking into account whether they fed: on one plant species (1), on more than one species from the same genus (2), on more than one genus from the same family (3), on more than one family from the same order (4), on more than one order from the same clade (5), and on more than one clade (6) (Graça et al., 2016). For each sampling plot, we then extracted the mean value of larval diet breadth according to the co-occurring species, in which values closer to 1 indicated specialist butterfly communities, whereas those closer to 6 indicated generalist butterfly communities. To control for species richness bias, we performed a null model (Swenson, 2014) with 999 randomizations. The null model generated 999 random species compositions for each sampling plot, from which we extracted 999 random values of community larval diet breadth. Randomizations were done within each site, and species selection was weighted by their prevalence in the site (i.e. number of transects in which a species occurred) to simulate their natural occurrence. Then, we calculated the standardized effect size (SES) by subtracting the mean null value from the observed value, and then dividing the result by the standard deviation of the null values. Positive values indicated communities more generalized than expected by chance, whereas negative values indicated communities more specialized than expected by chance.

Niche differentiation was calculated using a data table with butterfly species in the rows and host plant families in the columns, filled with 0 (not a host) and 1 (host). We extracted the mean Jaccard's distance between species for each sampling unit, as a measure of niche dissimilarity among co-occurring species. These values were also controlled for species richness bias via null models previously described. Here, positive values represented communities whose species were more different in their host use than expected by chance, while negative values represented communities whose species larval hosts overlapped beyond random expectation.

To validate the assumption that closely related species feed on similar host plants, we calculated the magnitude of the phylogenetic signal (Pagel's λ) in host plant composition. In this analysis, we used only the species whose hosts were documented ($n = 63$), and excluded all of those with estimated records ($n = 34$). A

phylogenetic tree was built according to proposed phylogenetic relationships among sampled butterfly species (e.g. Wahlberg et al., 2009; Ortiz-Acevedo & Willmott, 2013; Penz et al., 2012, 2013). Then, the tree was time-calibrated by gathering node ages from papers on systematics and biogeography of the focal lineages (Wahlberg et al. 2009; Matos-Maraví et al., 2013; Penz et al., 2011, 2012, 2015, 2017). Assuming a uniform distribution across the tree, dated nodes (~37% of all nodes) were used to adjust remaining branch lengths with the Branch Length Adjuster (BLADJ) algorithm in Phylocom (Webb et al. 2011-2017). Next, we conducted a Principal Coordinates Analysis (PCoA) using Jaccard's distance in which butterfly species were ordinated according to the host plant families they feed on. Thus, the scores of the first axis (variance explained = 66%) represented butterfly species and their respective distances to one another indicated dissimilarity in host plant composition. Ancestral states for host plant composition were estimated using the Brownian evolution model (Revell, 2012).

2.4. Taxonomic and phylogenetic diversity metrics

For each sampling plot, we obtained two measures from taxonomic (richness and species composition) and phylogenetic dimensions (MPD and phylogenetic composition). To estimate the variation in species composition, we ordinated sampling transects according to the presence/absence of species using Non-Metric Multidimensional Scaling (NMDS). A unidimensional solution of the NMDS ordination indicated the variation in butterfly species composition across our set of assemblages.

Table 4. Ninety-seven species of fruit-feeding nymphalids sampled in the Brazilian Amazon. LDB = Larval diet breadth. Ranks range from 1: more specialized to 6: more generalized, regarding host plant breadth.

| Species | Abundance | | | | LDB | Source for LDB |
|----------------------------------------------|-----------|-------|--------|-----------|-----|-----------------------------------------------------------------------------------|
| | Viruá | BDFFP | BR-319 | Chandless | | |
| Biblidinae | | | | | | |
| <i>Callicore eunomia</i> (Hewitson, 1853) | 0 | 0 | 0 | 1 | 3 | Estimated from <i>C. lyca</i> and <i>C. texa</i> in Janzen & Hallwachs (2009) |
| <i>Catonephele acontius</i> (Linnaeus, 1771) | 3 | 12 | 13 | 0 | 6 | HOSTS |
| <i>Diaethria clymena</i> (Cramer, 1775) | 0 | 0 | 0 | 2 | 6 | HOSTS, Janzen & Hallwachs (2009) |
| <i>Ectima iona</i> E. Doubleday, 1848 | 1 | 2 | 0 | 0 | 2 | Estimated from <i>E. erycinoides</i> in DeVries (1987), Janzen & Hallwachs (2009) |
| <i>Eunica anna</i> (Cramer, 1780) | 1 | 0 | 0 | 0 | 1 | Estimated from <i>E. malvina</i> |
| <i>Eunica bechina</i> (Hewitson, 1852) | 2 | 0 | 0 | 0 | 1 | Estimated from <i>E. malvina</i> |
| <i>Eunica clytia</i> (Hewitson, 1852) | 0 | 0 | 0 | 2 | 1 | Estimated from <i>E. malvina</i> |
| <i>Eunica malvina</i> H. Bates, 1864 | 1 | 0 | 0 | 0 | 1 | DeVries (1987) |
| <i>Eunica mygdonia</i> (Godart, [1824]) | 14 | 0 | 0 | 0 | 1 | DeVries (1987), Janzen & Hallwachs (2009) |
| <i>Eunica orphise</i> (Cramer, 1775) | 0 | 0 | 1 | 0 | 1 | DeVries (1987) |

| | | | | | | |
|---------------------------------------------------------|----|---|----|----|---|---------------------------------------------------------------------------------------------------|
| <i>Eunica sydonia</i> (Godart, [1824]) | 1 | 0 | 0 | 0 | 2 | Janzen & Hallwachs (2009) |
| <i>Eunica veronica</i> H. Bates, 1864 | 1 | 0 | 0 | 0 | 1 | Estimated from <i>E. malvina</i> |
| <i>Hamadryas amphinome</i> (Linnaeus, 1767) | 7 | 0 | 0 | 2 | 3 | DeVries (1987), HOSTS |
| <i>Hamadryas arinome</i> (Lucas, 1853) | 0 | 6 | 3 | 0 | 1 | DeVries (1987), HOSTS |
| <i>Hamadryas chloe</i> (Stoll, 1787) | 1 | 0 | 0 | 2 | 6 | Estimated from <i>H. feronia</i> |
| <i>Hamadryas feronia</i> (Linnaeus, 1758) | 10 | 0 | 0 | 0 | 6 | DeVries (1987), HOSTS |
| <i>Nessaea hewitsonii</i> (C. Felder & R. Felder, 1859) | 2 | 0 | 0 | 0 | 3 | Estimated from <i>N. aglaura</i> in Caterpillar Data Base, HOSTS, Janzen & Hallwachs (2009) |
| <i>Nessaea obrinus</i> (Linnaeus, 1758) | 0 | 0 | 7 | 9 | 3 | Estimated from <i>N. aglaura</i> in Caterpillar Data Base, HOSTS, Janzen & Hallwachs (2009) |
| <i>Paulogramma pyracmon</i> (Godart, [1824]) | 0 | 0 | 0 | 2 | 3 | Beccaloni et al. (2008) |
| <i>Pyrrhogyra crameri</i> Aurivillius, 1882 | 0 | 0 | 0 | 4 | 1 | Estimated from <i>P. otolais</i> |
| <i>Pyrrhogyra otolais</i> H. Bates, 1864 | 0 | 0 | 0 | 4 | 1 | Caterpillar Data Base |
| <i>Temenis laothoe</i> (Cramer, 1777) | 2 | 0 | 6 | 3 | 3 | DeVries (1987) |
| Charaxinae | | | | | | |
| <i>Archaeoprepona amphimachus</i> (Fabricius, 1775) | 0 | 0 | 1 | 0 | 2 | Warren et al. (2013) |
| <i>Archaeoprepona demophon</i> (Linnaeus, 1758) | 5 | 6 | 19 | 14 | 6 | Caterpillar Data Base, HOSTS, Janzen & Hallwachs (2009) |

| | | | | | | |
|-----------------------------------------------------|---|---|---|---|---|-------------------------------------------------------|
| <i>Archaeoprepona demophoon</i> (Hübner, [1814]) | 2 | 3 | 4 | 0 | 5 | DeVries (1987), Janzen & Hallwachs (2009) |
| <i>Fountainea halice</i> (Godart, [1824]) | 0 | 0 | 0 | 4 | 1 | Janzen & Hallwachs (2009) |
| <i>Fountainea ryphea</i> (Cramer, 1775) | 5 | 0 | 0 | 0 | 2 | Caldas (1994), HOSTS |
| <i>Memphis acidalia</i> (Hübner, [1819]) | 2 | 0 | 4 | 0 | 2 | Estimated from <i>M. beatrix</i> in DeVries (1987) |
| <i>Memphis appias</i> (Hübner, [1825]) | 0 | 0 | 0 | 2 | 2 | Estimated from <i>M. xenocles</i> |
| <i>Memphis glauca</i> (C. Felder & R. Felder, 1862) | 0 | 0 | 0 | 3 | 1 | Janzen & Hallwachs (2009) |
| <i>Memphis laertes</i> (Cramer, 1775) | 1 | 0 | 2 | 0 | 2 | Estimated from <i>M. beatrix</i> in DeVries (1987) |
| <i>Memphis leonida</i> (Stoll, 1782) | 0 | 0 | 4 | 2 | 2 | Estimated from <i>M. beatrix</i> in DeVries (1987) |
| <i>Memphis moruus</i> (Fabricius, 1775) | 4 | 0 | 0 | 2 | 6 | HOSTS |
| <i>Memphis oenomais</i> (Boisduval, 1870) | 0 | 0 | 2 | 0 | 2 | DeVries (1987), HOSTS, Janzen & Hallwachs (2009) |
| <i>Memphis phantes</i> (Hopffer, 1874) | 0 | 2 | 0 | 0 | 5 | Estimated from <i>M. cleomestra</i> in DeVries (1987) |
| <i>Memphis philumena</i> (E. Doubleday, [1849]) | 0 | 0 | 0 | 4 | 2 | Estimated from <i>M. oenomais</i> |
| <i>Memphis polycarmes</i> (Fabricius, 1775) | 2 | 0 | 2 | 0 | 5 | Estimated from <i>M. cleomestra</i> in DeVries (1987) |

| | | | | | | |
|----------------------------------------------------------------|-----|----|---|---|---|-------------------------------------------------------------------------|
| <i>Memphis xenocles</i> (Westwood, 1850) | 0 | 0 | 0 | 2 | 2 | DeVries (1987) |
| <i>Mesoprepona pheridamas</i> (Cramer, 1777) | 2 | 0 | 0 | 0 | 6 | Estimated from <i>Prepona laertes</i> |
| <i>Prepona claudina</i> (Godart, [1824]) | 1 | 0 | 6 | 0 | 6 | HOSTS |
| <i>Prepona dexamenus</i> Hopffer, 1874 | 2 | 0 | 2 | 0 | 6 | Estimated from <i>Prepona laertes</i> |
| <i>Prepona laertes</i> (Hübner, [1811]) | 4 | 0 | 2 | 2 | 6 | DeVries (1987), HOSTS, Janzen & Hallwachs (2009) |
| <i>Prepona narcissus</i> (Staudinger, [1885]) | 0 | 6 | 0 | 0 | 6 | Estimated from <i>Prepona claudina</i> |
| <i>Zaretis isidora</i> (Cramer, 1779) | 0 | 0 | 0 | 6 | 3 | Janzen & Hallwachs (2009) |
| <i>Zaretis itys</i> (Cramer, 1777) | 0 | 2 | 6 | 2 | 6 | Caterpillar Data Base, DeVries (1987), HOSTS, Janzen & Hallwachs (2009) |
| Nymphalinae | | | | | | |
| <i>Baeotus aeilus</i> (Stoll, 1780) | 0 | 2 | 5 | 0 | 3 | Estimated from <i>Historis</i> |
| <i>Colobura annulata</i> Willmott, Constantino & J. Hall, 2011 | 0 | 0 | 0 | 2 | 2 | Willmott et al. (2001) |
| <i>Colobura dirce</i> (Linnaeus, 1758) | 1 | 0 | 0 | 5 | 6 | HOSTS, Janzen & Hallwachs (2009), Willmott et al. (2001) |
| <i>Historis acheronta</i> (Fabricius, 1775) | 426 | 6 | 0 | 0 | 6 | DeVries (1987), HOSTS |
| <i>Historis odius</i> (Fabricius, 1775) | 2 | 0 | 0 | 0 | 6 | Caterpillar Data Base, DeVries (1987), HOSTS |
| <i>Tigridia aesta</i> (Linnaeus, 1758) | 1 | 18 | 5 | 2 | 3 | Caterpillar Data Base, DeVries |

(1987), Janzen & Hallwachs (2009)

Satyrinae

| | | | | | | |
|---------------------------------------------------|----|----|----|---|---|---------------------------------------------------------------------------------|
| <i>Bia actorion</i> (Linnaeus, 1763) | 3 | 0 | 3 | 0 | 3 | Freitas et al. (2002) |
| <i>Caeruleptychia coelestis</i> (A. Butler, 1867) | 4 | 0 | 0 | 4 | 4 | Estimated from <i>Magneptychia libye</i> |
| <i>Caeruleptychia romani</i> (Aurivillius, 1929) | 0 | 0 | 0 | 1 | 4 | Estimated from <i>Magneptychia libye</i> |
| <i>Catoblepia berecynthia</i> (Cramer, 1777) | 0 | 2 | 10 | 2 | 3 | HOSTS |
| <i>Catoblepia versitincta</i> Stichel, 1901 | 0 | 0 | 8 | 0 | 3 | Estimated from <i>Catoblepia</i> in Penz et al. (1999) |
| <i>Catoblepia xanthus</i> (Linnaeus, 1758) | 0 | 22 | 2 | 0 | 3 | Penz et al. (1999) |
| <i>Chloreptychia agatha</i> (A. Butler, 1867) | 0 | 0 | 2 | 0 | 5 | Estimated from <i>C. arnaca</i> in Caterpillar Data Base, DeVries (1987), HOSTS |
| <i>Chloreptychia chlorimene</i> (Hübner, [1819]) | 1 | 0 | 2 | 0 | 5 | Estimated from <i>C. arnaca</i> |
| <i>Chloreptychia herseis</i> (Godart, [1824]) | 1 | 0 | 4 | 0 | 5 | Estimated from <i>C. arnaca</i> |
| <i>Cissia palladia</i> (A. Butler, 1867) | 1 | 0 | 0 | 0 | 3 | DeVries (1987) |
| <i>Cissia terrestris</i> (A. Butler, 1867) | 19 | 0 | 0 | 0 | 4 | Estimated from <i>C. palladia</i> |
| <i>Eryphanis automedon</i> (Cramer, 1775) | 1 | 0 | 0 | 0 | 1 | Penz et al. (1999) |
| <i>Harjesia blanda</i> (Möschler, 1877) | 0 | 0 | 0 | 1 | 3 | Estimated from <i>Fosterinaria necys</i> |

| | | | | | | |
|--------------------------------------------------------|---|---|---|---|---|----------------------------------------------------------------------------------------|
| | | | | | | in HOSTS |
| <i>Magneuptychia fugitiva</i> Lamas, [1997] | 1 | 0 | 0 | 0 | 4 | Estimated from <i>Magneuptychia libye</i> in DeVries (1987), Janzen & Hallwachs (2009) |
| <i>Magneuptychia ocnus</i> (A. Butler, 1867) | 1 | 0 | 0 | 0 | 4 | Estimated from <i>Magneuptychia libye</i> |
| <i>Magneuptychia ocypete</i> (Fabricius, 1776) | 6 | 0 | 0 | 0 | 4 | Estimated from <i>Magneuptychia libye</i> |
| <i>Manataria hercyna</i> (Hübner, [1821]) | 0 | 0 | 0 | 2 | 2 | HOSTS |
| <i>Morpho achilles</i> (Linnaeus, 1758) | 0 | 0 | 2 | 6 | 3 | HOSTS |
| <i>Morpho deidamia</i> (Hübner, [1819]) | 0 | 0 | 0 | 2 | 1 | DeVries (1987), Feltwell (1993) |
| <i>Morpho hecuba</i> (Linnaeus, 1771) | 0 | 1 | 0 | 0 | 3 | Estimated from <i>M. hercules</i> in HOSTS |
| <i>Morpho helenor</i> (Cramer, 1776) | 0 | 0 | 0 | 4 | 6 | DeVries (1987), Janzen & Hallwachs (2009) |
| <i>Morpho rhetenor</i> Cramer, 1775) | 2 | 0 | 0 | 0 | 6 | HOSTS |
| <i>Narope cyllabarus</i> Westwood, 1851 | 0 | 0 | 0 | 2 | 2 | Penz et al. (1999) |
| <i>Opoptera hilaris</i> Stichel, 1901 | 0 | 0 | 0 | 2 | 1 | Estimated from <i>O. aorsa</i> in Penz et al. (1999) |
| <i>Opsiphanes cassina</i> C. Felder & R. Felder, 186 2 | 0 | 0 | 2 | 0 | 3 | Penz et al. (1999) |

| | | | | | | |
|-------------------------------------------------------|----|----|----|----|---|---------------------------------------------------------------|
| <i>Opsiphanes invirae</i> (Hübner, [1808]) | 32 | 28 | 22 | 6 | 5 | DeVries (1987), HOSTS, Penz et al. (1999) |
| <i>Opsiphanes quiteria</i> (Stoll, 1780) | 4 | 0 | 4 | 6 | 3 | Penz et al. (1999) |
| <i>Paryphthimoides ca argulus</i> | 7 | 0 | 0 | 0 | 3 | Estimated from <i>P. eous</i> in HOSTS |
| <i>Paryphthimoides difficilis</i> Forster, 1964 | 0 | 0 | 0 | 4 | 3 | Estimated from <i>P. eous</i> |
| <i>Paryphthimoides</i> sp. | 8 | 0 | 0 | 0 | 3 | Estimated from <i>P. eous</i> |
| <i>Pierella hortona</i> (Hewitson, 1854) | 0 | 0 | 1 | 1 | 3 | Estimated from <i>P. hyalinus</i> in DeVries (1987) |
| <i>Pierella lena</i> (Linnaeus, 1767) | 2 | 0 | 0 | 0 | 3 | Estimated from <i>P. hyalinus</i> |
| <i>Posttaygetis penelea</i> (Cramer, 1777) | 2 | 0 | 0 | 0 | 3 | Estimated from <i>Fosterinaria necys</i> in HOSTS |
| <i>Pseudodebis euptychidia</i> (A. Butler, 1868) | 0 | 0 | 0 | 29 | 2 | Estimated from <i>P. yphthima</i> in HOSTS |
| <i>Pseudodebis marpessa</i> (Hewitson, 1862) | 0 | 0 | 0 | 3 | 1 | Estimated from <i>P. celia</i> in Janzen & Hallwachs (2009) |
| <i>Pseudodebis valentina</i> (Cramer, 1779) | 1 | 0 | 0 | 4 | 1 | Estimated from <i>P. celia</i> in Janzen & Hallwachs (2009) |
| <i>Taygetis cleopatra</i> C. Felder & R. Felder, 1867 | 12 | 2 | 1 | 2 | 4 | Estimated from <i>T. thamyra</i> in Janzen & Hallwachs (2009) |
| <i>Taygetis echo</i> (Cramer, 1775) | 1 | 0 | 0 | 2 | 4 | Estimated from <i>T. thamyra</i> |

| | | | | | | |
|---------------------------------------------------|---|---|---|----|---|--------------------------------------------------|
| <i>Taygetis laches</i> Fabricius, 1793 | 3 | 0 | 0 | 0 | 5 | DeVries (1987), HOSTS, Janzen & Hallwachs (2009) |
| <i>Taygetis larua</i> C. Felder & R. Felder, 1867 | 0 | 0 | 0 | 3 | 3 | Estimated from <i>T. mermeria</i> |
| <i>Taygetis mermeria</i> (Cramer, 1776) | 0 | 0 | 0 | 5 | 3 | DeVries (1987) |
| <i>Taygetis sylvia</i> H. Bates, 1866 | 0 | 0 | 0 | 10 | 3 | Estimated from <i>T. sosis</i> |
| <i>Taygetis sosis</i> Hopffer, 1874 | 5 | 0 | 0 | 0 | 2 | DeVries (1983) |
| <i>Taygetis virgilia</i> (Cramer, 1776) | 0 | 0 | 0 | 17 | 2 | HOSTS |
| <i>Ypthimoides renata</i> (Stoll, 1780) | 3 | 0 | 0 | 0 | 3 | DeVries (1987) |
| <i>Ypthimoides</i> sp. | 1 | 0 | 0 | 0 | 3 | Estimated from <i>Y. renata</i> |

To characterize the phylogenetic component of communities, we built a second phylogenetic tree (Fig. 18), this time including all species collected in our system. We calculated the mean pairwise distance (MPD) of each sampling unit. We performed null models to account for bias introduced by differences in species richness by randomizing the phylogenetic tree tips 999 times and then calculating the SES, as described previously (Swenson 2014). Higher MPD values represented communities with species relatively distant in the phylogenetic tree (i.e. higher phylogenetic diversity). We also calculated the phylogenetic dissimilarity among sampling plots by estimating the proportion of shared evolutionary history (branch lengths) of their respective species. Most metrics of phylogenetic dissimilarity (distance- and tree-based) are tightly correlated, so we opted for a fast-computing pairwise measure (Swenson, 2014). We used the resulting pairwise matrix in NMDS to obtain one ordination axis, in which scores represented species composition, weighted by their phylogenetic relatedness (i.e. the higher the phylogenetic distance between species from different communities, the higher the dissimilarity between them). We refer to this measure as phylogenetic composition.

2.5. Environmental variables

We used five environmental variables as predictors for the butterfly diversity patterns: forest complexity, landscape type (continuous/fragmented), latitude, longitude and biogeographic region. We gathered information on vegetation from the Brazilian Institute for Geography and Statistics (IBGE, 2012) and the Program for Biodiversity Research (PPBio) website (<https://ppbio.inpa.gov.br>). We coded a quantitative metric of vegetation complexity based on canopy cover, tree density and light levels at understory level observed in the field. Hence, we obtained four increasing levels of vegetation complexity: open white-sand forest (1), closed white-sand forest (2), open ombrophilous forest (3) and dense ombrophilous forest (4).

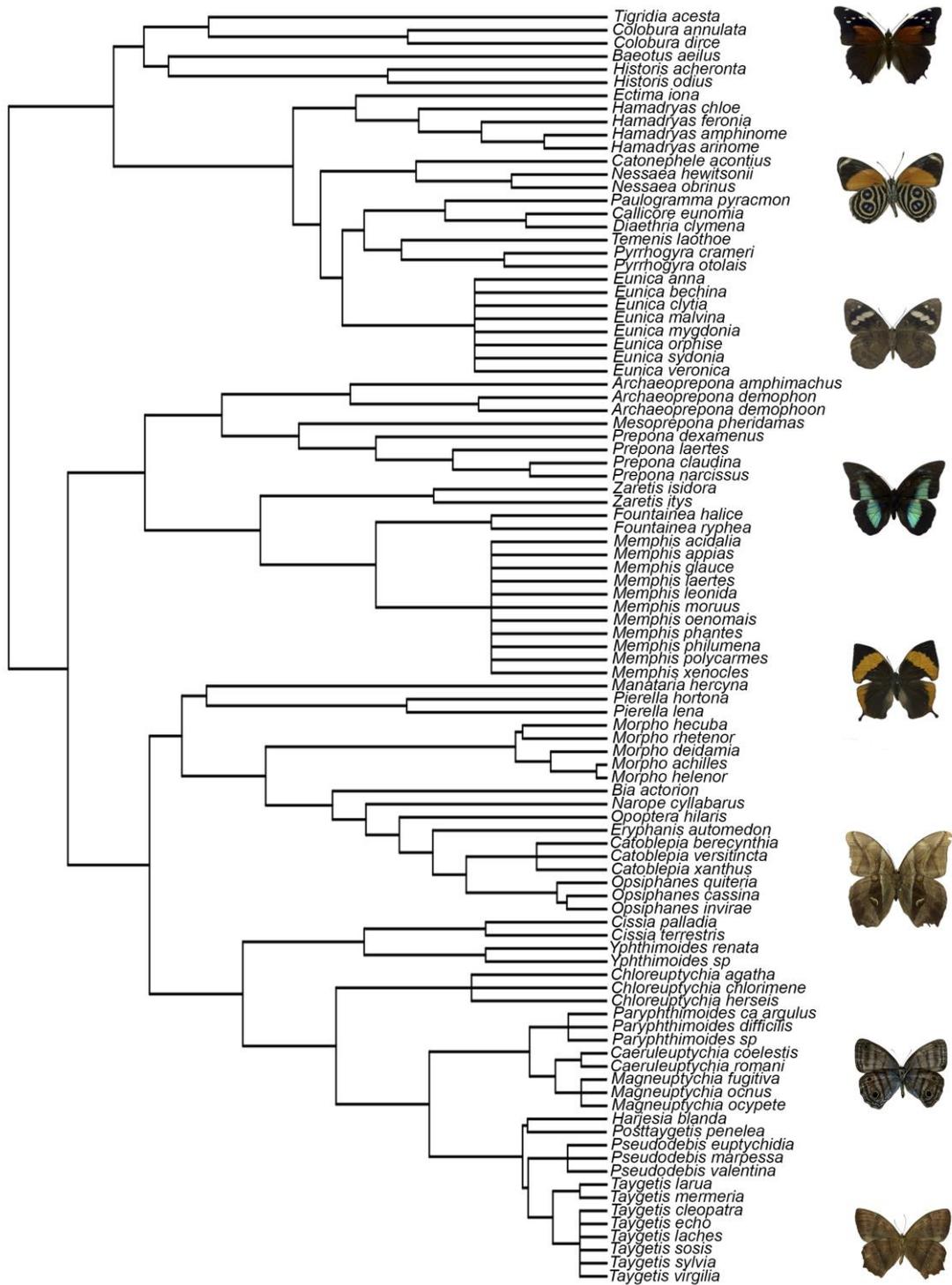


Figure 18. Phylogenetic tree containing all 97 studied butterfly species used to calculate metrics of phylogenetic diversity.

Because there were fragments of dense ombrophilous forests in our sample, we added the binary co-variable landscape type to the models to control for any confounding effects. We also used the PPBio repository to obtain data on latitude and longitude of each plot in Viruá, Manaquiri and Chandless, while those from the remaining areas were obtained from geographic coordinate software. Finally, we had transects in Guiana and Inambari biogeographic regions (*sensu* Wallace, 1852; Ribas et al., 2012; Santorelli Jr. et al., 2018), and this was coded as a binary variable.

2.6. Data analysis

Correlograms showed spatial autocorrelation at the level of sites in our data (Fig. 19). Thus, we used linear mixed effects models with site as a random factor. The first part of our analysis tested whether the environment explained the variation in species composition, richness, phylogenetic composition and diversity indirectly, *i.e.* via niche traits (red arrows, Fig. 17). To do so, we firstly fitted separate models with average larval diet breadth per plot as predictor variable versus species and phylogenetic composition as response variables. Secondly, we investigated whether niche differentiation influenced species richness and phylogenetic diversity (MPD). Lastly, we fitted two mixed effects models with the five environmental variables simultaneously to average larval diet breadth then to niche differentiation. In these models, we included a quadratic term for the predictor variables in order to identify any non-linear associations.

The second part of the analysis aimed at unraveling the direct effects of each environmental factor on butterfly species and phylogenetic patterns (green arrows, Fig. 17). Thus, we fitted four mixed effects models with the five predictors simultaneously to species richness, species composition, phylogenetic diversity and phylogenetic composition. Model predictive power was defined as the squared correlation between observed and predicted values. In these models, we also included quadratic terms for the explanatory variables.

We conducted all analyses in the statistical software R version 3.3.3. (R Development Core Team, 2017). We used packages *vegan* 2.3-5 (Oksanen et al., 2016) for ordination methods, *picante* 1.6-2 (Kembel et al., 2014) for calculating MPD, *ape* 3.5 (Paradis et al., 2016) for coding and plotting the phylogenetic tree, *phytools* 0.6-44 (Revell, 2017) for estimating phylogenetic signal and plotting the trait evolution tree, *nlme* 3.1-131 (Pinheiro et al., 2017) for running mixed effects models

and visreg 2.4-1 (Breheny & Burchett, 2017) for conditional plots (i.e. relationship between response and each predictor while holding remaining predictors at their means).

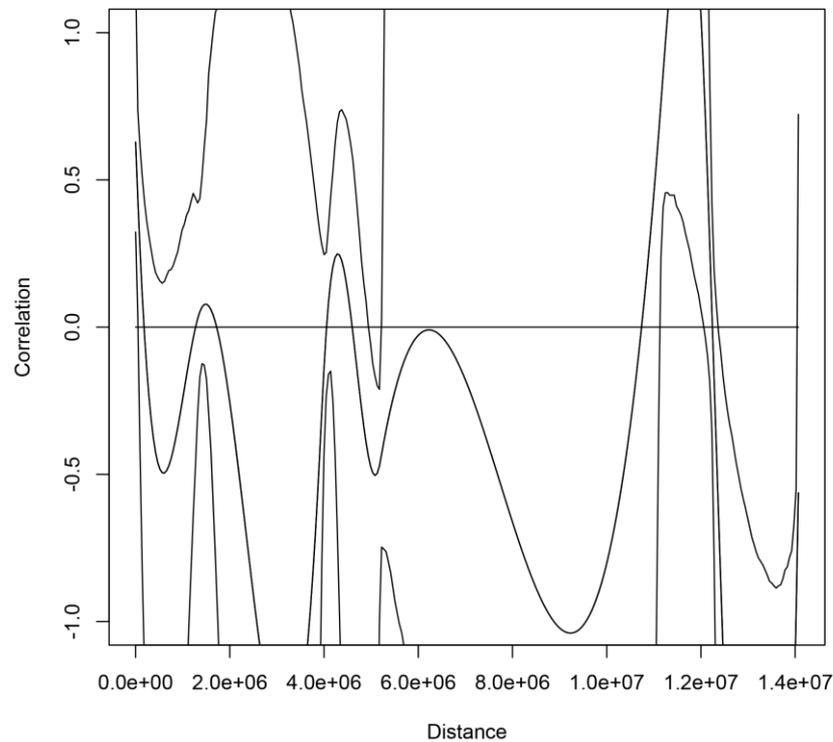


Figure 19. Correlogram evidencing the spatial autocorrelation among sampling units.

3. RESULTS

We collected 1105 butterflies, belonging to 97 species and all four frugivorous Nymphalidae subfamilies (Table 4). We found a strong phylogenetic signal in host plant composition ($\lambda = 0.99$, $p < 0.001$, Fig. 20), which corroborates that closely related species tend to share host plant families more often than distantly related ones. In this particular case, phylogenetic relatedness was a good indicator of similarity in niche.

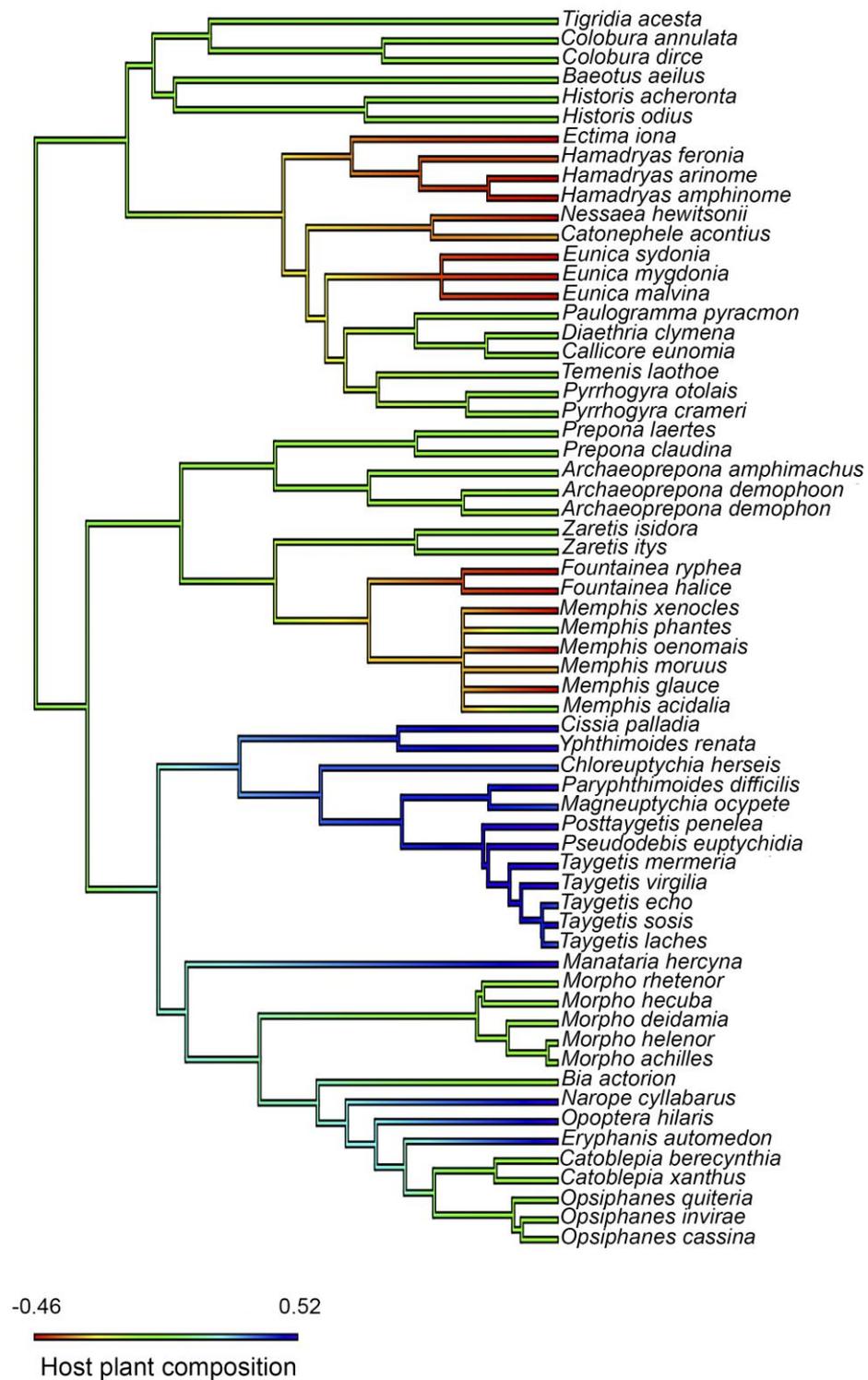


Figure 20. Pattern of evolutionary divergence in host plant composition across the studied butterfly lineages, showing strong phylogenetic signal. Similar color shades indicate similarity in host plant composition. Numeric range represents the ordination scores (PCoA Axis).

3.1. Indirect effect (via trophic niche)

We firstly investigated the indirect effect of the environment on butterfly taxonomic and phylogenetic diversity, using larval niche as a mediator. Our results showed that niche differentiation was a marginally significant predictor for variation in species richness ($t_{41, 49} = -1.866, p = 0.069$), and significantly increased with phylogenetic diversity ($t_{41, 47} = 8.144, R^2 = 0.60, p > 0.001$, Fig. 21). Conversely, larval diet breadth did not correlate with either species ($t_{41, 49} = -0.187, p = 0.851$) or phylogenetic composition ($t_{41, 49} = 0.126, p = 0.899$).

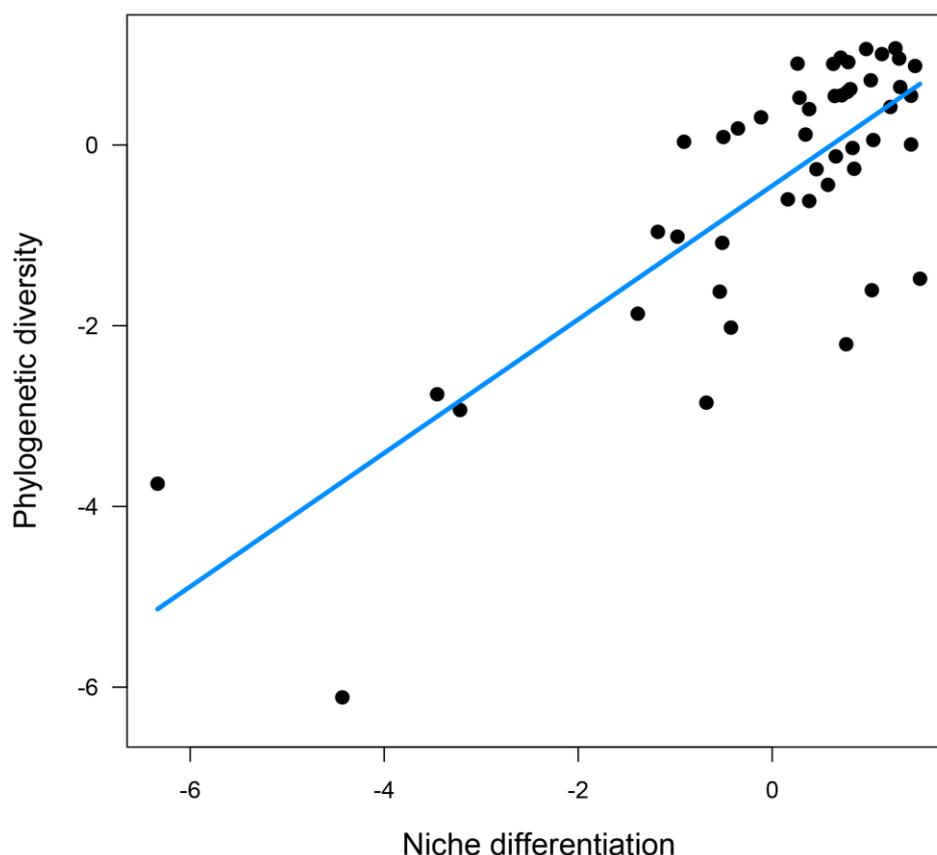


Figure 21. The positive influence of larval niche differentiation on butterfly phylogenetic diversity.

We detected a significant influence of forest complexity on larval diet breadth ($t_{38, 47} = 5.210, R^2 = 0.25, p = 0.032$, Fig. 22), but not on niche differentiation ($t_{38, 47} = 1.589, p = 0.124$). The former relationship was unimodal, and generalist communities were mainly found in vegetation with intermediate complexity (closed white-sand forest and open ombrophilous forest), whereas specialist communities were

concentrated on both ends of the vegetation complexity gradient (open white-sand forests and dense ombrophilous forests). Geographic position and biogeographic region did not predict changes in either larval diet breadth or niche differentiation.

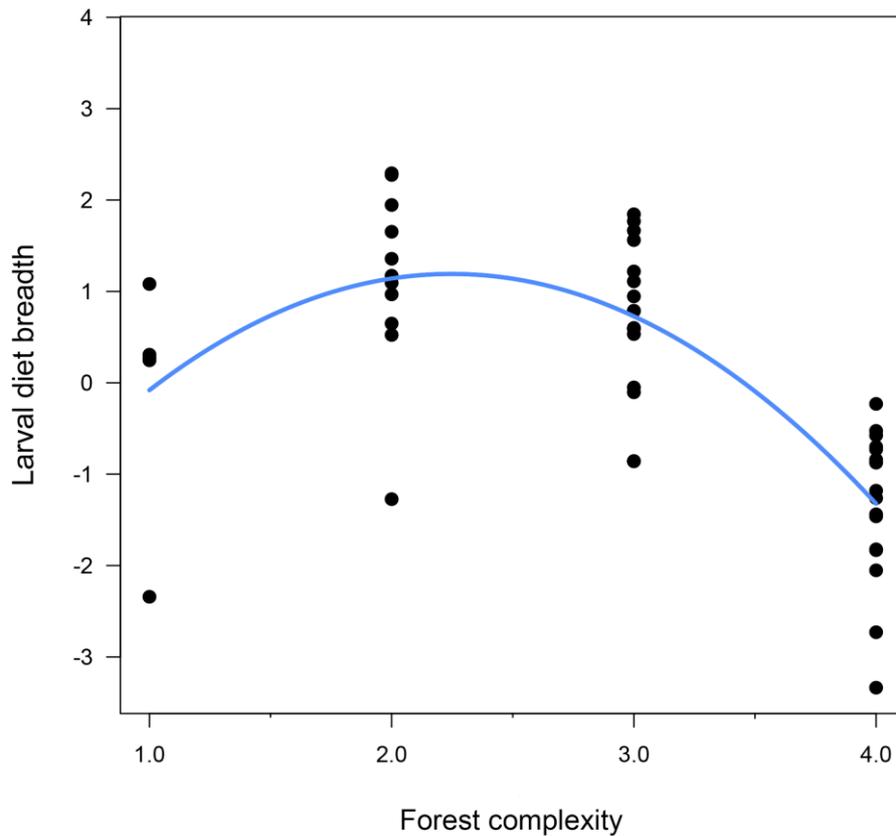


Figure 22. Unimodal relationship between larval diet breadth and forest complexity in Amazonia, in which lowly and highly complex landscapes tended to contain more specialized butterfly communities on average.

3.2. Direct effect

We did not observe any influence of the environmental variables on butterfly species richness or on phylogenetic diversity. On the other hand, butterfly species composition varied strongly with forest complexity ($t_{40, 50} = -4.459$, $p < 0.001$), latitude ($t_{40, 50} = -2.468$, $p = 0.018$), longitude ($t_{40, 50} = 3.678$, $p < 0.001$) and biogeographic region ($t_{4, 50} = -3.112$, $p = 0.035$) (Fig. 23). Together, the four predictors explained around 69% of the variation in butterfly species composition. Variation in phylogenetic composition was also triggered by forest complexity ($t_{40, 50} = 4.516$, $p = 0.001$) latitude ($t_{40, 50} = 2.923$, $p = 0.005$) and longitude ($t_{40, 50} = -4.398$, $p = 0.001$) (Fig. 24), whose model had overall explanatory power around 44%. In

particular, the southwestern site (lower latitude and longitude) contained communities phylogenetically more similar to each other than to the other sites.

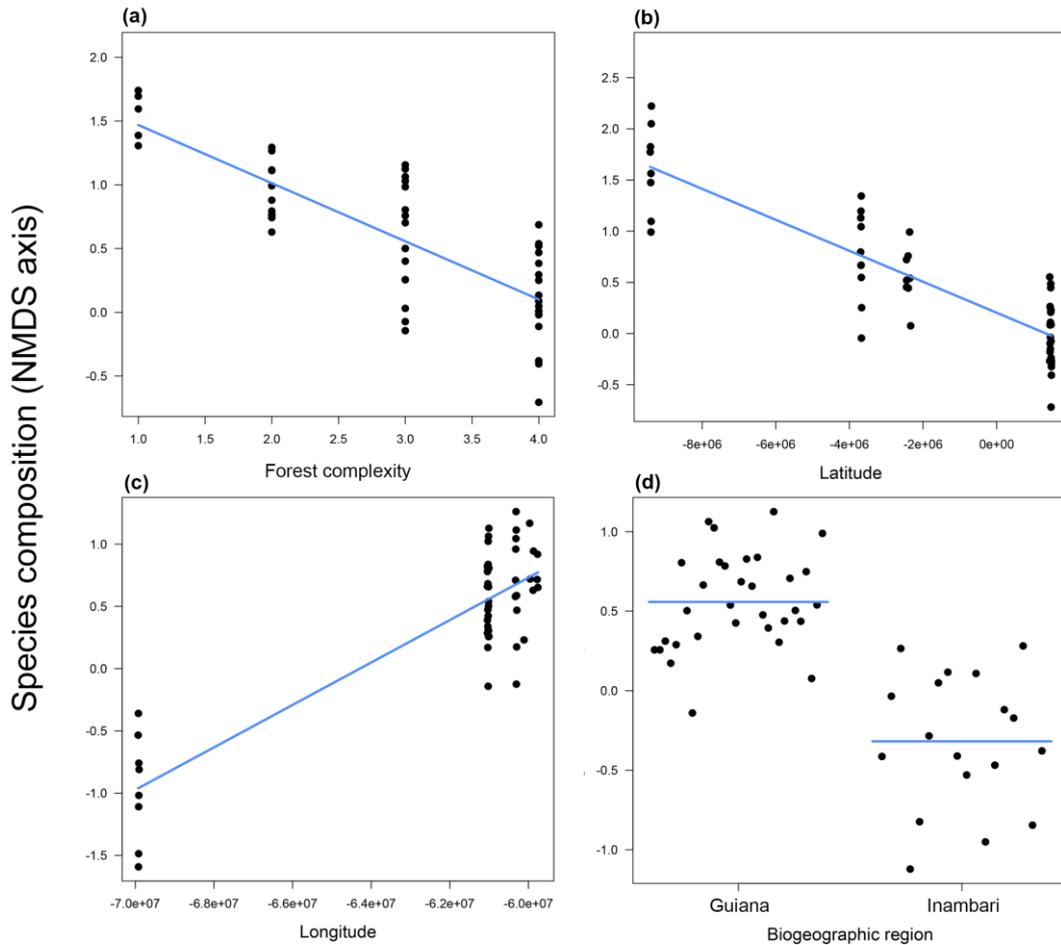


Figure 23. The response of variation in butterfly species composition (first NMDS axis) to all four Amazonian predictors tested: (a) forest complexity; (b) latitude; (c) longitude; (d) biogeographical region.

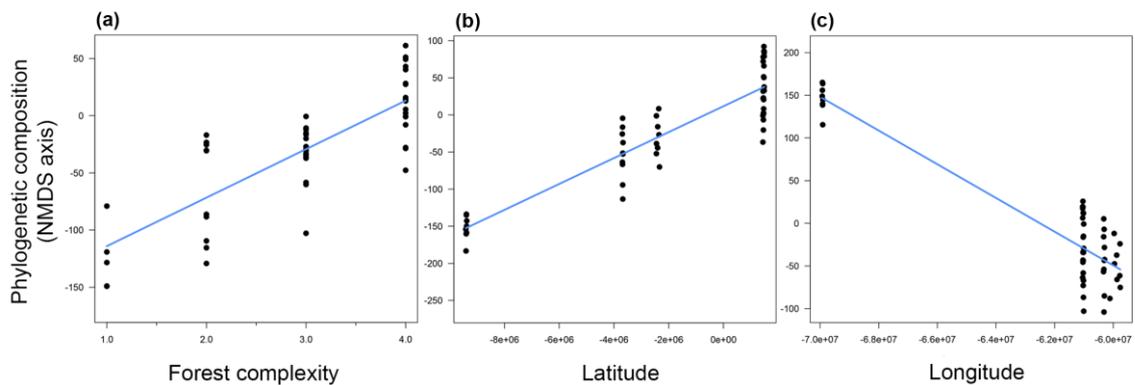


Figure 24. Effect of forest complexity (a) and geographic position (b, c) in Amazonia on butterfly phylogenetic composition.

4. DISCUSSION

Our study focused on juvenile trophic niche (overlap and breadth) as cornerstone for species coexistence in the adult stage and community assembly across wide spatial scales. There is evidence that species occurrence is correlated with juvenile feeding niche (Curtis et al., 2015; Graça et al., 2017) and performance (Bell & Stoka, 2012), suggesting that adult choice for habitats mirrors early stages' requirements as well. To address this issue, we used a dominant group of herbivores in tropical forests as models: butterflies.

4.1. Indirect effect of environmental predictors on butterfly distribution

Niche differentiation was a weak predictor for species richness. Further, and contrary to our expectation, this relationship was negative, as species richness tended to decrease with increasing niche differentiation. This pattern suggests that proximity in larval niche actually accounts for a higher number of coexisting species, thus at first contesting the Competitive Exclusion Principle (Hardin, 1960). On the other hand, the prediction that phylogenetic diversity would increase with niche differentiation was significantly supported (Fig. 21). Communities with little niche overlap on average contained distantly related species, and very few communities contained large niche overlap. In this case, as host plant composition was constrained by phylogeny (Fig. 20), congener spatial exclusion may occur via ecological similarity. Two main reasons led us to consider that host similarity limits coexistence. First, female butterflies prefer to lay eggs on undamaged plants due to direct resource competition (Shiojiri et al., 2015), thus they might avoid colonizing habitats with congeners. Second, depending on the level of damage inflicted by herbivores, plants may emit volatile chemicals to attract the infesters' parasitoids (van Poecke et al., 2003), which is important given that parasitoids often associate with closely related hosts (Korenko et al., 2011; Desneux et al., 2012), undermining the odds of survival for both sibling groups. Therefore, larval niche overlap may negatively affect closely related species, eventually driving adult phylogenetic overdispersion, contrary to the evidence of weak interspecific competition among closely related chewing phytophagous insects (Kaplan & Denno, 2007). Further, Nakadai et al. (2018) suggested that co-occurrence of butterflies in islands is more affected by filtering on larval resource niche than by competition. Because our study involves communities in mainland landscapes, this

may suggest that butterfly co-existence may undergo distinct dynamics between continental and insular landscapes.

No effect of forest complexity on phylogenetic diversity was encountered ($P = 0.321$), diverging from Lamarre et al. (2016), who detected overall phylogenetic overdispersion of lepidopterans (butterflies and moths) in white-sand forests of French Guiana and Peru. Such divergence stresses the impact of taxonomic coverage on community assembly community, since we surveyed butterfly assemblages only. On the other hand, the lack of associations between vegetation and phylogenetic diversity of fruit-feeding butterflies was reported at a local scale in northern Amazonia (Graça et al. 2017), and even after adding dense ombrophilous forest plots to our analyses, no pattern emerged.

Surprisingly, larval diet breadth did not explain variation in species composition as reported previously for ombrophilous forests (Graça et al., 2016), but the regional scope of our study, which includes other vegetation types, may have resulted in the non-significant effect. Vegetation complexity nonetheless triggered a unimodal variation in larval diet breadth, with specialist communities occurring in both simplified and complex forest types (Fig. 22). White-sand forests are harsh habitats, with low plant diversity, low quantity of nutrients, high temperatures and periodical flood regime (Baraloto et al., 2011; do Vale et al., 2014; Guevara et al., 2016), and open white-sand habitats portray the extreme of such conditions, such as wetter soil and higher solar incidence (Coomes & Grubb, 1996; Graça et al., 2017). In addition, white-sand plants are acknowledged herbivory-resistant for having evolved high levels of sclerophylly (Fine et al., 2006; Fortunel et al., 2014) and many lineages are endemic to such habitats (Fine et al., 2010; Guevara et al., 2016). For that reason, few very specialized herbivores should be able to explore them as resource (Lamarre et al., 2016), thus rendering overall communities more specialized. Yet, these communities contained on average less specialist butterflies than those in dense ombrophilous forests, which harboured the most specialized butterfly communities in our system. As previously conveyed (Coley & Aide, 1991; Graça et al., 2016), plant-richer environments may have favoured herbivore specialization as a means of alleviating competition within plant hosts. This is consistent with the assumption that despite the strong filters imposed by white-sand vegetation on herbivore diet, sites with higher plant diversity (herbivore hosts) still accounts for greater levels of herbivore specialization (Graça et al., 2017).

We are aware of possible shortcomings regarding our metric of larval diet breadth, mostly due to rough categorization and neglect of intraspecific variation (see Swenson, 2013). This is a common problem faced when studying functional traits, especially in diverse regions, such as the tropics, and diverse groups, such as insects. In this light, obtaining individualized and quantitative metrics of species traits in some communities may be impractical in face of money and time constraints (Swenson, 2013). Accordingly, we believe our measure of diet breadth more likely loses information that would strengthen the encountered patterns (type II error) than conjures inexistent relationships.

4.2. Direct effect of environment predictors on butterfly distribution

Forest complexity governed variation in butterfly species (Fig. 23a) and phylogenetic composition (Fig. 24a). Not only vegetation structure and composition defines larval host availability and quality (Blau, 1980), it directly regulates abiotic elements, such as sunlight incidence (Montgomery & Chazdon, 2001; Graça et al., 2017). Different groups of butterflies respond distinctively to such biotic and abiotic effects of vegetation change, due to species-specific habitat preferences (Willott et al., 2000; Hamer et al., 2003; Pardonnet et al., 2013), which thus contributes to the turnover in taxonomic composition and may be filtering species with shared evolutionary histories. For example, we found out that *Manataria hercyna*, whose genus is a bamboo feeder (DeVries, 1987), was associated with bamboo-dominated habitats, while many phylogenetically close biblidines such as *Callicore eunomia*, *Diaethria clymena*, *Paulogramma pyracmon* and *Pyrrhogyra* spp. occurred only in open ombrophilous forests.

Geographic position accounted for variation in species (Fig. 23b, 23c) and phylogenetic composition between sites (Fig. 24b, 24c). Sampling plots in the southwestern region harboured strikingly distinct species composition and were phylogenetically more similar to each other. While these patterns may simply imply the importance of unmeasured variables, such geographical isolation may result from historical events of the area. For instance, the structure of soils in southwestern Amazon has been under strong Andean geology influence (Latrubesse et al., 1997), differing from the characteristic Amazon soils (Gama et al., 1997; Daly et al., 2006). These peculiarities gave rise to the establishment of unique phytophysionomies, such as extensive bamboo-dominated stands and *salão* formations (Daly et al., 2006;

Griscom et al., 2007), which likely affected herbivore colonization. Alternatively, range occurrence may link to species-specific dispersal constraints. Butterflies are active dispersers, but factors such as morphology, sex and mating behaviour particular to each species interfere in dispersal capacity (Tufto et al., 2012; Penz et al., 2015), rendering some species more stationary than others.

The Amazon River separates the Guiana and Inambari biogeographic regions in Central Amazon and seemingly reflects the separation in the species composition of butterfly communities (Fig. 23d). We have not analyzed genetic drift or phylogeography of any butterfly population, thus implying events regarding speciation processes would be erroneous. Nevertheless, studies demonstrated that while the Amazon River may not function as a barrier for species with enhanced dispersal skills (e.g. *Morpho*, Penz et al., 2015), for less dispersive species, it might have driven allopatry at its largest widths (e.g. Central Amazon) between populations from each margin (e.g. *Bia*, Penz et al., 2017). This may be an ongoing process in the taxonomically and phylogenetically similar communities in BDFFP areas (northern margin) and Manaquiri (southern margin) for example, but detailed phylogeographic examinations are indispensable to identify evolutionary divergence between riverbanks.

4.3. Concluding remarks

Larval niche differentiation influenced phylogenetic diversity of butterfly communities, but was not influenced by the environment. Contrariwise, larval niche breadth did not explain variation in species or phylogenetic composition, but was driven by environment and geographic gradients. Measured predictors directly explained variation in butterfly species and phylogenetic composition. We therefore conclude that while butterfly larval niche is indeed important for adult spatial distribution, it does not mediate the environmental influence on taxonomic and phylogenetic structure of communities. Rather, other functional traits are likely mediating the effect of vegetation, geographic position or biogeographical region on butterfly diversity. Additionally, community taxonomic composition was significantly different between biogeographic regions, which highlights that policies should consider the biogeographical background when electing priority conservation areas. We ultimately hope our results provide the foundation and the encouragement for

further investigations regarding the role of juvenile functional traits on species assembly.

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SÍNTESE E CONSIDERAÇÕES FINAIS

O intento da presente tese foi determinar fatores que dirigem a ocorrência espacial de assembleias de borboletas frugívoras no bioma Amazônico. A nível de microhábitat, verificamos que a morfologia do voo (razão asa-tórax) está ligada à segregação de espécies entre dossel e sub-bosque, de modo que espécies com corpo mais robusto e maior capacidade de voo habitam preferencialmente o dossel florestal. Essa associação parece ter ocorrido por radiação adaptativa com o surgimento de novos nichos ecológicos durante a estruturação das florestas tropicais. Além disso, machos e fêmeas apresentam dimorfismo sexual acentuado quanto à morfologia de voo, com machos investindo relativamente mais em voo do que fêmeas, o que pode estar refletindo trade-offs fisiológicos entre voo e reprodução. Por fim, detectamos que espécies habitantes do sub-bosque possuem um dimorfismo sexual mais acentuado do que espécies de dossel. A nível local, foi demonstrado que a mudança de florestas ombrófilas de solo argiloso para florestas de areia amazônicas gera um trade-off entre abundância e riqueza de borboletas frugívoras. As campinas são dominadas principalmente por *Historis acheronta*, possivelmente refletindo a tolerância dessa espécie a condições de alta temperatura e ressecamento, bem como a sua capacidade de explorar os recursos de produtividade primária abundantes nesses locais. Futuros estudos com essa espécie em particular são necessários para elucidar seus mecanismos adaptativos. Não somente, essa variação ambiental afeta características intrínsecas das borboletas, como comprimento da asa e razão asa-tórax, o que indica que a instabilidade da paisagem tende a selecionar espécies com maior capacidade de voo e dispersão. É possível que esses traços funcionais sejam os mediadores para a ocorrência de espécies particulares entre as diferentes fitofisionomias da Amazônia. Ao investigar a segregação espacial a nível regional, foi possível observar que a vegetação (variável local) ainda determina a estruturação taxonômica e filogenéticas das assembleias de borboletas frugívoras. Variações nos padrões de diversidade de borboletas não explicadas pela vegetação podem ser atribuídas à posição geográfica das comunidades, bem como à biogeografia, visto que pudemos detectar uma diferença significativa entre as faunas da região Guiana e Inambari. Adicionalmente, o nicho trófico larval é um fator importante para determinar a coexistência entre espécies, porém não serve como mediador para a influência dos gradientes locais ou regionais nas assembleias de borboletas frugívoras. Nossos resultados tratam de três

escalas espaciais distintas, desde o nível de microhábitat, passando por gradientes locais, até o nível regional. Essas escalas interagem entre si, possivelmente iniciando com processos históricos que determinam padrões em larga escala (e.g. biogeografia e dispersão). Filtros locais (tipo de vegetação) selecionam, então, as espécies melhores adaptadas, as quais colonizam microhábitats compatíveis com as suas características intrínsecas.

Nossos resultados são baseados em um modelo ecológico integrativo na tentativa de entender a estrutura e diversidade das comunidades de borboletas na Amazônia. Esperamos que estudos similares sejam desenvolvidos no futuro, evidenciando a importância do componente funcional, bem como do parentesco entre as espécies para a diversidade dos ambientes amazônicos. Inúmeras localidades não foram amostradas e a expectativa é que futuras investigações possam completar tais lacunas. Da mesma forma, fica evidente que a heterogeneidade da Amazônia, desde seus tipos vegetacionais até sua origem biogeográfica, é determinante para a organização das comunidades biológicas. Na presente tese, estudamos especificamente borboletas frugívoras, mas supomos que esse seja a tendência para a grande maioria dos organismos. Seja qual for a hipótese mais acertada para a formação da Amazônia atual, os inúmeros nichos e oportunidades ecológicas que surgiram ao longo dos milhões de anos da história amazônica permitiram uma ampla diversificação biológica, que acaba por si só se mantendo em homeostase. Se formos pensar por esse lado, todos os ambientes e microhábitats amazônicos são importantes para a sua regulação, o que diretamente influencia a tomada de decisões para o uso de recursos naturais, o desenvolvimento de atividades primárias, a implementação de grandes projetos de infraestrutura como estradas e hidrelétricas e a criação de áreas de proteção ambiental. As borboletas nos mostraram que a retirada da cobertura vegetal, e conseqüente ruptura da estratificação vertical, pode levar à perda de uma ampla porção da comunidade e coloca um fim em processos evolutivos que têm durado por milhões de anos em apenas alguns minutos. É imperativo manter, por exemplo, os ambientes de campina, onde a estrutura das comunidades é totalmente oposta àquela de florestas fechadas, e contêm espécies com funções ecológicas que dificilmente serão desempenhadas por outras. As florestas ombrófilas abrigam uma alta riqueza de borboletas com jovens bastante especializados do ponto de vista alimentar, os quais não sobreviverão à derrubada de suas plantas hospedeiras e à deterioração de seus hábitats. Por fim, a biogeografia da Amazônia não pode ser mais deixada de lado em

políticas conservacionistas, visto que as assembleias de diferentes origens biogeográficas carregam consigo diferentes pedaços da história amazônica, os quais precisam ser preservados. Assim, espera-se que o que foi mostrado aqui com as borboletas sirva de base para futuros estudos com outros organismos da Amazônia, e mais ainda, que tenha utilidade no contexto da proteção do maior bioma brasileiro.

Muitos ainda pensam que os biólogos são contra o desenvolvimento e o progresso da humanidade, pois estes não entendem que a natureza precisa ser modificada e usada a favor do homem. A atual conjuntura político-econômica do Brasil parece usar dessa ideia deturpada para conspirar sobre o afrouxamento da legislação ambiental brasileira. Na verdade, nós sabemos muito bem que os organismos tendem a modificar o ambiente circundante para sobreviver e que as ações de um organismo podem inerentemente prejudicar outros coexistentes. As atividades humanas e os grandes projetos precisam ser desenvolvidos, e por isso, nós biólogos (e outros cientistas) nos entregamos ao estudo das mais diversas formas de sustentar o progresso para que a natureza sofra o mínimo de agressão possível, até porque a nossa própria sobrevivência depende dela. É imprescindível que não desviemos do caminho do desenvolvimento sustentável e lutemos contra o retrocesso nas questões ambientais. A dimensão e magnitude da ação humana é, muitas vezes, injusta com os outros seres, pois nossa espécie tem uma capacidade imensa de modificar a natureza, muitas vezes a extremos irreversíveis. Porém, é importante lembrar sempre que somos apenas mais uma dentre as ainda incontáveis espécies da Terra – todas as quais com direitos iguais de habitá-la. Costumamos nos distanciar do restante dos organismos pela nossa capacidade cognitiva e habilidades intelectuais, e achamos que todas as outras formas de vida precisam servir aos nossos interesses. Na verdade, o *Homo sapiens*, que por capricho da evolução passou a ser uma espécie pensante capaz de agir e refletir sobre suas ações, carrega consigo a responsabilidade e o fardo de proteger todas as outras, e não destruí-las. Esperamos que os resultados trazidos por esse trabalho sirvam para pararmos e ouvirmos a história do mundo e da natureza contada por organismos como as borboletas.

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