

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

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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 modelling to estimate stratum preference. We detected a strong phylogenetic signal in wing–thorax ratio in both sexes. Stoutier fast-flying species preferred the canopy, whereas 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 stoutier 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.

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, that is 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 unfavourable conditions (Norberg, 1990; Grimaldi &

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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; Céspedes *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, 2015; Walther, 2002; 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, whereas 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 analyse 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) and 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, for example relative thorax mass, forewing area, wing loading and wing centroid position (Chai, 1990; Chai & Srygley, 1990; Dudley, 2000; Berwaerts *et al.*, 2002; DeVries *et al.*, 2010; Céspedes *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 data set on morphological and ecological traits of frugivorous nymphalids obtained with standardized sampling at seven locations across the Amazon basin.

Materials and methods

Material origin

The species used in our study are all native to the Amazon rainforest. In total, we covered a 3341-ha area across seven localities in the Brazilian States of Roraima, Amazonas and Acre (Fig. S1). Roraima State: (1) Viruá National Park (1°27'49.28"N, 61°1'30.59"W) encompasses a mosaic landscape of white sand forests on sandy soils and open ombrophilous forests on clayey soils (Damasco *et al.*, 2013). Amazonas State: the forest fragments in (2) Dimona (2°20'10.11"S, 60°06'46.80"W), (3) Porto Alegre stations (2°21'16.07"S, 59°57'26.47"W) and

(4) Colosso stations (2°24'17.83"S, 59°52'17.43"W); (5) the continuous dense ombrophilous forest on clayey soils at KM-41 reserve (2°26'56.87"S, 59°46'11.26"W) and (6) the lowland dense ombrophilous forest on hydromorphic soils adjacent to the BR-319 road (IBGE, 1997) (3°41'31" S, 60°19'52"W). Acre State: (7) Chandless State Park (9°23'1"S, 69°55'37"W) comprises an open ombrophilous forest on clayey soils with scattered patches of bamboo- and palm-dominated vegetation (PPBio, 2017).

Sampling was conducted using understory (height: 1.5 m–2.2 m) and canopy (height: ≥ 15 m) traps baited with a rotting mixture of plantains and sugarcane juice. Each area was visited one time between May 2015 and October 2016. We followed studies on vertical stratification of butterfly and other insects to choose the appropriate height for canopy traps (e.g. DeVries *et al.*, 1997; Grimbacher & Stork, 2007), while contemplating the particular forest structure in each sampling site. Our sampling units were 250-m-long transects, at least 1 km apart, and were composed of three canopy and three understory traps (subsamples) at least 50 m apart (one sampling unit = six traps) within each transect. The seven study sites accounted for 50 sampling units (transects) and 300 subsamples (traps). Trap activity ran for five consecutive days with 24-hour intervals for visiting to remove individuals captured and replace the bait. Butterflies were retrieved for subsequent identification and measurements and are housed at the Invertebrate Collection of the National Institute for Amazonian Research (INPA), Manaus City, Brazil.

Morphological traits and stratum preference

We measured 1092 individuals when fresh, that is prior to dehydration for mounting and within the first twelve hours of sampling. Also, the estimation of all morphological traits and habitat preference was performed for each sex separately. We obtained three morphological measurements: forewing length, thorax length and thorax width. Using a millimetre ruler, we estimated forewing length as the linear distance between the base of the discal cell and the interception of vein R5 with the wing margin (Cespedes *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, whereas 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 understory as input (Fordyce & DeVries, 2016). Values close to 1 indicate high canopy fidelity, whereas those close to 0 indicate preference for the understory. The analysis was conducted in R (R Development Core Team, 2017) using package bayespref 1.0 (Fordyce *et al.*, 2011) (data are available on <https://doi.org/10.5061/dryad.db827>).

Phylogenetic signal in wing–thorax ratio

The phylogenetic relationships among sampled species (Fig. 1) were reconstructed based on the nymphalid generic topology proposed by Wahlberg *et al.* (2009), with further resolution whenever available, for example 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 (nor could be estimated) 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 analysed whether absolute thorax volume (regardless of wing size) and wing aspect ratio correlated with stratum preference in parallel PGLS analyses (see Supplementary Information for details).

Sexual dimorphism in morphology and stratum preference

We investigated whether males and females from the same species differed regarding wing–thorax ratio and

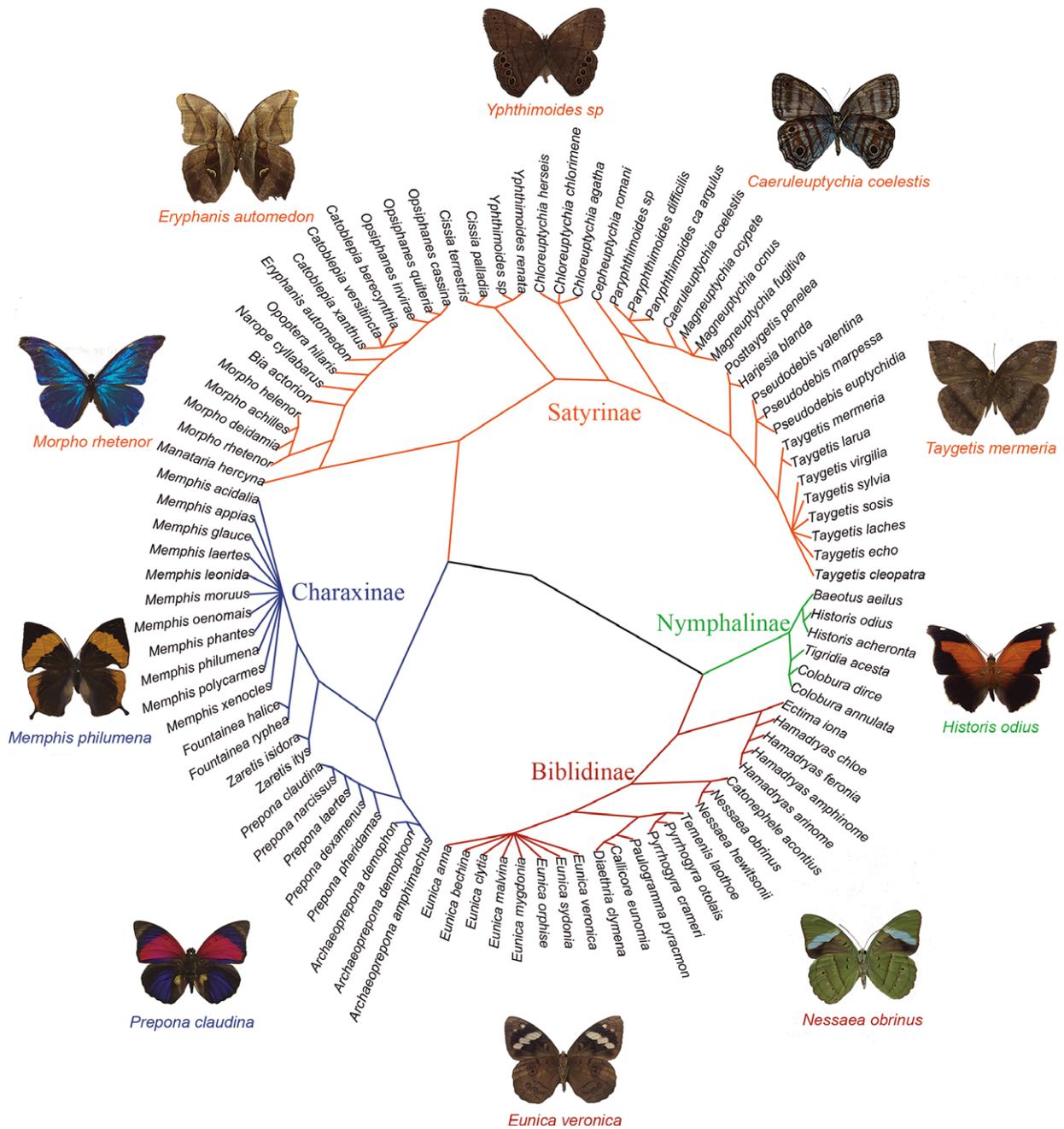


Fig. 1 Phylogenetic tree reconstructed considering all 94 studied species. All branch lengths are standardized to 1.

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 S1). 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*.

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

Our PGLS models retrieved negative relationships between butterfly wing–thorax ratio and canopy fidelity (Fig. 2). 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), whereas a minority showed transitional values, not exhibiting a clear preference (Fig. 2).

The parallel PGLS tests revealed that neither absolute thorax volume (Fig. S2, males: $t_{2, 71} = 1.374$, $P = 0.17$; females: $t_{2, 59} = 1.592$, $P = 0.11$) nor wing aspect ratio (Fig. S3, males: $t_{2, 71} = 1.635$, $P = 0.10$; females: $t_{2, 59} = 1.282$, $P = 0.20$) correlated with canopy fidelity.

Regarding between-sex differences, we found that females were significantly more slender than males of the same species (Fig. 3, $t_{1, 39} = 6.820$, $\mu = 1.33$, $P < 0.001$), but did not differ from conspecific males in stratum preference (Fig. 3, $t_{1, 39} = -0.414$, $\mu = -0.01$, $P = 0.681$). Additionally, sexual dimorphism in wing–thorax ratio decreased as canopy fidelity increased (Fig. 4, $t_{2, 38} = -3.054$, $R^2 = 0.21$, $P = 0.004$), thus indicating that in canopy species, males and females had more similar flight morphology than in those associated with the understorey.

Discussion

This study represents an endeavour 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

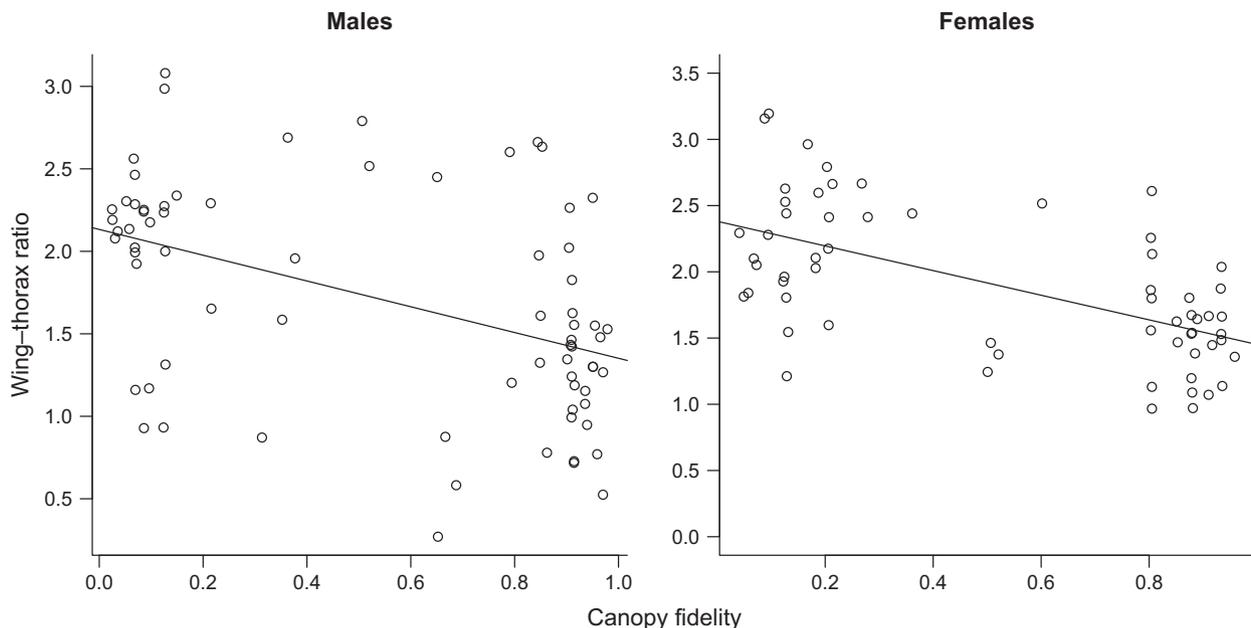


Fig. 2 PGLS models for the relationship between canopy fidelity (0 = understorey only; 1 = canopy only) and wing–thorax ratio (log-transformed). Each dot represents a species (males, $n = 73$; females, $n = 61$).

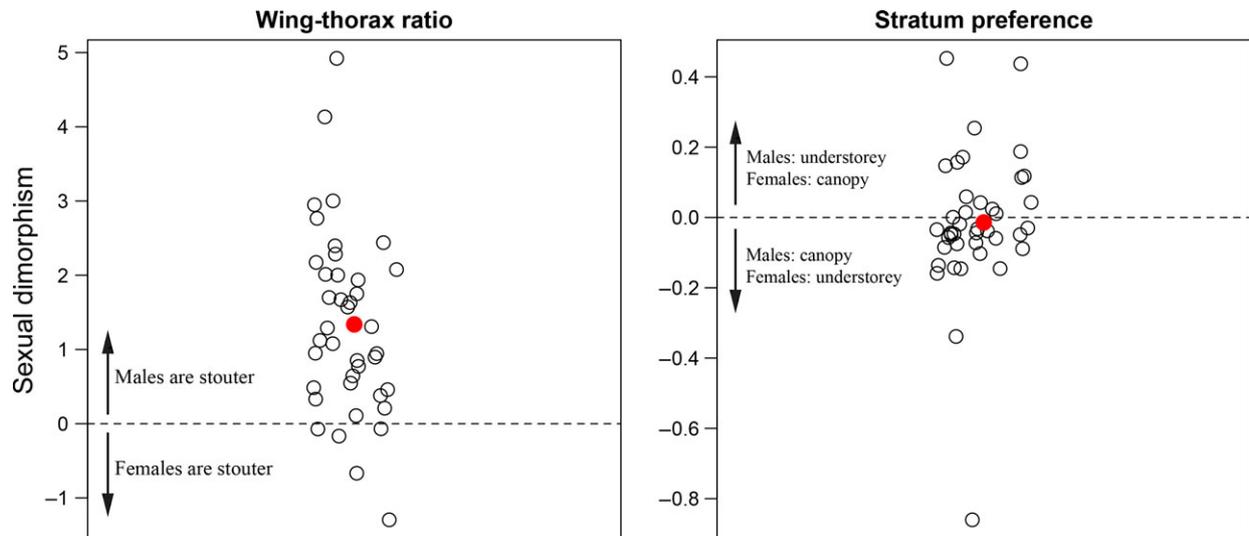


Fig. 3 Sexual dimorphism regarding wing–thorax ratio and stratum preference. The dashed line represents the mean difference expected under the null hypothesis. The filled red dots represent the observed mean difference. Each empty dot represents a species ($n = 40$).

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, 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

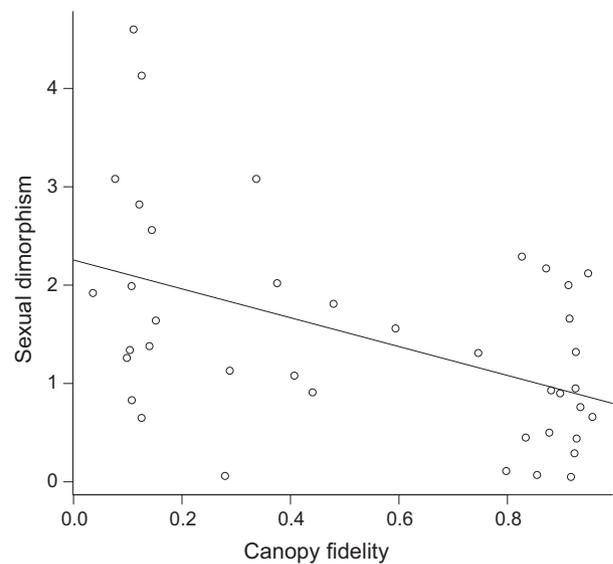


Fig. 4 PGLS model for the relationship between sexual dimorphism in wing–thorax ratio and canopy fidelity (0 = understorey only; 1 = canopy only). Each dot represents a species ($n = 40$).

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 unfavourable. We further theorized that species in the understorey might rely more on thermoregulation (e.g. shivering, Srygley, 1994), as 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; Nitepöld *et al.*, 2011). Nevertheless, males and females differ in reproduction: males may perch or patrol territories for mating encounters, whereas 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, that is 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. 3). 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. 4). 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 wing–thorax ratio, because their flight morphology varies more strongly between strata than that of males (Fig. 2).

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 reflects 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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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Material and Methods.

Table S1 List of the 94 species of fruit-feeding nymphalids studied, with their respective sex, wing-thorax ratio (WTR) and stratum preference (CF = canopy fidelity, 0 = understorey only, 1 = canopy only) and abundance per site. 1 = Viruá National Park; 2 = Dimona Station; 3 = Porto Alegre Station; 4 = Colosso Station; 5 = KM41 Forest; 6 = BR-319 Road Adjacent Forest; 7 = Chandless State Park.

Figure S1 Location of the seven studied sites (filled dots) in three states of the Brazilian Amazon.

Figure S2 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 S3 PGLS models for the relationship between canopy fidelity (0 = understorey only; 1 = canopy only) and wing aspect ratio (log-transformed). Each dot represents a species (males, $n = 73$; females, $n = 61$).

Data deposited at Dryad: <https://doi.org/10.5061/dryad.db827>

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