

Combining Taxonomic and Functional Approaches to Unravel the Spatial Distribution of an Amazonian Butterfly Community

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Abstract

This study investigated the spatial distribution of an Amazonian fruit-feeding butterfly assemblage by linking species taxonomic and functional approaches. We hypothesized that: 1) vegetation richness (i.e., resources) and abundance of insectivorous birds (i.e., predators) should drive changes in butterfly taxonomic composition, 2) larval diet breadth should decrease with increase of plant species richness, 3) small-sized adults should be favored by higher abundance of birds, and 4) communities with eyespot markings should be able to exploit areas with higher predation pressure. Fruit-feeding butterflies were sampled with bait traps and insect nets across 25 km² of an Amazonian ombrophilous forest in Brazil. We measured larval diet breadth, adult body size, and wing marking of all butterflies. Our results showed that plant species richness explained most of the variation in butterfly taxonomic turnover. Also, community average diet breadth decreased with increase of plant species richness, which supports our expectations. In contrast, community average body size increased with the abundance of birds, refuting our hypothesis. We detected no influence of environmental gradients on the occurrence of species with eyespot markings. The association between butterfly taxonomic and functional composition points to a mediator role of the functional traits in the environmental filtering of butterflies. The incorporation of the functional approach into the analyses allowed for the detection of relationships that were not observed using a strictly taxonomic perspective and provided an extra insight into comprehending the potential adaptive strategies of butterflies.

Key words: body size, environmental filtering, larval diet breadth, plant species richness, predation pressure

Functional traits comprise morphological, physiological, phenological, behavioral, and life-history characteristics of organisms that underlie their ecological performance and evolutionary fitness (Violle et al. 2007). Hence, the environmental forces governing species distribution are likely to be reflected on these characteristics (Swenson and Weiser 2010) in both temporal (Swenson et al. 2012) and spatial (Arnan et al. 2013) scales. By incorporating functional variability in analyses, ecologists enhance their predictive power and their capacity to detect patterns along environmental gradients as well as gain insight into possible ecological adaptations of the targeted organism (McGill et al. 2006, Swenson 2013). The functional approach has been widely explored in communities of plants (Kraft et al. 2008, Dubuis et al. 2013) and aquatic organisms (Poff et al. 2006). However, fewer studies have investigated turnover in functional composition of terrestrial arthropods (Öckinger et al. 2010,

Liu et al. 2015), even though they represent most eukaryote diversity in terrestrial ecosystems (Basset et al. 2012).

Butterflies represent an interesting model in which to explore functional beta diversity because there is a good amount of knowledge on their traits (Öckinger et al. 2010). Furthermore, butterflies are tightly associated with their habitats in all life stages (Freitas et al. 2003), so that environmental gradients are expected to trigger marked variations in species taxonomic and functional composition.

Body size, larval diet breadth, and eyespot patterns of the wings are reported to be significant traits in the ecological performance of butterflies (Ewers and Didham 2006, Öckinger et al. 2010, Kodandaramaiah 2011). For example, large-sized European nymphalids tended to occur in highly diverse landscapes with more heterogeneous vegetation (Barbaro and van Halder 2009), and stouter fruit-feeding species are known to explore gap environments in

tropical forests (Hill et al. 2001, Pardonnet et al. 2013). Similarly, smaller, specialist butterflies with lower dispersal ability tended to be more affected by habitat loss (Öckinger et al. 2010), while larval diet breadth increased with altitude and decreased with plant species richness in the temperate zone (Pellissier et al. 2012). Also, the presence and the pattern of eyespots on butterfly wings are thought to be devices that enhance the effectiveness of their getaways and of intimidation of enemies (Merckx and Van Dyck 2002, Hill and Vaca 2004, Stevens 2005). Moreover, there is evidence that a generalist diet of larvae might allow for a higher mobility of imagoes (Komonen et al. 2004), and that large-winged adults are less likely to successfully escape from birds' attacks than small-sized ones, as documented by feeding assays (Chai and Srygley 1990). In this light, it is essential to investigate how these traits may influence community assembly of tropical butterflies, to better understand their community-wide response to environmental changes and adaptation strategies.

Gradients of vegetation and birds' occurrence are intuitive drives of butterfly assembly, because they serve as food supply and population regulators, respectively, for these insects. For that reason, we hypothesized that plant species richness and abundance of insectivorous birds would be important predictors of butterfly community patterns. Changes in vegetation create gradients of both host plant availability and physical environmental features, such as temperature and moisture, which are known to influence the spatial segregation of fruit-feeding butterflies (Ribeiro and Freitas 2010, 2012). As for the abundance of insectivorous birds, they are used as surrogates to predation pressure to which winged butterflies are exposed, as arthropod-feeding birds are thought to impose a strong selective pressure on butterflies (Bowers et al. 1985, Stevens 2005).

The aim of our study was to investigate the spatial distribution of an Amazonian community of fruit-feeding butterflies, linking the traditional taxonomic approach (species name-based) to the functional one, while addressing the five following questions: 1) Is butterfly species turnover responding to the spatial patterns of plants and birds? 2) Is the butterfly community more specialized in plant-richer areas? 3) Are smaller-sized butterfly communities found in areas with higher abundance of insectivorous birds? 4) Are communities whose butterflies possess eyespot markings occurring where insectivorous birds are more abundant? 5) Is the butterfly functional turnover reflected on the species taxonomic segregation across the space?

Materials and Methods

Study Area

The study was conducted in Ducke Reserve (02° 55' and 03° 01' S, 59° 53', and 59° 5' W), north of Manaus, State of Amazonas, Brazil (Supp Fig. 1A [online only]). It occupies an area of 100 km² of virtually untouched forest surrounded by Manaus City (Baccaro et al. 2008). The forest is ombrophilous, dense with a closed canopy, which represents the type of forest of nearly 80% of the Brazilian Amazon (IBGE 2013). The climate is characterized by a rainy season from November to May and a relatively dry season (less than 100 mm of monthly rainfall) from August to October (Marques-Filho et al. 1981). Mean daily humidity and mean daily temperature between 2008 and 2011 were 77.7% and 25.7°C, respectively (Coordination of Environmental Dynamics, INPA).

Study Community

The community studied comprises the butterflies that gain most of their nutrients from rotting fruits, plant sap, and decaying material,

known as the fruit-feeding guild (DeVries 1987). Fruit-feeding butterflies are nymphalids belonging to the subfamilies Biblidinae, Charaxinae, Nymphalinae, and Satyrinae (DeVries 1987), which may represent up to 75% of the Neotropical nymphalid species richness (Brown 2005).

Butterfly Sampling

Sampling was carried out in transects at 30 plots, apart at least 1 km, which cover a 25-km² area of the reserve (Supp. Fig. 1B [online only]), from June to August 2013. Each plot consisted of one transect (250 m in length by 2 m in width) that followed altitudinal contours to minimize within-plot variation in soil and its correlates (Costa and Magnusson 2010).

Two sampling methods were used: bait trap and active seeking with insect net. In the former method, traps were baited with a mixture of liquefied brown sugar, transversely sliced plantains, and a tablespoon of bakery yeast, fermented for 24 h and hung at 1.80–2.20 m from the ground on tree branches. Each plot received five bait traps, placed at least 50 m apart, resulting in 150 traps in total. Traps were left active in the field for 8 straight days and were visited every 48 h to remove trapped butterflies and to replace the bait. Trapping was done only in the understory for logistic constraints. A few species regarded as canopy inhabitants were sampled and included in the analyses because some of them may visit lower strata, especially if gaps are nearby. In the active method, fruit-feeding butterflies were sampled with standard insect nets (37 cm diameter frame) by two individuals, along the 250 m of the plots for 30 min. This procedure was replicated for 5 d, always starting at 8:30–9:00 a.m. To minimize bias in this method, the same two individuals sampled all 30 transects. Also, as five plots were worked at a time, we were able to start (early morning) and end (early afternoon) with a different transect in each of the 5 d, thus controlling for day period and butterfly level of activity.

Functional Trait Measurements and Statistics

Larval Diet Breadth

Records of host plant for all species were gathered from the following sources: the databases "HOSTS" (<http://www.nhm.ac.uk/research-curation/research/projects/hostplants>) and "Caterpillar Data Base" (<http://caterpillars.unr.edu>) the project of Guanacaste Conservation Area (Janzen and Hallwachs 2009), as well as from various scientific contributions (e.g., DeVries 1987, Willmott et al. 2001). For species not listed in any of these sources, their diet breadth was estimated from a congeneric. For example, data on *Cithaeris andromeda* (F.) was estimated from *Cithaeris pireta* (Stoll). Larval diet breadth scored as six ranks: 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". Scoring was done according to the latest systematic review of the angiosperms (APG III 2009) and "clade" encompasses six groupings named Magnoliids, Commelinids, Fabids, Malvids, Lamiids, and Campanulids. The average diet breadth of each community was estimated by calculating the mean value of the ranks (1–6) attributed to the species co-occurring in each sample, in a way that values next to 1 indicate a more specialized community, whereas values next to 6 indicate a more generalized community. This was done with abundance-weighted and presence-absence data matrices to control for abundant species.

Body Size

We used forewing length as a measure of adult size. Forewing length is highly correlated with adult biomass ($R^2 = 82\text{--}87\%$), and thus it is a good proxy for adult size in Lepidoptera in general (Miller 1977) and fruit-feeding butterflies in particular (Ribeiro and Freitas 2011). Not surprisingly, forewing length has been a frequent measure of adult size in lepidopteran studies (Öckinger et al. 2010, Cespedes et al. 2014). To measure wing length, we adapted the protocol described by Van Hook et al. (2012). Here, forewing length is the linear distance from the base of the Sc vein to the wing apex, between the R4 and R5 veins. We also calculated the average body size of each community, based on the forewing length of the co-occurring species, using abundance-weighted and nonweighted matrices.

Wing Markings

We refer to *eyespot*s as those circular markings with three-dimensional effect that imitate a pupil (like those of *Caligo* spp.), while spots with a bi-dimensional appearance (like those of *Prepona claudina* (Godart)) are referred to as *circular markings* (Blest 1957, Stevens 2005). Samples were ordinated by principal coordinate analyses (PCoA) according to the relative abundance of butterfly species with no markings (NM), circular markings (CM), and eyespot markings (EM). We extracted the first PCoA axis (axis explained variance = 83%) to represent the turnover in wing-marking pattern across the sampled communities.

Environmental Variables

All information used as environmental gradients in this study was obtained from the online database of the Brazilian Biodiversity Research Program (PPBio). Plants and birds were sampled by other researchers for previous studies and are available on the PPBio online database. We highlight that these biotic factors were collected in the exact same plots as we sampled the butterflies. Data on herbs, lianas, palm trees, diameter-at-breast-height (DBH) >10-cm trees, and birds are available on the [supplementary material](#).

Plant species richness represents a sum of the richness of herbs, lianas, palm trees, and trees with DBH >10 cm in each plot (Costa 2006, Castilho et al. 2006, Costa et al. 2009, Nogueira et al. 2011, for sampling details). Because herb species were not sampled in four plots, all analyses with plant species richness as a predictor include 26 samples. Vegetation data were collected at a different time from the butterfly data (see [supplementary material](#)); however, we reckon they are still informative because vegetation patterns in the reserve are correlated with soil and topography (Costa 2006, Castilho et al. 2006, Costa et al. 2009), in a way that between-plot variation in plant richness and composition should not change drastically in the short-term. Also, for the specific case of DBH >10-cm trees, a 3-year census starting 7 years after the first sampling showed that species richness per plot stayed equivalent ($R = 0.97$; C. V. Castilho, unpublished data). We tested the correlation between plant species richness and plant species composition, because vegetation composition could also influence butterfly distribution. Plant species composition was accessed by performing PCoA ordinations with abundance-weighted and nonweighted matrices of plant data, and extracting the first axes of the resulting ordinations (variance explained: 76% for abundance-weighted and 74% for nonweighted). We found most of the variation in the first PCoA axis could be explained by plant species richness ($R = 0.75$; $R = 0.72$; [Supp. Fig. 2](#) [online only]), so that the usage of these two variables concomitantly would lead to multicollinearity in multiple regressions. The second

PCoA axes captured very little variance in plant species composition (weighted: 17%; nonweighted: 19%), and were not correlated with species richness ($P = 0.109$; $P = 0.084$). Then, we used these second axes as a third predictor in multiple regressions to detect any influence of plant species composition on butterflies independently from plant richness. However, no effect was detected, and results for the remaining predictors (plant richness and abundance of birds) were qualitatively the same when ignoring this variable. For that reason, we decided to maintain plant species richness as our independent variable to match our original hypothesis more precisely, knowing that its variation carries along information on plant species turnover.

From the bird data set, we selected the abundance of the species that only feed on insects/arthropods (Bueno et al. 2012, for sampling details). Diet information followed Cintra and Naka (2012) and Henriques et al. (2003), who described the avifauna in central and eastern Amazonia, respectively. Knowing that most Amazonian birds are sedentary and resident (Cohn-Haft et al. 1997) and that those species recorded in Ducke Reserve very likely breed in the area (Willis 1977), their distribution patterns should not change significantly in a few years. In addition, there is evidence for a 10-year stability in abundance patterns of tropical insectivorous birds residing in undisturbed forests and low-intensity disturbed areas (Karp et al. 2011), and their population density tends to remain stable for up to 8 years (Greenberg and Gradwohl 1986). Hence, even though the bird data set was not obtained simultaneously to the butterfly one (see [supplementary material](#)), we believe that the avian abundance patterns analyzed are still informative for the present study.

Statistical Analysis

Taxonomic Approach

First, species abundances were standardized by calculating the samples standardization to equal totals (SAT). This was done to reduce the discrepancy between abundant species (maximum abundance = 98) and rare species ($n = 1$), while accounting for the effect of abundance variation. SAT has been shown to be one robust standardization method for ecological ordinations (Faith et al. 1987). Second, the samples were ordinated according to their butterfly species composition to reduce the dimensionality of the data. So, a PCoA was applied to Bray–Curtis pairwise dissimilarities between samples. By definition, the first axis resulting from this ordination captures the highest variance of community composition, in a way that samples in opposite ends of this axis display the sharpest dissimilarities. In this case, the variance explained by the first PCoA axis was 41%. This axis was used to represent butterfly species composition against both plant species richness and abundance of insectivorous birds (independent variables) in multiple regressions to detect whether these variables were associated with butterfly species turnover.

Functional Approach

Each sample received an average value of larval diet breadth and body size according to the co-occurring butterflies, while the PCoA scores indicated the distribution of the wing-marking patterns. These three trait vectors were used as dependent variables in multiple regressions against both predictors as well, to investigate whether the environmental variables were filtering butterflies based on these functional traits, rather than on species identity. Abundance-weighted and nonweighted values of the functional traits (diet and size) of each community were used as

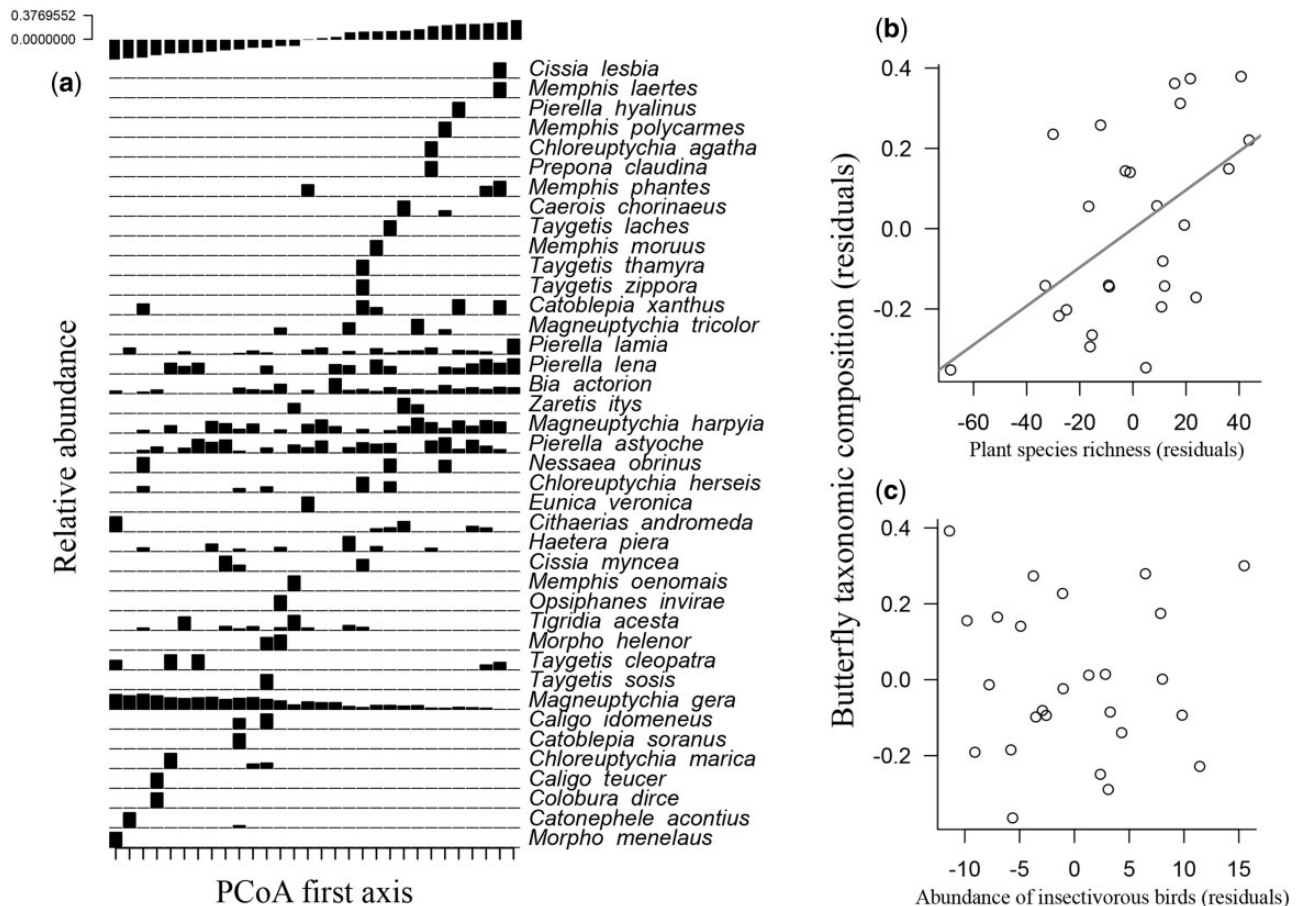


Fig. 1. The first axis of PCoA ordination showing the pattern of butterfly species turnover (A) and how it associated with the gradients of plant species richness (B) and abundance of insectivorous birds (C) as said by the partial regressions. Each dot represents a sampling unit ($n = 26$).

complementary measures to estimate butterfly functional turnover, and were analyzed separately (as in Arnan et al. 2013).

Taxonomic Versus Functional Composition

Butterfly taxonomic composition (PCoA ordination axis) was regressed against the values of the functional traits of each sample to detect whether species segregation could be reflecting the spatial variation in these attributes. Because these analyses were done using only the butterfly data set, they included all original samples ($n = 30$).

We did not perform phylogenetic controlled analyses because our study does not contain comparative analyses between any taxa. All questions were addressed considering the variation in traits at the community level. All analyses were performed using packages *vegan* 2.2-1 and *car* 2.0–25, inside the statistical software R 3.1.3 (R Development Core Team 2015).

Results

We sampled 41 species of fruit-feeding butterflies, belonging to subfamilies Satyrinae (28), Charaxinae (8), Biblidinae (3), and Nymphalinae (2) (details in Supp. Table 1 [online only]).

Taxonomic Approach

The first PCoA axis captured a pattern of butterfly species turnover, considering their relative abundance (Fig. 1A). Multiple regressions

showed that plant species richness explained the turnover in butterfly taxonomic composition, whereas abundance of birds did not (global model: $F_{2,23} = 4.675$; $R^2 = 0.28$; $P = 0.019$; Fig. 1B and C; Table 1). Specifically, the PCoA scores increased with plant species richness (Fig. 1B).

Functional Approach

Nonweighted variation in community diet breadth was best predicted by plant species richness, whereas the effect of abundance of birds was not significant (global model: $F_{2,23} = 4.173$; $R^2 = 0.27$; $P = 0.028$; Fig. 2A and B; Table 1). Conversely, abundance of insectivorous birds was a good predictor for changes in nonweighted variation in community body size, with plant species richness displaying null influence (global model: $F_{2,23} = 5.902$; $R^2 = 0.34$; $P = 0.008$; Fig. 2C and D; Table 1). We found no evidence regarding the effect of plant and bird gradients on community wing-marking pattern ($P = 0.750$). The global models containing the abundance-weighted data on both community diet breadth and body size against the environmental variables were not significant (diet breadth: $P = 0.125$; body size: $P = 0.228$).

Taxonomic Versus Functional Composition

Butterfly species composition was associated with abundance-weighted turnover in diet breadth (Fig. 3A), while the association with body size was marginally significant and nonsignificant with wing-marking pattern (global model: $F_{3,26} = 7.054$; $R^2 = 0.45$;

Table 1. Summary of multiple regressions results

Approach utilized	Partial regressions	<i>t</i>	<i>P</i>
Taxonomic approach	Butterfly PCoA scores*		
	Plant species richness	2.954	0.007
Functional approach	Birds abundance	-0.175	0.862
	Diet breadth (nonweighted)*		
	Plant species richness	-2.888	0.008
	Birds abundance	-0.536	0.596
	Diet breadth (weighted)		
	Plant species richness	-2.088	0.048
	Birds abundance	0.011	0.991
	Body size (nonweighted)**		
	Plant species richness	-1.334	0.195
	Birds abundance	2.832	0.009
	Body size (weighted)		
	Plant species richness	0.596	0.556
Birds abundance	1.756	0.092	
Taxonomic vs. functional composition	Wing marking		
	Plant species richness	0.101	0.920
	Birds abundance	-0.720	0.479
	Butterfly PCoA scores**		
	Diet breadth (nonweighted)	-1.911	0.067
	Body size (nonweighted)	2.813	0.009
Wing marking	-0.769	0.448	
	Butterfly PCoA scores**		
Diet breadth (weighted)	-2.714	0.011	
Body size (weighted)	1.999	0.056	
Wing marking	-0.687	0.498	

Butterfly PCoA scores represent the scores of the first axis of the ordination performed regarding butterfly taxonomic composition. Response variables in each regression model are in bold. Asterisks (* < 0.05; ** < 0.01) indicate statistically significant global models, and bold values are partial significant effects.

$P = 0.001$; Table 1). As for the nonweighted matrices of trait statistics, we detected a significant effect of body size in species assembly (Fig. 3B), a marginally significant association with diet breadth and still no relationship with wing-marking patterns (global model: $F_{3,26} = 5.305$; $R^2 = 0.38$; $P = 0.005$; Table 1).

Discussion

Vegetation diversity patterns are well-known key factors shaping the structure of fruit-feeding butterfly assemblages (Ramos 2000, Barlow et al. 2007), and our results give further support to this assumption, as plant species richness predicted changes in both species and functional composition of the studied butterflies (Figs. 1B and 2A). The species turnover (Fig. 1A) exposed how the butterfly community is structured and tended to follow the vegetation richness. For example, from the low-flying Haeterini, *Pierella hyalinus* (Gmelin) and *Pierella lamia* (Sulzer) apparently are more successful in plant-richer areas, whereas *C. andromeda* was mainly found in the plot with the lowest plant species richness. As *C. andromeda* is known to feed on Araceae (Janzen and Hallwachs 2009), it may be consuming the *Dieffenbachia* and *Urospatha* observed there. The remaining Heaterini, *Haetera piera* (L.), *Pierella astyoche* (Erichson), and *Pierella lena* (L.), did not show a clear tendency in following the vegetation gradient. In addition, congeneric species *Magneuptychia gera* (Hewitson) and *Magneuptychia harpyia* (C. Felder & R. Felder) displayed a preference for opposite types of habitat, as the former tended to inhabit plant-poorer (lowest richness = 174) areas, and the latter had a tendency to be found in plant-richer areas (highest richness = 236). This species substitution might be owing either to preference for the habitat condition *per se*, or because their rather similar niches lead them to compete and exclude each other.

As expected, vegetation species richness was associated with community diet breadth (Fig. 2A). The average diet breadth of fruit-feeding butterflies decreased with the increase of plant species richness, so more specialized communities were found in areas with higher plant diversity, as previously observed for nontropical Papilionoidea (Pellissier et al. 2012). Specialization might be a direct effect of the evolutionary arms race between herbivores and plants (Coley and Aide 1991). Herbivory pressure on plants would lead to the development of plant defenses, thus plant diversification. Then, selective pressure would favor herbivores capable of overcoming particular defensive strategies, thus leading to a higher level of feeding specialization. This cycle could be chaining herbivore diet breadth to plant diversity evolutionary-wise, ultimately determining the more specialized diet of butterfly communities found in areas with higher plant richness. Although our study does not depict a marked gradient of plant diversity, as would an elevation gradient, for instance (Pellissier et al. 2012, Carneiro et al. 2014), there is evidence that herbivore pressure on plants is more intense in lower latitudes (Pennings et al. 2009, Schemske et al. 2009), which should strengthen herbivore-plant interactions even in nonaltitudinal tropical landscapes, such as our study area.

There was no influence of the abundance of insectivorous birds on butterfly taxonomic composition (Fig. 1C). In contrast, a significant association appeared when the community body size variation was used as response variable (Fig. 2D). Butterfly adult size increased with the abundance of predators, contrary to the hypothesis that smaller size improves escaping mechanisms. Rather, the selective pressure by predatory birds appears to be favoring large-sized communities. One possibility is that larger wings may work as deflection tools against predators, misdirecting attacks from vital body parts, such as the abdomen (Poulton 1890, Stevens 2005, Olofsson

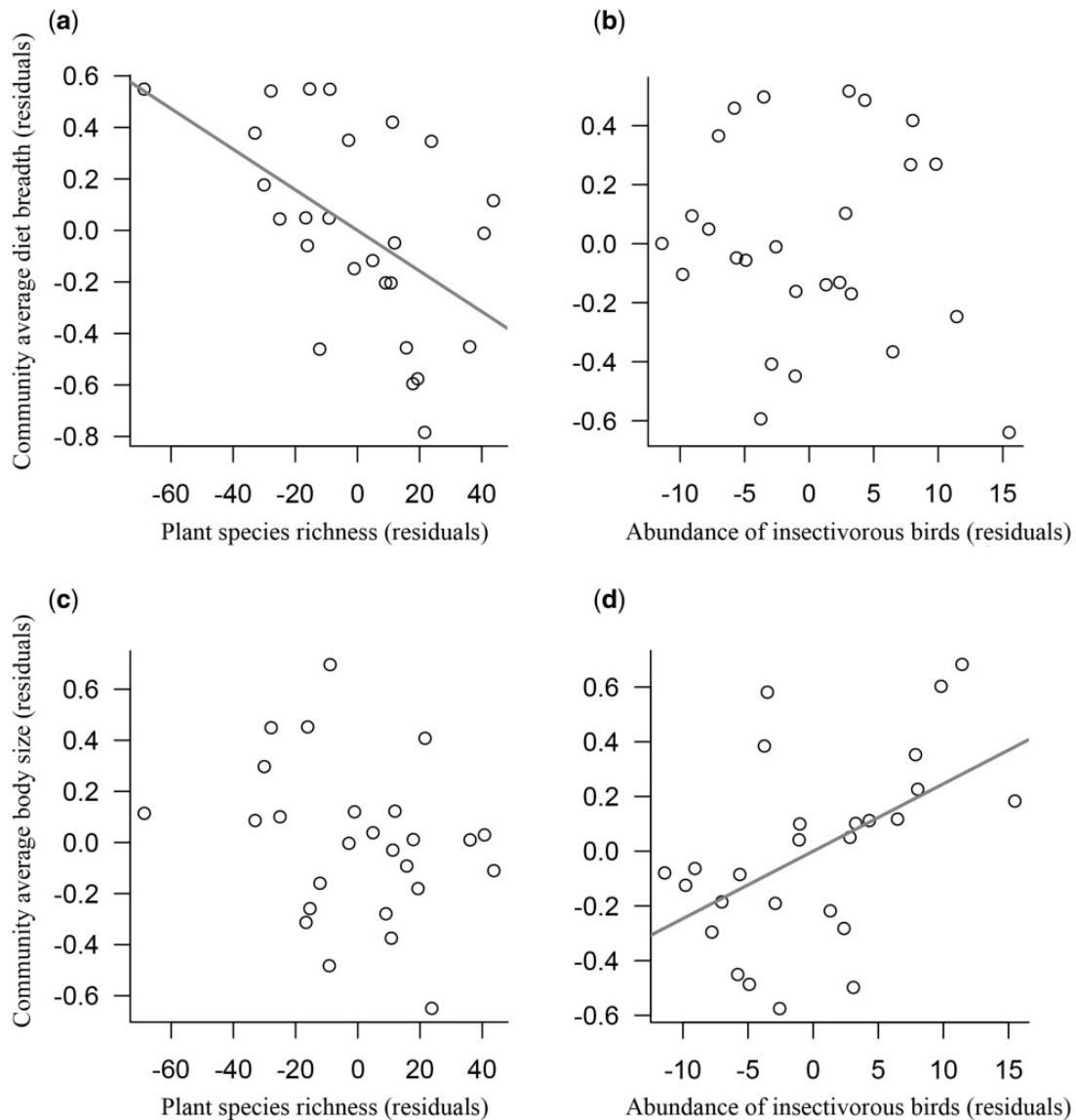


Fig. 2. Partial regressions of the influence of plant species richness and abundance of insectivorous birds on average diet breadth (A and B) and body size (C and D) of butterfly communities. Each dot represents a sampling unit ($n=26$).

et al. 2010). As a consequence, species with larger wings may escape more readily from predation by detaching disposable bitten wing fragments, and may thus be more likely to succeed in areas with higher predation pressure.

Even though wing marking are thought to work as deflective devices as well (Hill and Vaca 2004, Kodandaramaiah 2011), we did not detect an association between the presence of eyespots and the abundance of birds across the space (Table 1). Considering that the largest species found in our survey (*Morpho helenor* (Cramer), *Morpho menelaus* (L.), *Caligo idomeneus* (L.), and *Caligo teucer* (L.)) do have big eyespot markings, body enlargement may enhance the efficacy of such signals and be itself a better adaptation than the mere presence of the eyespots. The deflection role of butterfly wing characteristics has been disputed because of the conflicting results provided by those experiments that aimed to test it (Hill and Vaca 2004, Vlieger and Brakefield 2007, Olofsson et al. 2010). Nonetheless, the community-level pattern of size variation unraveled here is consistent with larger-winged butterflies performing better (or smaller-winged ones performing worse) under higher predation risk.

Our results revealed that community variation in diet breadth and body size contributed to butterfly species assembly (Fig. 3). This is evidence that the butterfly species distribution observed reflects how the environment filters their functional composition, and thus their performance regarding intrinsic features. The interactivity of the studied traits is possibly part of a complex network that defines the segregation of the targeted butterfly assemblage, as our analyses revealed unexplained variance. The development of more studies regarding butterfly functional composition may help elucidate which traits and mechanisms contribute for the small-bodied *Chloreuptychia agatha* (A. Butler) to succeed under higher predation risk, for instance. Besides, butterflies are amenable to experimental manipulation, thus allowing for direct tests of the mechanisms implied by our results.

In this study, the goal was to couple taxonomic and functional approaches to understand how environmental gradients influenced the spatial distribution of fruit-feeding butterflies. The fact that the functional approach was able to detect relationships that were not evident in the taxonomic one (Figs. 1C vs. 2D) signals the importance of a complementary type of study to enhance the detectability of biological

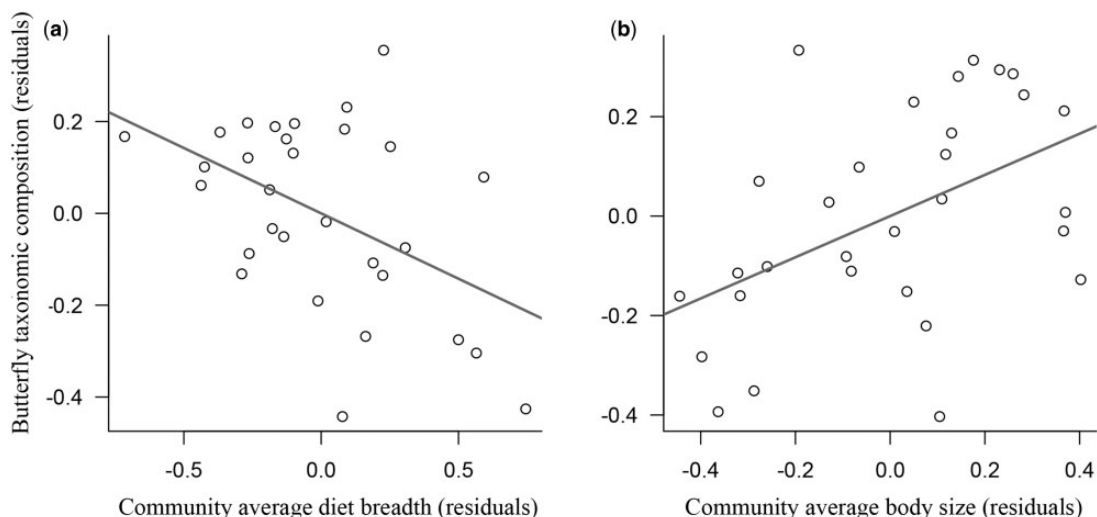


Fig. 3. Partial regressions between average trait value and taxonomic composition (scores of the first PCoA ordination axis) across local butterfly assemblages. Abundance-weighted community diet breadth (A) and nonweighted community body size (B) associated with species turnover. Each dot represents a sampling unit ($n=30$).

associations, as well as obtain a more holistic view into the diversity patterns and functionality of ecosystems. In addition, when analyzing community-wide variation in functional traits, it is possible to gain extra insight into adaptations underlying species responses to the environment and facilitate comparisons between patterns of different regions (Verberk et al. 2013). Therefore, we consider that the functional composition should represent an additional device for the establishment of conservation efforts and the comprehension of the linkage between current distribution patterns and evolutionary biology of insects.

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Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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