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Temporal Diversity Patterns and Phenology in Fruit-feeding Butterflies in the Atlantic Forest

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ABSTRACT

The Atlantic Forest deserves special attention due to its high level of species endemism and degree of threat. As in other tropical biomes, there is little information about the ecology of the organisms that occur there. The objectives of this study were to verify how fruit-feeding butterflies are distributed through time, and the relation with meteorological conditions. Species richness and Shannon index were partitioned additively at the monthly level, and β diversity, used as a hierarchical measure of temporal species turnover, was calculated among months, trimesters, and semesters. Circular analysis was used to verify how butterflies are distributed along seasons and its relation with meteorological conditions. We sampled 6488 individuals of 73 species. Temporal diversity of butterflies was more grouped than expected by chance among the months of each trimester. Circular analyses revealed that diversity is concentrated in hot months (September–March), with the subfamily Brassolinae strongly concentrated in February–March. Average temperature was correlated with total abundance of butterflies, abundance of Biblidinae, Brassolinae and Morphinae, and richness of Satyrinae. The present results show that 3 mo of sampling between September and March is enough to produce a nonbiased sample of the local assemblage of butterflies, containing at least 70 percent of the richness and 25 percent of abundance. The influence of temperature on sampling is probably related to butterfly physiology. Moreover, temperature affects resource availability for larvae and adults, which is higher in hot months. The difference in seasonality patterns among subfamilies is probably a consequence of different evolutionary pressures through time.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp.

Key words: additive partitioning; fragmentation; Nymphalidae; seasonality; temporal variation.

Species richness is not evenly distributed throughout the planet, with certain habitats showing an exceptional concentration of biodiversity (Gaston 2000). Tropical rain forests in particular have received much attention, because they harbor nearly half of the world's species diversity (Olson & Dinerstein 2002). Among the Brazilian biomes, the Atlantic Forest deserves special attention due to its high level of endemism and degree of threat (Brown & Brown 1992), making it a 'hotspot' for conservation (Myers *et al.* 2000). Despite its great importance and high level of anthropogenic conversion, little information is available about the biology of the organisms that occur in the Atlantic Forest, as well as in all other tropical biomes.

The temporal distribution of organisms is related to different aspects of their evolutionary strategies, such as foraging strategies, mating, predator avoidance, and their consequent reproductive success. Classic phenological studies are usually of great help in generating basic data for these inferences, and a further promising approach to understanding the patterns of temporal distribution of the organisms is the additive partitioning of species diversity. This idea was proposed by some authors in the 1960s (reviewed by Veech *et al.* 2002) and analytically demonstrated by Lande (1996). It consists of partitioning species diversity (γ) into additive components representing within-community diversity (α) and among-community diversity (β), where diversity can be measured as species richness, or through a diversity index (*e.g.*, Shannon; Veech *et al.* 2002). This analytical approach allows the evaluation of importance of a hierarchy of temporal or spatial scales to the structuring of biological diversity in communities.

Butterflies are widely used as biological models in ecological studies (Brown 1991, New 1997, Steffan-Dewenter & Tscharntke 1997, Brown & Freitas 2000, Schulze *et al.* 2004) because of their relatively large size, conspicuity, ease in sampling, and relatively well-known taxonomy (Brown 1991, 1992; DeVries *et al.* 1997; Veddeler *et al.* 2005). The assemblage of fruit-feeding butterflies (Satyroid lineage of Nymphalidae; *sensu* Freitas & Brown 2004) constitutes 50–75 percent of all Nymphalidae richness in different Neotropical butterfly communities (Brown & Freitas 2000, Brown 2005), and can be sampled easily with traps using rotting fruit as bait. Consequently, fruit-feeding species are largely used in biological studies (Devries & Walla 2001; Hamer *et al.* 2005; Uehara-Prado *et al.* 2005, 2007). Moreover, fruit-feeding butterflies are excellent models to study temporal diversity variation, because of their seasonal distribution (Hamer *et al.* 2005, Molleman *et al.* 2006) and are good predictors of the community responses of other taxa (Barlow *et al.* 2007). Although some authors have presented data about seasonal distribution of butterflies in the Atlantic Forest (Ebert 1969, Brown 1992), seasonality in this group has never been tested with quantitative analyses. In view of this, the objectives of the present study were to: (1) verify quantitatively how fruit-feeding butterflies are distributed

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through time, and what are the main temporal sources of their diversity and (2) verify if meteorological conditions affect temporal distribution.

METHODS

STUDY SITE.—Fieldwork was carried out in the city of São Luiz do Paraitinga, São Paulo State, southeastern Brazil (23°20′ S, 45°20′ W), near to scarps of the Serra do Mar mountain range. The average altitude in this region is 740 m asl; the relief is composed of a complex landscape with rolling hills, steep escarpments, and deep, narrow valleys (Ministério das Minas e Energia [MME] 1983). The climate is humid without a marked dry season; annual average temperature is 20.2°C (monthly minimum [July]: 9.5°C; maximum [January]: 28.6°C) and the average annual rainfall is 1340 mm (MME 1983).

The original vegetation of this area was mainly a dense humid forest (MME 1983); however, the process of forest fragmentation drastically changed the land cover in the region (Petrone 1959, Dean 1997). Today, a large part of the native vegetation has been removed, resulting in small patches of disturbed forest scattered in a matrix of ranching areas and abandoned pastures, with some eucalyptus plantation areas (Fig. 1).

SAMPLING METHODS.—The butterfly sampling method is detailed in Ribeiro *et al.* (2008), where each fragment received five portable traps baited with a mixture of banana and sugarcane juice fermented for 48 h. The traps were deployed along a linear transect, 30 m apart from each other, suspended from low branches such that the platform hung at 1–1.5 m above the ground. Ten fragments with similar structural characteristics were chosen at random, but divided into two different landscapes of similar size (*ca* 7000 ha) according to matrix composition, in adjacent river basins. In total, we used 50 traps; however, for the temporal analysis described above, captures from all traps were pooled together. The butterflies were sampled from June 2004 to May 2005. In each month, the traps remained open in the field for 8 d and were visited at 48-h intervals. In each visit, the bait was replaced and each captured individual was identified, marked, and released. Species not identified in the field were taken for later identification. The recaptures were not used in the analyses so as not to overestimate the butterfly abundance.

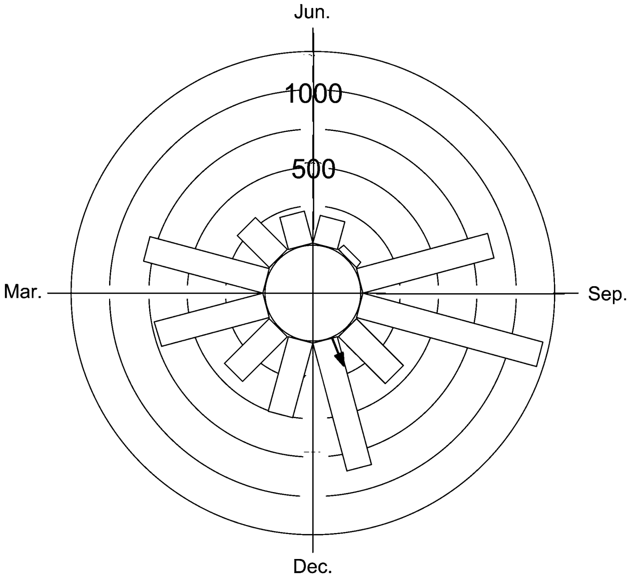

FIGURE 1. Circular histogram of the number of fruit-feeding butterfly individuals observed in a fragmented landscape. The arrow represents the average vector length (*r*) and indicates the average date (26 November).

DATA ANALYSES.—The null hypothesis that fruit-feeding butterfly diversity is randomly distributed through time was tested by additive partitioning of total diversity, using species richness and the Shannon index as measures of diversity, which fulfill all the criteria for this analysis (Lande 1996). Both measures of diversity were used in all comparisons.

To assess temporal variation in species diversity, the pooled data for all forest patches were aggregated by month, trimester, and semester; thus, resulting in a hierarchy with 12, 4, and 2 units, respectively. Average diversity (α) at each level was calculated, and the differences between them express β diversity, used in the present work as a hierarchal measure of temporal species increase when we look to a superior level (Lande 1996). Thus, α diversity at the month level is the mean of the 12 sampling months, at the trimester level is the mean of four sampling trimesters, and at the semester level is the mean of the two semesters. β diversity among months is the difference between α of trimesters and α of months etc. as explained above for α diversity. Note that, in additive partitioning, α and β diversity have the same units, and both are means. For species richness, for example, α diversity is the mean number of species in a given level, and β is the mean number of species added if we move to the next level (Veech *et al.* 2002).

Part of β diversity is due to sampling variation because it is improbable that two samples have the same species at the same abundance, even if they are from the same assemblage. Hence, to attribute β diversity to an ecological process, first we have to prove that it is larger or smaller than the value expected by random variation due to the sampling design. In other words, we have to test the null hypothesis that all samples came from the same assemblage, and that β diversity is a sampling artifact. If so, the observed β value would not differ from the value obtained if the data were shuffled at random among samples. Hence, the significance of observed β can be estimated through permutation tests by which the diversity expected at each level is simulated by shuffling the units of the lower level (Crist *et al.* 2003). For such, captured individuals are shuffled among months (within a trimester) to test for significance of β at the month level. Then, in separate randomizations, months are shuffled within trimesters (of a semester). Because of the low number of possible permutations, we have not shuffled trimesters between either semester, but calculated β at semester level only for descriptive purposes. Because whole lower-level units are permuted within higher-level units, intraspecific aggregation in each level is preserved. Crist *et al.* (2003) named this procedure 'sample-based randomization', in contrast to a single independent randomization of individuals among units at all levels, which they call 'individual-based randomization'.

The randomization process is then repeated many times to obtain null distributions of the β diversity estimates at each hierarchical level (Crist *et al.* 2003). The null hypothesis is tested by determining how often a larger or smaller value than the observed result was obtained in the randomizations. If this occurs in < 5 percent of randomizations, we assume that the observed value is significantly different than expected by chance (Gotelli & Graves 1996, Veech 2005). For randomization at each level, we carried out 1000 trials with a routine written with R Language 2.4.0 (R Development Core Team 2006), using the Package boot 1.2–27 (Canty & Ripley 2006; code available upon request to the authors).

Circular analyses were used to test whether butterflies are evenly distributed throughout the year and to calculate how concentrated the distribution of fruit-feeding butterflies is throughout the year. In this analysis, the date of capture of each observed specimen was transformed into degrees, and the mean vector (μ) and its length (r) were then calculated (Fisher 1983, Zar 1999). The length of the mean vector could range from zero to one, and describes how concentrated the occurrence of the species is throughout the year. A value of zero would indicate that the probability of occurrence is the same on every day of the year, whereas a value of one would indicate that all butterflies occur on the same day of the year.

To test the null hypothesis that the butterflies were uniformly distributed through time, Rao's Spacing test was used because it is less sensitive to polymodal data (Bergin 1991). The analyses were conducted for the entire community and for each subfamily by itself. The PAST software (Hammer *et al.* 2001) and the trial version of ORIANA 2.0 (Kovach 2002) were used for the circular analyses.

The relationship between meteorological conditions, butterfly richness, and abundance was tested with linear regression analysis, using total sampled assemblage richness and abundance. We also tested the abundance of each subfamily and the richness of Biblidinae and Satyrinae, the most rich and abundant subfamilies. The richness was rarefacted before analysis to avoid the effect of abundance in richness. We log-transformed all data before analysis to fit the normal distribution assumption of linear regression. We use the false discovery rate correction to avoid Type I errors in this multiple analysis and also because this is more powerful than family wise error rate (*e.g.*, Bonferroni, Hochberg's) corrections (Benjamini & Hochberg 1995).

RESULTS

In total, 6488 individuals of 73 butterfly species were captured during the 12 sampling periods, representing all groups of fruit-feeding Nymphalidae: Satyrinae, Brassolinae, Morphinae, Charaxinae, Biblidinae, and the tribe Coeini (Nymphalinae). Butterfly diversity was not randomly distributed across the analyzed hierarchic temporal levels. The mean monthly diversity included 58.9 percent of the species richness and was lower than expected ($P < 0.001$; Table 1). The observed $\beta 1$ richness (among months in a trimester) included 14.6 percent of the total richness and was greater than expected for $\beta 1$ richness ($P < 0.001$; Table 1). The Shannon (H') diversity index showed a similar pattern of temporal partitioning (Table 1). The mean monthly diversity of the Shannon index included 90.7 percent of the total diversity, lower than the expected α diversity ($P < 0.001$; Table 1). The observed $\beta 1$ diversity included 4.6 percent of the total Shannon diversity ($\gamma H'$) and was greater than the expected $\beta 1$ diversity ($P < 0.001$; Table 1). The observed $\beta 2$ (among trimesters) diversities (S, H') were not different than expected by the null model (Table 1). These results show that the observed temporal turnover of butterfly species cannot be attributed only to sampling chance (Table 1). Fruit-feeding butterflies are not randomly distributed across the months of a year, due to the aggregation of species at this temporal scale. As β diversity among months was significantly higher than expected both for richness and Shannon diversity, we can infer that the monthly turnover occurs both for rare and abundant species. However, on the higher temporal scale, among trimesters ($\beta 2$), the observed increase of diversity was not different from that expected by chance, and can be attributed to sampling variation only.

TABLE 1. *Temporal partitioning of species diversity in the assemblage of fruit-feeding Nymphalidae in Upper Paraíba River Basin, São Paulo State, Brazil. Results in bold type indicate that the observed diversity is significantly different from that expected in a random distribution. S, species richness;* H′, *Shannon diversity index; and NS, nonsignificant. β diversity at the semester level was not tested due to the small number of possible permutations (only 4! = 24).*

Diversity		Observed	%	Expected	P
S					
α	Within months	43.0	58.9	45.9	< **0.001**
$\beta 1$	Among months	10.7	14.6	7.79	< **0.001**
$\beta 2$	Among trimesters	8.01	11.0	7.39	NS
$\beta 3$	Between semesters	11.3	15.5		
γ	Total	73.0			
H'					
α	Within months	2.69	90.7	2.81	< **0.001**
$\beta 1$	Among months	0.136	4.6	0.019	< **0.001**
$\beta 2$	Among trimesters	0.064	2.2	0.045	NS
$\beta 3$	Between semesters	0.076	2.6		
γ	Total	2.97			

Circular analyses of the captured butterflies showed that the total sampled assemblage (Fig. 1) and each tested subfamily (Fig. 2) presented nonuniform distributions throughout the year. The mean vector (μ) of the total sampled assemblage and for each subfamily was between 90° and 180° (September–March), and the subfamily Brassolinae showed a strong concentration around these months (length of mean vector [r] = 0.8045; Fig. 2). Because of this temporal concentration, all combinations of three consecutive months between September and March contained at least 70 percent of the total richness and 25 percent of the total abundance, and the best combination (November–January) showed 83.8 percent of the total richness and 26 percent of the total abundance.

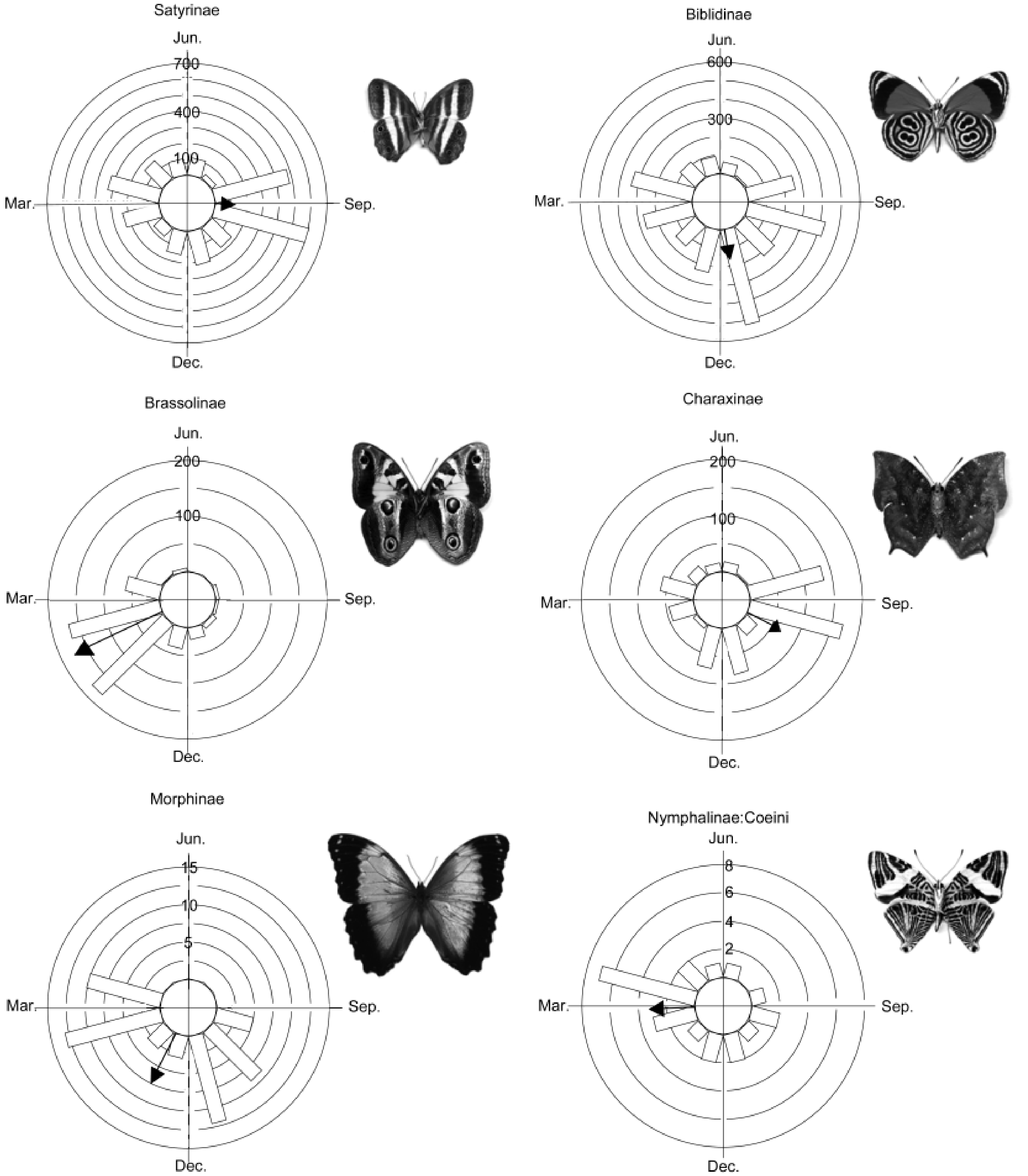

FIGURE 2. Circular histogram of the number of individuals observed for six subfamilies of fruit-feeding butterflies in a fragmented landscape. The arrows represent the average vector length (*r*) of each subfamily and indicate the average dates.

Total abundance and Biblidinae, Brassolinae, and Morphinae abundance were shown to be strongly related with mean temperature (Table 2). The total and the Biblidinae richness were not related to mean temperature and only the Satyrinae richness showed a significantly positive association with mean temperature (Table 2). Monthly precipitation was not significantly associated with any

TABLE 2. *Coefficients of determination (*R^2*) between butterfly rarefacted richness and abundance and meteorological conditions (mean temperature, rainfall) of the assemblage of fruit-feeding Nymphalidae in Upper Paraíba River Basin, São Paulo State, Brazil. Only significant linear regressions, after the false discovery rate (FDR) correction, are shown. NS indicates that the linear regression was not significant after FDR correction.*

	Temperature		Precipitation	
	R^2	P	R^2	P
Abundance				
Total	0.6895	0.0091	− 0.1549	NS
Biblidinae	0.7664	0.0022	− 0.0132	NS
Brassolinae	0.8310	0.0004	0.2321	NS
Morphinae	0.8276	0.0005	− 0.2154	NS
Charaxinae	0.4364	NS	0.5425	NS
Nymphalinae	0.4197	NS	0.1083	NS
Satyrinae	0.3544	NS	− 0.3701	NS
Rarefacted richness				
Total	0.5581	NS	0.4242	NS
Biblidinae	0.4085	NS	0.0760	NS
Satyrinae	0.6639	0.0133	0.4497	NS

measure of richness and abundance measured in the present study (Table 2).

DISCUSSION

In the present study, the additive partitioning of species diversity across temporal scales showed a clear pattern of aggregation of species only within months, which was also found in other studies (DeVries *et al.* 1999, Hirao *et al.* 2007), suggesting that this could be a characteristic of butterfly communities in general, and not an idiosyncrasy of the studied system. Aggregation of individuals at small temporal and spatial scales is a plausible explanation of β diversity at this level (Crist *et al.* 2003), and reflect processes at the individual level, such as dispersal, mating, and habitat selection. The unequal distribution of richness among months, combined with the great turnover of species between months, shows that no single month is representative of the total sampled assemblage, and a representative sample can only be achieved by sampling in more than 1 mo. Additionally, the circular analyses showed that fruit-feeding butterflies are not uniformly distributed throughout the year, but rather concentrated between September and May. Moreover, subfamilies Brassolinae and Morphinae were strongly concentrated in January and February. Based on the facts above, our data show that sampling during 3 mo in the hot season (September–March) is enough to produce a representative sample of the local assemblage, containing at least 70 percent of the actual richness and 25 percent of the abundance of individuals. A similar pattern was observed for the total butterfly community in two previous studies at high-altitude sites (500–1500 m) in the Atlantic Forest of southeastern Brazil (Ebert 1969, Brown 1992). Knowledge of the patterns of temporal distribution can be helpful in planning future studies on fruit-feeding butterflies in the studied region. Our results show that year-round sampling is not required if only a rapid portrait of the assemblage is needed, saving time and money in future studies.

In the present study, we found positive relationships among richness, abundance, and temperature (Table 2). The increase in total abundance in hot months was led to some extent by the increase in the most seasonal subfamilies (Brassolinae and Morphinae) and one of the most abundant (Biblidinae; Table 2). The Biblidinae abundance increase is probably influenced by species that only fly during hot months as indicated by the positive relation between richness and mean temperature (Table 2). Of the physical factors assessed, mean temperature could be an important factor driving this pattern. Among several factors that could produce this pattern, two of them are likely to be the most important: (1) seasonal variation in resource availability and (2) temperature as a factor affecting butterfly activity (as a measure based on capture rates *sensu* Ribeiro & Freitas 2010). These two factors would be acting together, making it difficult to distinguish the contribution of each one to the sampled butterfly abundance. The first factor, seasonal variation in resource availability, could be a key factor affecting the structure of fruit-feeding butterfly assemblages at intermediate scales of time. Specifically for these butterflies, the availability of decaying fruits and larval host plants are both subject to seasonal variation in the Atlantic Forest (Morellato *et al.* 2000). Seasonal variation in the availability of plant biomass, including leaves and new plant tissues, determines the optimum period for caterpillar development at each site (New 1991, Murakami *et al.* 2008). For adults, which obtain the majority of their nutritional requirements from rotten fruit and fermented plant sap, the temporal availability of these resources can also influence their seasonal pattern of activity (Hamer *et al.* 2006). The adults use the energy gathered from these food sources in essential activities such as territoriality, egg production, courting, and host plant location, so it is reasonable that some fruit-feeding butterflies could have been selected to synchronize their cycles so as to fly simultaneously with the highest offering of fruits (Brown 1992). If this is true, we could expect that fruit-feeding butterflies should peak in different months, following the variation in availability of fleshy fruits at different sites, for it is known that production of fruits peaks in different months at different Atlantic Forest sites (Morellato & Leitão-Filho 1992, Morellato *et al.* 2000).

The second factor, temperature, could also be a key factor in increasing butterfly activity in warm days. Butterflies need to warm up before initiating their daily activities, resulting in earlier and higher adult activity on hot days as compared with cold days, and this can directly influence the effective richness and abundance of fruit-feeding butterflies at a given site (Ribeiro & Freitas 2010).

In conclusion, the present work shows that different subfamilies may employ different strategies of reproduction and resource use. For example, Biblidinae, Satyrinae, and Charaxinae peaked in the hottest months, but adults can be sampled all year-round, showing that species in these families may mate and breed all throughout the year. In contrast, captures of Brassolinae were strongly concentrated in February–March, showing a different reproductive strategy. In the latter case, concentration of individuals in a short flight period possibly enhances the probability of finding a sexual partner. Additionally, flight period in this case could be synchronized with the best season for both high resource offer and low enemy pressure (D. B. Ribeiro & A. V. L. Freitas, unpubl. data). An intermediate, not so concentrated strategy is shown by the Morphinae, which has a flight period that extends from October to April. These results quantitatively confirm the previous naturalistic observations that fruit-feeding butterflies present different flight periods in the Atlantic Forest, which could indicate that different taxa use different strategies of reproduction and are subject to different evolutionary pressures over time in the Neotropical region.

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