

# Adult feeding moths (Sphingidae) differ from non-adult feeding ones (Saturniidae) in activity-timing overlap and temporal niche width

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**Abstract** According to classic ecology, resource partitioning by segregation along at least one of the three main niche axes (time, food, and space) must take place for the coexistence of species with similar ecological requirements. We used nocturnal light traps to investigate the assemblage structuration of two moth families: Sphingidae (23 species) and Saturniidae (13 species). Because competition for food among adults potentially occurs only among sphingids, only for this family did we expect less overlap of diel activity patterns than expected by chance and also a greater temporal niche width compared to saturniids. Moreover, we expected a greater number of sphingid species pairs to differ in activity timing compared to saturniid pairs. We also hypothesized that in the case of a lack of temporal structuration, sphingids would be morphologically structured in relation to proboscis length. Contrary to

what we expected, both families overlapped their activity patterns more than expected by chance alone and sphingid moths were not morphologically structured. Nevertheless, there were 173 significant pairwise differences in temporal activity between sphingids, contrasting with no interspecific differences between saturniids. Sphingid species also showed a wider temporal niche width than saturniids, as expected. Predation risk and abiotic factors may have caused the overall similarities in activity patterns for both families. The temporal niche seemed not to be determinant for the assemblage structuration of moths as a whole for either of the studied families, but segregation along the temporal niche axis of some potentially competing species pairs can be a relevant factor for the coexistence of nectar-feeding species.

**Keywords** Competition · Chronoecology · Predation · Assemblage structure · Resource partitioning

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## Introduction

The understanding of how many species can coexist while sharing similar resources has been considered a pivotal question for ecologists around the globe for decades (e.g., McArthur 1958; Schoener 1968; Pianka 1973; Barbault and Maury 1981; Winemiller and Pianka 1990; Chesson 2000). If two species show high ecological overlap in a niche axis, segregation will probably occur along at least one of the other niche dimensions (Schoener 1974a; Jiménez et al. 1996). Thus, to maintain sustainable populations, species with similar ecological requirements must achieve a certain degree of resource partitioning (Schoener 1974a), which may be a reflection of evolutionary relatedness (Walter 1991; Roll et al. 2006) or ecological factors (Pianka 1980;

Walter 1988). Therefore, ecological studies on assemblage structure should ideally take into account the investigation of the three main niche axes that can facilitate coexistence between species: the spatial, trophic, and temporal axes (Schoener 1974a, b).

Although divergences in the temporal activity patterns among species are less common in communities compared to the other niche dimensions (Schoener 1974a), time of activity is also considered an important niche dimension (MacArthur and Levins 1967). Changes in the frequency of interspecific encounters can decrease the competition between species that exploit similar resources. Thus, species in a temporally partitioned community might gain exclusive access to food and space within a certain time interval (Kronfeld-Schor and Dayan 2003). Temporal partitioning is considered to be a viable mechanism for reducing resource competition in the case of differences in activity times of shared limiting resources (Schoener 1974a) or else if there is renewal of limiting resources within the time involved in the separation (MacArthur and Levins 1967).

Some empirical studies showed that several animal assemblages, such as those of bats (Adams and Thibault 2006), rodents (Vieira and Baumgarten 1995; Jones et al. 2001; Castro-Arellano and Lacher 2009), lizards (Pianka 1973), and ants (Albrecht and Gotelli 2001), show evidence of community structuring regarding temporal activity. However, despite efforts to investigate this niche aspect in some organisms (especially vertebrates), relatively few studies have been conducted on temporal niche structuring, and insect assemblages seem to have been even less examined until the present (however, see Albrecht and Gotelli 2001; Prieto and Dahners 2009; Santos and Presley 2010).

Alternatively to temporal segregation in order to avoid interspecific competition, differences in body size or morphology might arise among co-occurring species as a result of this negative interaction (Diamond 1975; Simberloff and Connor 1981). Such morphological differences would reduce the overlap of resource utilization (Schoener 1974a). This pattern has been observed, for example, in the canine teeth diameter of carnivores (Pimm and Gittleman 1990), the incisor arcade structure in herbivorous mammals (Du Toit 1990), and the body size of congeneric spiders (Nieto-Castañeda and Jiménez-Jiménez 2009).

Among insects, moths can prove to be good models for improving the understanding of niche segregation patterns since assemblages may be composed of several species that are functionally diverse. Saturniidae and Sphingidae, for example, are two moth families that differ in ecology, morphology, and behavior. Adults of the Saturniidae are incapable of feeding due to a lack of feeding apparatus (i.e., proboscis) (Bartholomew and Casey 1978; Janzen 1984). These insects have a wide variety of wing sizes and shapes designed for distinct flight strategies, which evolved for

escaping predators and searching for mates. On the other hand, adult sphingids feed on flowers with different corolla heights (Bullock and Pescador 1983; Haber and Frankie 1989) and show a correspondent wide range of proboscis length (e.g., Moré et al. 2012). Moths of this family have relatively geometric and similar-shaped wings adapted for high velocity and long distance flights (Bartholomew and Casey 1978). Since these features differ markedly between these two moth families, patterns of niche partitioning can also arise differently in their assemblages. Sphingid species fulfil the two basic conditions for temporal partitioning to be a viable mechanism for reducing resource competition (see Kronfeld-Schor and Dayan 2003). These moths feed on nectar, which is a resource that may be renewed throughout the night, and flowers usually present specific periods of peak nectar production (e.g., Wolff et al. 2003; Rocca and Sazima 2006).

In the present study, we investigated patterns of niche use by Saturniidae and Sphingidae. Firstly we verified the potential role of phylogeny on the observed temporal niche patterns, testing whether possible differences in moth activity timing are derived from distinct evolutionary relatedness of the species. Assuming the relevance of ecological factors for determining temporal segregation, we expected that phylogenetic constraints are less determinant than ecological constraints for temporal structuration in the moth families. The proposed hypothesis of closely phylogenetically related species having similar activity patterns (Dann 1981) implies a limited capacity for flexibility in adaptation to environmental adversities (Kronfeld-Schor and Dayan 2003). Considering the potential role of ecological factors in the activity patterns of both families, we investigated specifically the following aspects:

1. We evaluated whether these moth families are temporally structured at assemblage level (i.e., assemblages temporally arranged consistent with avoidance of competition). As competition for food among adults potentially occurs only among the sphingid species, we expected that this family would have a structured assemblage. Inversely, as saturniid adults do not feed, we expected released competitive pressure leading to a temporally unstructured assemblage.
2. We compared the degree of pairwise segregation at species level along the temporal axis within families, taking into consideration interspecific (i.e., comparisons between species pairs coexisting in the same sampling session) and intraspecific (i.e., comparisons for the same species between different sampling sessions) differences in daily activity patterns. Considering that even unstructured assemblages may present some potentially competing pairs of species due to ecological similarities, we expected a greater number of

pairwise differences in temporal activity patterns for sphingid species than within the Saturniidae.

3. We evaluated whether the Sphingidae is trophically structured based on proboscis length. More specifically, we tested whether a minimum difference in proboscis length would be required for different resource exploration, thus potential avoidance of competition. Because species with high overlap in some niche axes will possibly segregate along another niche axis (Schoener 1974a), we also expected that in the case of a lack of temporal structuration, species of the Sphingidae would be morphologically structured in relation to proboscis length. This structure is well recognized as a useful indicator of adult foraging ecology (Bullock and Pescador 1983; Haber and Frankie 1989; Stang et al. 2009). According to Rodríguez-Gironés and Santamaría (2007), when there is competition for resources, long-tongued moths feed preferentially at deep flowers and short-tongued moths at shallow flowers.
4. Finally, we compared temporal niche breadth between the Saturniidae and Sphingidae. We expected that competition for food would cause a greater niche width (considering time as a resource) in sphingids compared to saturniids. Considering that other main evolutionary forces (e.g., predator pressure, competition for oviposition site) would be similar for both families, niche expansion onto new “resources” (i.e., time periods, in this specific case) is a valid mechanism for reaching a less severe level of competition only within the adult feeding family (e.g., Lister 1976; Bolnick 2001).

## Materials and methods

### Study area

Data collection took place in the Serra do Pardo National Park (SPNP), in the mid-west of the state of Pará in the Brazilian Amazon (data collection point at 5°56′41.30″S, 52°37′21.80″W), located in the municipalities of Altamira and São Félix do Xingu. The SPNP has an area of 445,392 ha and comprises open and closed submontane rain forests and campo cerrado (open vegetation of Brazilian savanna-like biome, i.e., cerrado) (Fávaro 2011). The rainy season begins in January and lasts for 5–6 months (R. A. J. Oliveira and C. F. de Angelis, unpublished data).

### Sampling methods

The evaluation of activity patterns of the studied moth families took place during 2010 in four sampling sessions (April, May, September, and December). We used three mounted light traps, 500 m from each other. Each light

trap was composed of two 250-W lamps mounted in front of two 1.5 × 2.0-m white sheets arranged in an L-shape. In each sampling session, we continuously registered the activity pattern of the moths by capturing and counting the adults attracted to the light traps. Each sampling session lasted 13 nights with approximately 12 consecutive hours of sampling (sunset to sunrise), totaling 156 trapping nights. For further species confirmation, all captured individuals were deposited in the entomological collection of the Research Center for the Cerrado of the Brazilian Agricultural Research Corporation, located in the city of Brasília, Federal District of Brazil. All species identifications were performed by an expert taxonomist (A. J. A. de Camargo). The identification of any potentially cryptic species was confirmed through genitalia dissection.

### Statistical analysis

To evaluate whether phylogenetic constraints are relevant for the determination of temporal activity patterns, we tested the correlation between the matrix of pairwise values of the Pianka index and the matrix of phylogenetic distances among species. For this comparison, we performed a permutational Mantel test with 10,000 iterations. To obtain the genetic distances of moth species, we used a molecular phylogeny based on the mitochondrial cytochrome gene using genetic sequences obtained from GenBank [accession numbers are given as electronic supplementary material (ESM), Appendix 1]. We aligned the cytochrome sequences using the CLUSTALW multiple alignment software (Thompson et al. 1994) and then calculated the matrix of phylogenetic distance using Kimura two-parameter distances. This method takes into account the unequal frequencies of transition versus transversion changes that are typical and well known for mitochondrial DNA (Kimura 1980). The analyses were conducted using the MEGA 5 software (Tamura et al. 2011).

We evaluated the activity patterns of the moth assemblages considering only species with a minimum of 20 individuals captured during a sampling session. Each session was analyzed separately, as composition and abundances can change drastically from one capture session to another, thus also changing the interspecific interactions among potentially competing species. Since closely related species are more likely to interact due to their similar ecological requirements (Schoener 1974a), all comparisons on niche overlap were made separately for each family. We pooled the moth occurrences in 2-h intervals, starting at 1900 hours. Because we recorded only one capture of the analyzed species between 1800 and 1900 hours during the entire study, we opted to exclude this time interval from the analysis. Thus we considered six time intervals (1900–0700 hours). We chose this interval length in order to keep

a minimum number of individuals per interval in the analysis, even considering the less abundant species. Each 2-h time interval was considered to be a resource state, and the number of individuals registered in the light traps during each time interval was an estimate of the use of this resource state by each species (Presley et al. 2009).

To evaluate the temporal structuration of all species (i.e., at the assemblage level) during each sampling session, we used the software TimeOverlap (Castro-Arellano et al. 2010). This software is based on the algorithm Rosario, which calculates the mean observed niche overlap using the Pianka or Czechanowski indexes and compares this overlap to randomly assorted assemblages by Monte Carlo simulations (10,000 iterations) using a species-by-interval matrix. The algorithm randomly generates the activity patterns of each species and calculates the amount of niche overlap maintaining the empirical structure of the data (Castro-Arellano et al. 2010). Thus, this analysis is capable of detecting a higher overlap in temporal niche than expected by chance alone (temporal coincidence) or a lower overlap than expected by chance alone (temporal avoidance). In this study, we opted to present only the Pianka index results due to the consistent and similar values compared to the Czechanowski index obtained during analyses.

Although the Rosario algorithm can be an important tool for understanding the role of time as a basis for niche partitioning at the assemblage level, the model conceals significant segregation between species pairs (Castro-Arellano et al. 2010). Therefore, pairwise comparisons and the identification of which species differ in activity pattern also are important for interpreting the mechanistic processes of niche segregation. For this reason, first we obtained the pairwise Pianka index for each species and then we tested the interspecific differences in temporal activity patterns in each sampling session with a Kolmogorov–Smirnov two-sample test using the software Past 2.17c (Hammer et al. 2001). Due to the great number of species tested in this analysis, we opted to show the pairwise results only for the three least abundant and the three most abundant species in each sampling session (see the Results section for more details). However, the full set of pairwise comparisons can be assessed in the supplementary files. We also tested for intraspecific differences comparing the temporal activity of each species registered in at least two sampling sessions, also via Kolmogorov–Smirnov two-sample tests. Therefore, we were able to determine whether the activity patterns of moth species were similar between sample sessions.

As proboscis length is well recognized as a useful indicator of foraging ecology (Bullock and Pescador 1983; Haber and Frankie 1989; Rodríguez-Gironés and Santamaría 2007; Stang et al. 2009), we used this trait to evaluate a possible morphological structuration in the Sphingidae

assemblage. For that we used the size-overlap module in the software EcoSim 7 (Gotelli and Entsminger 2001). This analysis originally tested for patterns in the body sizes of coexisting species and compared these patterns to expected values in randomly assorted assemblages (10,000 permutational iterations) with no competitive interactions. We performed this analysis using the average proboscis length of each species considering the full set of species composition for each family in each sampling session (i.e., species co-occurring in time). We measured only the proboscis of individuals captured during the study. For each species, we considered the total number of individuals captured during all sampling sessions for the average calculations, due to the low abundance of some species per sampling session. Proboscis lengths were obtained in the laboratory by measuring the individual proboscis, distended to its maximum length, to the nearest 0.01 mm with a digital caliper. We set the following options of EcoSim: variance in segment length, logarithmic transformation, and no rounding. In this analysis, the segment length represents the difference in “body size” (proboscis length, in our case) between two consecutive species, and a structured assemblage would have an observed variance significantly smaller than that in random assemblages.

To compare the temporal niche widths between sphingids and saturniids, we first used the standardized index proposed by Levins (1968), considering 2-h intervals as distinct resource states (as in Vieira and Paise 2011). We calculated this index for each species, considering the sampling sessions separately. Using this index of temporal niche width (dependent variable), we performed an analysis of covariance (ANCOVA) considering the moth families as a fixed factor, each sampling session as blocks, and the number of captured individuals of each species as a covariate. Through this analysis, we compared the niche widths of both moth families by controlling possible sources of variability from different sampling sessions and discrepant abundances of the species.

## Results

We recorded 11,212 individuals of 80 sphingid species and 112 saturniid species. However, we excluded the first sampling session from the analyses, as we recorded only species with less than 20 individuals during this session. We performed analyses regarding the activity patterns of 23 sphingid species, using sampling session (SS) and session number (as indicated by the subscript),  $SS_2 = 9$ ,  $SS_3 = 19$ ,  $SS_4 = 21$ , and 13 saturniid species,  $SS_2 = 7$ ,  $SS_3 = 6$ ,  $SS_4 = 7$ .

The evaluation of phylogenetic constraints on activity patterns performed with a Mantel test showed, for all

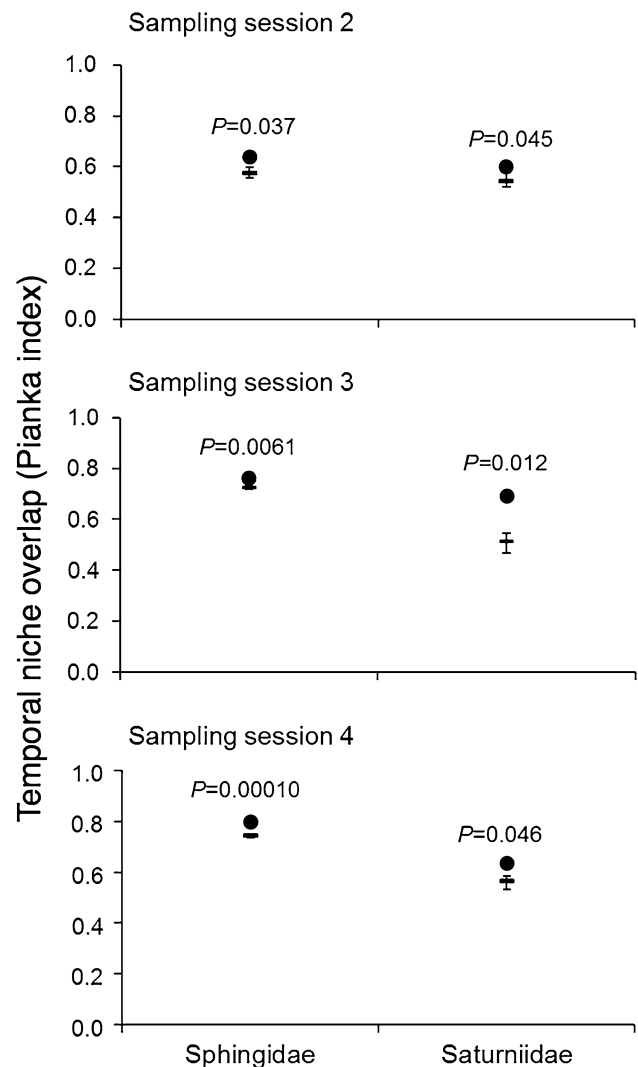
sampling sessions, no correlation between temporal niche overlap (Pianka index) and phylogenetic distance matrices for both Sphingidae ( $SS_2$ ,  $r = -0.08$ ,  $P = 0.643$ ;  $SS_3$ ,  $r = -0.08$ ,  $P = 0.754$ ;  $SS_4$ ,  $r = 0.05$ ,  $P = 0.355$ ) and Saturniidae ( $SS_2$ ,  $r = 0.17$ ,  $P = 0.184$ ;  $SS_3$ ,  $r = 0.02$ ,  $P = 0.457$ ;  $SS_4$ ,  $r = 0.20$ ,  $P = 0.380$ ) families.

Results from simulations using the values of the Pianka index showed that neither the Sphingidae nor the Saturniidae segregated as a whole along the temporal niche axis in any of the sampling sessions. These analyses on assemblage structuration, however, showed that assemblages of sphingids ( $SS_2$ ,  $P = 0.037$ ;  $SS_3$ ,  $P = 0.006$ ;  $SS_4$ ,  $P < 0.001$ ) and saturniids ( $SS_2$ ,  $P = 0.045$ ;  $SS_3$ ,  $P = 0.012$ ;  $SS_4$ ,  $P = 0.046$ ) overlap their activity patterns significantly more than expected by chance alone. Such significant differences were opposite to what would be expected under niche segregation (Fig. 1).

Despite the observed lack of overall temporal niche segregation for both families, the within-family pairwise comparisons in temporal activity showed strikingly different patterns for each family. Kolmogorov–Smirnov tests showed 173 significant between-species differences in the Sphingidae ( $SS_2 = 5$ ,  $SS_3 = 77$ ,  $SS_4 = 91$ ; Table 1; Fig. 2; see also ESM, Appendix 2 for the full set of species) and no significant between-species differences in the Saturniidae (Table 2; Fig. 3; see also ESM, Appendix 3 for the full set of species). Moreover, we observed a pattern in which the less abundant sphingid species tended to differ in activity pattern in relation to the most abundant ones (Table 1; Fig. 2; see also ESM, Appendix 2). We also detected 15 significant intraspecific differences in the temporal activity of sphingid species as registered in at least two sampling sessions and no intraspecific differences for pairs of saturniid species (Table 3).

In the measurement of proboscis length (722 individuals of 80 species), we verified that the sphingid *Neococytius cluentius* had the longest proboscis length and *Nycerix riscus* had the shortest proboscis length (see ESM, Appendix 4). The size-overlap analysis based on the variance segment length showed that the observed variance was not significantly smaller than expected by chance alone in all sampling sessions (Fig. 4). Therefore, the analyses indicated a lack of morphological niche structure in the Sphingidae. Instead, the observed distribution of proboscis lengths tended to show a lumpy species distribution, with groups of species with similar lengths (see insets, Fig. 4).

The comparison between niche widths (mean  $\pm$  SD) indicated that sphingids ( $4.26 \pm 0.84$ ) had significantly wider niches than saturniids ( $2.24 \pm 0.65$ ) (ANCOVA,  $F_{1,65} = 24.798$ ;  $P < 0.001$ ), with a significant effect of sampling sessions ( $F_{1,65} = 3.402$ ;  $P = 0.039$ ) but no effects of species abundances ( $F_{1,65} = 2.170$ ;  $P = 0.146$ ).



**Fig. 1** Observed and expected temporal niche overlap (obtained by the Pianka index) within two moth families (Sphingidae and Saturniidae) for each sampling session conducted in the Brazilian Amazon (Serra do Pardo National Park). Filled circle indicates the observed Pianka index. Horizontal bars indicate averages of the simulated Pianka indexes. Vertical bars indicate the 95 % confidence intervals of the simulated indexes. P-values are probabilities of simulated distributions (10,000 simulations) overlapping more than expected by chance alone (i.e., temporal coincidence and no temporal niche segregation)

## Discussion

We showed that at the assemblage level, neither Sphingidae nor Saturniidae moths segregate over time. Instead, members of these families overlapped their activity patterns more than expected by chance alone. Pairwise comparisons of niche segregation, however, indicated that only sphingid species pairs significantly differ in their daily temporal patterns. Additionally, the Sphingidae presented a wider temporal niche than the Saturniidae.

**Table 1** Pairwise comparisons of activity patterns of the three least abundant and the three most abundant sphingid species in the three sampling sessions (SS) conducted in the Brazilian Amazon (Serra do Pardo National Park)

	<i>C. duponchel</i>	<i>E. oenotrus</i>	<i>X. tersa</i>	<i>E. alope</i>	<i>E. ello</i>	<i>X. chiron</i>
<b>SS<sub>2</sub></b>						
<i>Cocytius duponchel</i> (29)	–	0.891	0.87	0.845	0.784	0.82
<i>Erinnyis oenotrus</i> (34)	0.742	–	0.676	0.934	0.923	0.884
<i>Xylophanes tersa</i> (34)	1.000	1.000	–	0.615	0.534	0.600
<i>Erinnyis alope</i> (210)	0.109	0.480	0.414	–	0.993	0.989
<i>Erinnyis ello</i> (242)	0.048	0.355	0.421	1.000	–	0.983
<i>Xylophanes chiron</i> (332)	0.003	0.024	0.027	0.848	0.469	–
	<i>P. ficus</i>	<i>M. florestan</i>	<i>A. palmeri</i>	<i>P. tetrio</i>	<i>E. ello</i>	<i>X. chiron</i>
<b>SS<sub>3</sub></b>						
<i>Pachylia ficus</i> (25)	–	0.595	0.704	0.826	0.893	0.881
<i>Manduca florestan</i> (27)	0.842	–	0.434	0.643	0.548	0.556
<i>Adhemarius palmeri</i> (28)	0.639	1.000	–	0.805	0.835	0.904
<i>Pseudosphinx tetrio</i> (460)	0.002	0.002	0.002	–	0.882	0.894
<i>Erinnyis ello</i> (534)	0.002	0.002	0.001	0.928	–	0.989
<i>Xylophanes chiron</i> (827)	0.002	0.002	0.001	0.476	0.478	–
	<i>P. resumens</i>	<i>P. eurycles</i>	<i>P. darceta</i>	<i>C. duponchel</i>	<i>X. chiron</i>	<i>E. ello</i>
<b>SS<sub>4</sub></b>						
<i>Pachyliooides resumens</i> (20)	–	0.886	0.769	0.733	0.375	0.551
<i>Protambulyx eurycles</i> (20)	0.844	–	0.883	0.948	0.569	0.703
<i>Pachylia darceta</i> (21)	1.000	0.347	–	0.805	0.376	0.514
<i>Cocytius duponchel</i> (303)	0.002	0.002	0.002	–	0.735	0.812
<i>Xylophanes chiron</i> (492)	0.002	0.002	0.002	0.467	–	0.974
<i>Erinnyis ello</i> (729)	0.002	0.003	0.002	0.025	0.110	–

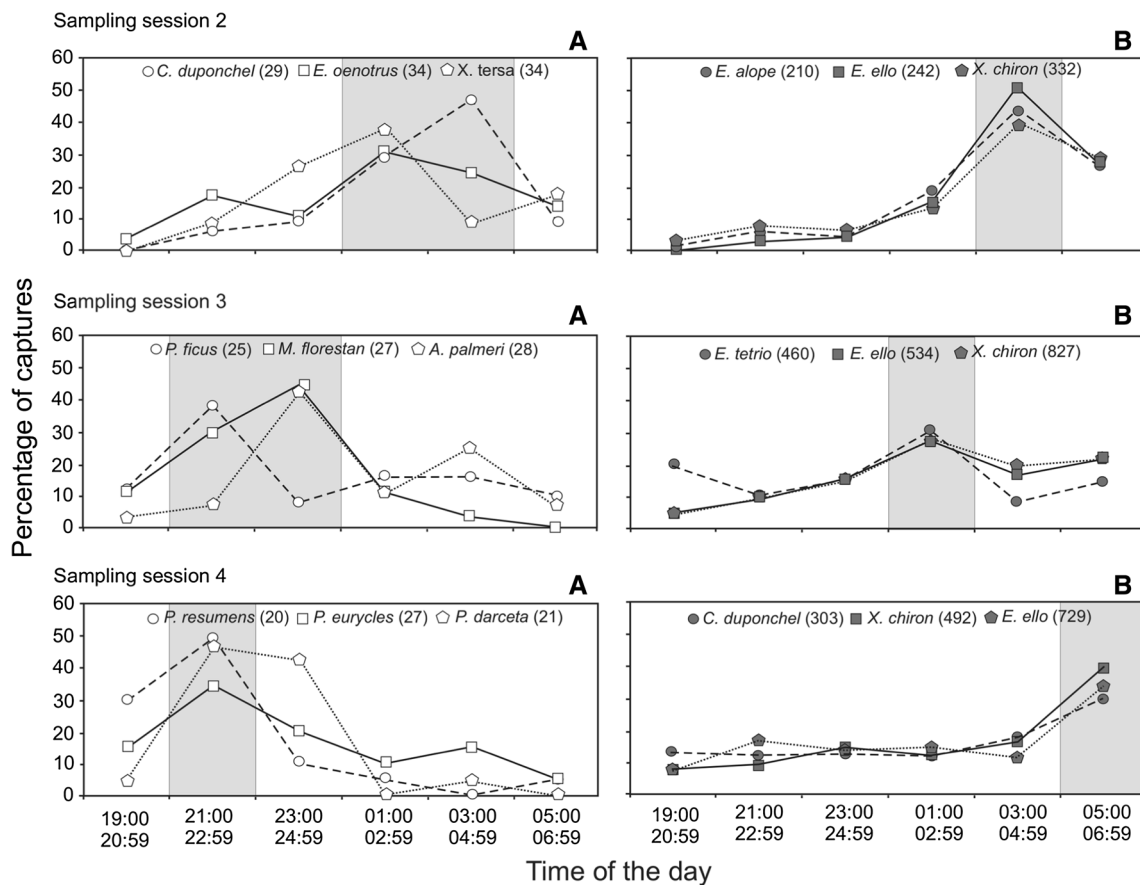
Values below the main diagonal correspond to *P*-values obtained via Kolmogorov–Smirnov tests. Values above the diagonal correspond to niche overlap (Pianka index). Species are arranged in ascending order of abundance (*in parentheses*)

Significant values are indicated in italic ( $P < 0.05$ )

The observed absence of overall temporal structuration was expected for the saturniids due to their lack of feeding, but was unexpected for sphingids due to their foraging activity during the night, and thus was due to a possible resource competition among species. Therefore, our results seemed to indicate that the food resource is not the major limiting factor for the Sphingidae, at least at the assemblage level. Our analyses were performed for only the dry-season data, when flowering peaks are more frequent and nectar availability is potentially greater in the Amazon rain forest (e.g., Araújo 1970; Haugaasen and Peres 2005; Bentos et al. 2008). Thus, at this time of the year it is possible that there was no strong competition for food resources or else other factors would have determined the observed patterns. Both alternatives would thus lead to the observed absence of general temporal structuring of the assemblages.

Moreover, we registered the lowest abundance and richness of the Sphingidae and Saturniidae in the first sampling session, precluding activity-pattern analyses. This may suggest a synchronism in which individuals tend to emerge in

the high-resource period, when flowering and the production of new leaves peak (e.g., Haugaasen and Peres 2005) that serve as an oviposition substrate and food resource for moth caterpillars (e.g., Auerbach and Simberloff 1989; Barone 1998; Kessler and Baldwin 2002). Additionally, the lack of competition for food in sphingids at the assemblage level was also reinforced by our results regarding proboscis structuration. As no minimum difference in proboscis length is required for different resource exploration, availability of food resources seems not to be an important issue, at least for the assemblages as a whole. This looseness in morphological similarity allowing many species to have similar proboscis lengths may be the result of two main factors: (a) the wider temporal niche width found for sphingids, permitting some species to forage not only during an optimal and specific range of time but at different times during the night; and (b) the several between-species differences that we found in activity patterns, indicating a finer division of time between many potentially competing species pairs.



**Fig. 2** Temporal activity patterns of the three least abundant (A) and the three most abundant (B) species of Sphingidae in the Brazilian Amazon. The numbers of individuals in each sampling session are given in parentheses. Light-grey bars indicate the highest peak of activity considering the three species of each group (least or most

abundant) combined. Peaks were defined by the highest proportion of sampled individuals of each species along time intervals. Species names and pairwise comparisons based on Kolmogorov–Smirnov two-sample tests are shown in Table 1

Alternatively, our results may indicate a different pattern of assembly structuration (contrary to our expectations of segregation), as suggested by Scheffer and van Nes (2006). These authors proposed a new view of assembly structuration, in which species-rich communities tend to show a lumpy species distribution, being organized in groups of similar species. Such a pattern appears when strong competitor species occupy intermediate positions between species that are distant in niche space (Scheffer and van Nes 2006). In other words, for this pattern to arise in an assemblage, some species must be sufficiently different to create intermediate niche spaces, and some species must be sufficiently similar to occupy such spaces (Scheffer and van Nes 2006). Indeed, our results show a trend of this lumpy pattern, in terms of species distribution according to proboscis length in each sampling session. Thus, under this assembly structuration view, our results on proboscis length may suggest structured moth assemblages.

As expected, we also found no relation between activity pattern and phylogeny in either the Sphingidae or the

Saturniidae. Phylogenetic imprints can be much stronger than ecological factors (Roll et al. 2006). In this case, ecological traits are the result of historical and evolutionary effects, limiting the plasticity of species in the use of niche axes for ecological segregation (Schoener 1974a; Kronfeld-Schor and Dayan 2003; Roll et al. 2006). The observed lack of phylogenetic imprints suggests that the activity time of the studied assemblages is driven mainly by environmental and ecological selective forces. As competition for food seems not to be the determining factor in the activity pattern of the assemblages (more specifically, for sphingids), other aspects should be considered. According to Presley et al. (2009), if an assemblage is not structured by competition, the activity patterns of ecologically similar species may be molded by other external factors, resulting in more temporal overlap. Indeed, our results on assemblage structuration pointed to such patterns for both families in all sampling sessions.

Another factor that might be causing the observed patterns of temporal niche convergence is predation.

**Table 2** Pairwise comparisons of activity patterns of the three least abundant and three most abundant saturniid species in the three SS conducted in the Brazilian Amazon

	<i>A. liberia</i>	<i>T. timur</i>	<i>A. boisduvalii</i>	<i>H. ebalus</i>	<i>S. molina</i>	<i>D. panamensis</i>
<b>SS<sub>2</sub></b>						
<i>Automeris liberia</i> (23)	–	0.76	0.849	0.342	0.236	0.195
<i>Titaea timur</i> (23)	1.000	–	0.957	0.347	0.633	0.586
<i>Adeloneivaia boisduvalii</i> (25)	1.000	1.000	–	0.209	0.445	0.383
<i>Hylesia ebalus</i> (35)	1.000	1.000	0.819	–	0.789	0.817
<i>Syssphinx molina</i> (42)	0.739	0.741	0.654	0.843	–	0.992
<i>Dirphia panamensis</i> (62)	0.842	0.840	0.775	0.768	0.769	–
	<i>C. hamifera</i>	<i>E. barnesi</i>	<i>S. molina</i>	<i>D. panamensis</i>	<i>A. plateada</i>	<i>A. pelias</i>
<b>SS<sub>3</sub></b>						
<i>Citheronia hamifera</i> (20)	–	0.869	0.457	0.61	0.907	0.73
<i>Eacles barnesi</i> (24)	0.737	–	0.676	0.731	0.894	0.817
<i>Syssphinx molina</i> (28)	0.821	0.738	–	0.215	0.504	0.277
<i>Dirphia panamensis</i> (51)	0.843	0.718	0.765	–	0.837	0.974
<i>Adelowalkeria plateada</i> (100)	0.114	0.845	0.114	0.472	–	0.901
<i>Adeloneivaia pelias</i> (265)	0.470	0.768	0.824	0.843	0.467	–
	<i>S. molina</i>	<i>C. anthonilis</i>	<i>A. subangulata</i>	<i>C. hamifera</i>	<i>E. barnesi</i>	<i>A. pelias</i>
<b>SS<sub>4</sub></b>						
<i>Syssphinx molina</i> (20)	–	0.536	0.743	0.426	0.899	0.770
<i>Citioica anthonilis</i> (23)	0.844	–	0.615	0.811	0.401	0.783
<i>Adeloneivaia subangulata</i> (23)	0.738	1.000	–	0.832	0.887	0.369
<i>Citheronia hamifera</i> (32)	0.820	1.000	1.00	–	0.563	0.668
<i>Eacles barnesi</i> (33)	0.768	0.762	0.814	0.649	–	0.305
<i>Adeloneivaia pelias</i> (65)	0.842	0.847	1.000	1.000	1.000	–

Values below the main diagonal correspond to *P*-values obtained via Kolmogorov–Smirnov tests. Values above the diagonal correspond to niche overlap obtained (Pianka index). Species are arranged in ascending order of abundance (in parentheses)

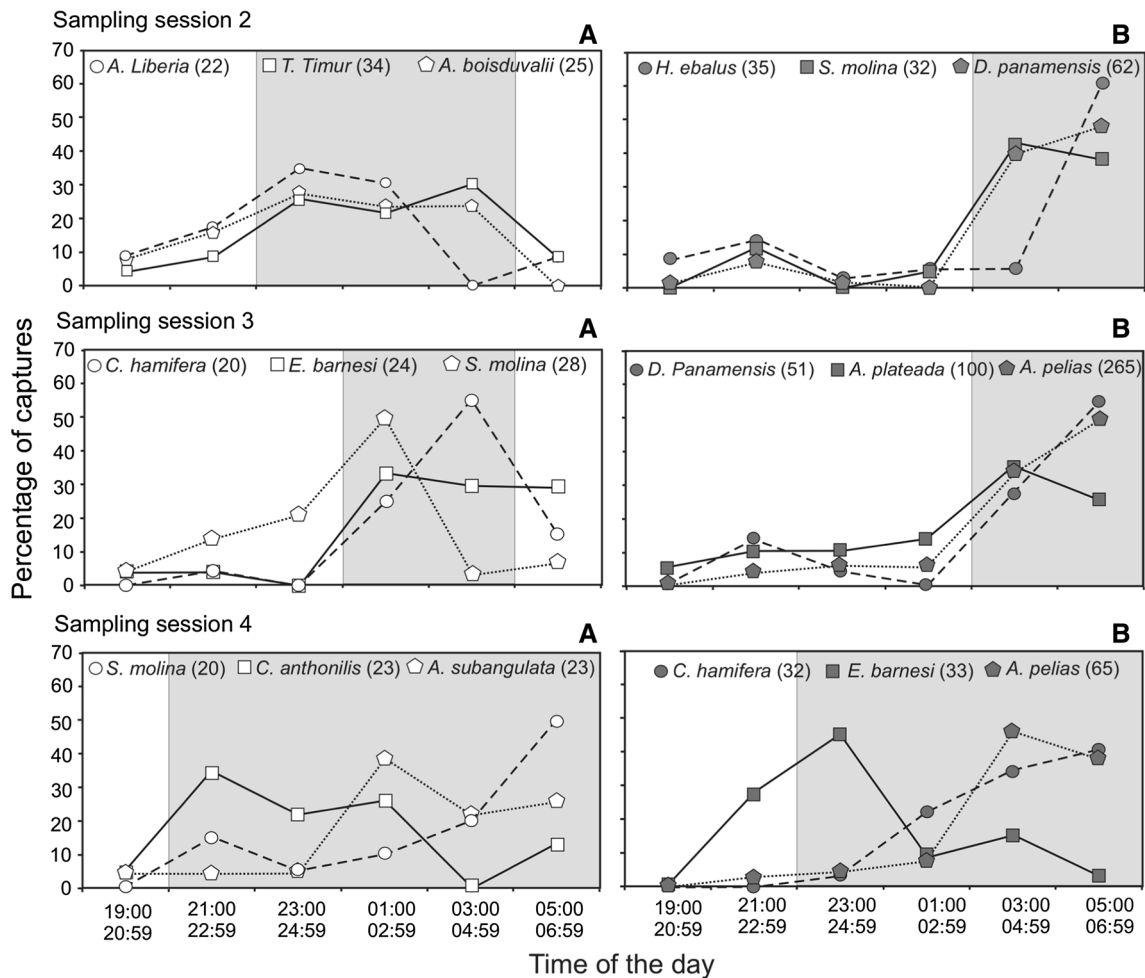
Convergence of individuals in time might dilute the chance of individual capture, a kind of multispecies “schooling effect.” For moths, insectivore bats can be considered to be major nocturnal predators (Fullard 1987). The bimodal activity pattern of these mammals with a higher peak after sunset and a smaller one before sunrise (Hayes 1997), may constrain moths to be more active between these two periods. Our data support this view, since the activity peaks of most of species occurred between 2100 and 0500 hours. In fact, studies evaluating temporal activity patterns showed a relation to predation risk for some organisms such as bats (e.g., Rydell et al. 1996; Presley et al. 2009), rodents (e.g., Kotler et al. 1994; Castro-Arellano and Lacher 2009), and fishes (e.g., Reeb 2002).

In addition to biotic factors, mutable abiotic factors such as humidity, temperature, wind velocity, and vapor pressure are important and can influence moth and butterfly activity at the diel scale (e.g., Pitcairn et al. 1990; Prieto and Dahners 2009). For example, an overlap was found in the response of butterfly species to environmental temperature due to the required optimal temperature for flight and

mate searching (Prieto and Dahners 2009). For nocturnal and ectothermic organisms, such abiotic factors should also contribute to determining a general pattern of activity in moths at the assemblage level. Thus, physiological constraints would force most of the assemblage species to be active in the same optimal range of abiotic factors (Prieto and Dahners 2009).

In addition to the several interspecific differences among sphingids and the lack of them in saturniids, we also found within-species differences in the activity of sphingids sampled in at least two sampling sessions. These intraspecific differences indicate a greater plasticity in sphingids possibly due to competitive interactions between species of this family. Thus, it is likely that such differences will arise depending on which species are present in the assemblage and whether they are competing at that moment. Furthermore, the wider niche width in sphingids compared to saturniids indicates that, different from the analyses regarding assemblage level, competition for food resources (both intra- and interspecific) can be responsible for distinct diel activity patterns at the species level.





**Fig. 3** Temporal activity patterns of the three least abundant (A) and the three most abundant (B) species of Saturniidae in the Brazilian Amazon. The numbers of individuals in each sampling session are given in parentheses. Light-grey bars indicate the highest peak of

activity considering the three species of each group (least or most abundant). Species names and pairwise comparisons based on Kolmogorov–Smirnov two-sample tests are shown in Table 2

Alternatively, such differences in activity pattern may be the result of reproductive isolation among some congeneric or more related species pairs, which thus avoid hybridization (Devries et al. 2008). Indeed, we found some differences between congeneric species, but at the same time did not find any correlation between phylogeny and activity patterns of sphingids. Our results suggest that the differences between congeneric species seem to be more related to abundances (which varied widely among sampling sessions) than to relatedness among species. For example, *Enyo lugubris* and *Enyo ocypte* differed in activity pattern in SS<sub>3</sub> but did not differ in SS<sub>4</sub>. This result is probably due to the marked differences in abundance between these species in SS<sub>3</sub> (*E. lugubris* = 45 individuals, *E. ocypte* = 252 individuals), while in SS<sub>4</sub>, these species presented more similar abundances (*E. lugubris* = 38 individuals, *E. ocypte* = 29 individuals).

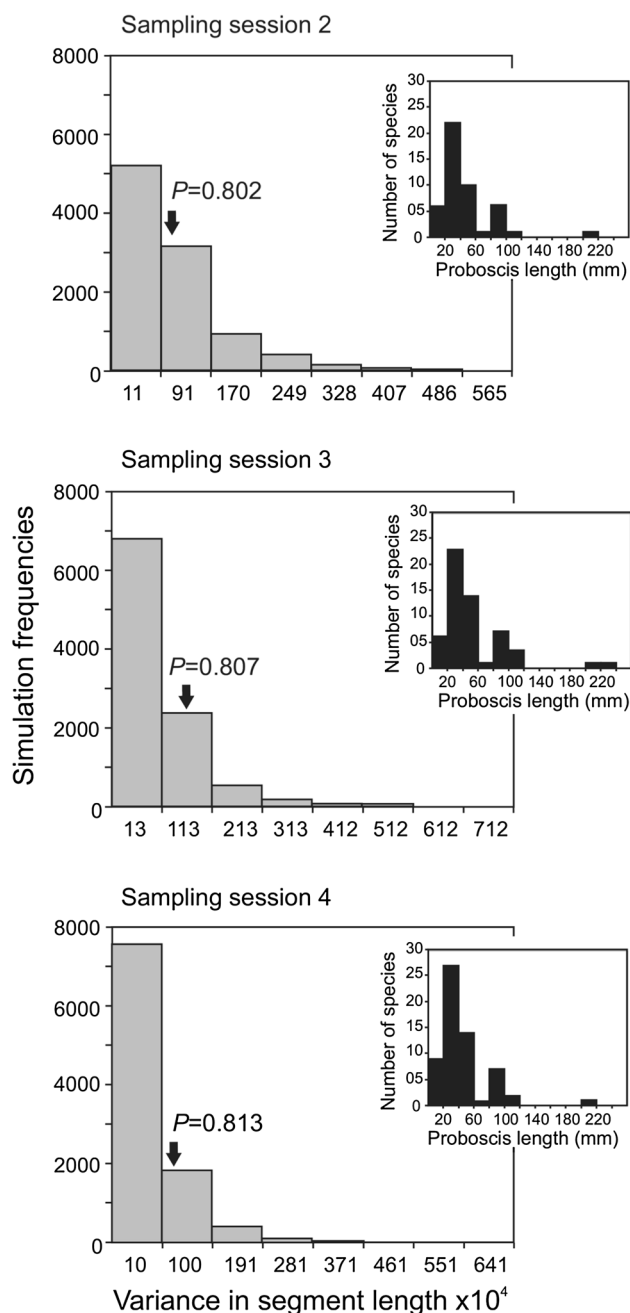
Interestingly, our results showed a pattern in which more abundant species tended to differ in temporal activity in relation to less abundant ones. A possible explanation for such a pattern is that numerical bias between more and less abundant species may produce statistical significant differences. In some cases, however, even less abundant species did not differ from more abundant species in temporal activity in both sphingids [e.g., *Cocytius duponchel* (29 individuals) and *Erinnyis alope* (210 individuals)—SS<sub>2</sub>] and saturniids [e.g., *Citheronia hamifera* (20 individuals) and *Adeloneivaia pelias* (265 individuals)—SS<sub>3</sub>], suggesting that differences in abundance per se did not account for the observed differences. Additionally, we observed a pattern in which the more abundant species of sphingids are more active in the last hours of the night, while the less abundant species are more active in the first hours of the night. It is possible that even with the lack of temporal structuration at the

**Table 3** Results (*P*-values) of Kolmogorov–Smirnov two-sample tests comparing the temporal activity patterns of the Sphingidae and Saturniidae species captured at least in two different SS in the Brazilian Amazon (Serra do Pardo National Park)

	SS <sub>2</sub> vs. SS <sub>3</sub>	SS <sub>2</sub> vs. SS <sub>4</sub>	SS <sub>3</sub> vs. SS <sub>4</sub>
<b>Sphingidae</b>			
<i>Adhemarius palmeri</i> (28, 34)	–	–	0.350
<i>Callionima parce</i> (130, 34)	–	–	0.002
<i>Cocytius duponchel</i> (29, 237, 303)	0.001	0.003	0.469
<i>Enyo lugubris</i> (45, 38)	–	–	0.646
<i>Enyo ocypte</i> (101, 252, 29)	0.142	0.070	0.002
<i>Erinnyis alope</i> (210, 186, 59)	0.849	0.471	0.025
<i>Erinnyis ello</i> (242, 534, 729)	0.476	0.111	0.836
<i>Erinnyis oenotrus</i> (34, 212, 52)	0.115	0.112	0.026
<i>Eumorpha anchemolus</i> (110, 209, 279)	0.847	0.116	0.470
<i>Eumorpha satellitia</i> (140, 139)	–	–	0.769
<i>Manduca florestan</i> (27, 55)	–	–	0.812
<i>Neococytius cluentius</i> (44, 79)	–	–	0.842
<i>Protambulyx eurycles</i> (34, 20)	–	–	0.846
<i>Protambulyx strigilis</i> (300, 98)	–	–	0.028
<i>Pseudosphinx tetrio</i> (460, 34)	–	–	0.002
<i>Xylophanes chiron</i> (332, 827, 492)	0.482	0.475	0.111
<i>Xylophanes pluto</i> (42, 106, 26)	0.142	0.736	0.025
<i>Xylophanes tersa</i> (34, 38)	0.845	–	–
<b>Saturniidae</b>			
<i>Adeloneivaia boisduvalii</i> (25, 25)	–	0.844	–
<i>Adeloneivaia pelias</i> (265, 65)	–	–	0.843
<i>Citheronia hamifera</i> (20, 32)	–	–	0.712
<i>Dirphia panamensis</i> (62, 51)	1.000	–	–
<i>Eacles barnesi</i> (24, 33)	–	–	1.000
<i>Syssphinx molina</i> (42, 28, 20)	0.474	0.850	0.114

Species abundances tested in each SS are shown in parentheses in chronological order

Significant values are indicated in italic ( $P < 0.05$ )



**Fig. 4** Observed and expected proboscis size overlap (log scale) for Sphingidae moths in the Brazilian Amazon. *P*-values indicate probabilities that observed values are smaller than expected by chance alone (10,000 simulations). *Insets* show the species distribution according to proboscis length in each sampling session

assemblage level, some species may save time and energy avoiding interactions (Richards 2002; Prieto and Dahners 2009). As the activity of bats in general can be intense in the

first hours after sunset as soon as they leave their roosts for feeding (e.g., Tayllor and Oneill 1988; Rydell et al. 1996; Hayes 1997; Bernard 2002; Presley et al. 2009), the more abundant moth species could tend to avoid predation by being more active in the last hours of the night. On the other hand, to avoid interactions with other moths, the less-abundant sphingid species would be forced to be more active earlier during the night. However, it is likely that this pattern may depend on which species make up the assemblage and the intensity at which the species are interacting.

## Conclusion

Our study revealed that neither the Sphingidae nor the Saturniidae are temporally structured, when considering whole assemblages. Moreover, sphingid moths, whose individuals feed during the adult stage, are not morphologically structured (based on proboscis length), at least based on the classic assemblage structuration view of diverging species. The results indicated, however, that only the sphingid species, the group that potentially competes for food, present several significant differences between species pairs in their diel activity patterns considering all possible species pairs for each family. This family also showed a wider niche width than that of the saturniid moths. We conclude that the temporal niche is not determinant for the overall assemblage structuration of moths as a whole (i.e., assemblage level) but that segregation of some potentially competing pairs of moth species (i.e., species level) along the temporal niche can be a relevant factor for promoting the coexistence of adult feeding sphingids. Although our findings show temporally unstructured moth assemblages, these differences among potentially competing species (apparently due to differences in abundance) also can be an important mechanism for maintaining high diversities. Such interspecific differences in sphingids (feeding moths) and the lack of them in saturniids (non-feeding moths) suggest that nectar resources may trigger such pattern.

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