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RESEARCH ARTICLE

Vertical stratification of Sphingidae moths (Lepidoptera: Bombycoidea: Sphingidae) in the Tapajós National Forest, Pará, Brazil

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ABSTRACT. The present study analyzed the vertical stratification of hawkmoths in an area of the Dense Ombrophylous Forest in the Amazon. The moths were captured through light traps with ultraviolet lamps F15 T12 LN installed in three strata (canopy, midstory, and understory) from 6 pm to 7 am, during the first quarter to new moon period, on three consecutive nights per month during May 2019 to February 2020, in the Tapajós National Forest located in the state of Pará, Brazil (02°51'23.3"S, 54°57'31.0"W). This study analyzed 33 species (S) and 775 specimens (N) of Sphingidae. The sphingofauna had a high concentration, mainly in the upper strata, with greater emphasis on richness (S = 28), abundance (N = 687), and Berger Parker dominance (BP = 0.72) found in the forest canopy. The canopy's dominance stood out because the species *Erinnyis ello* (Linnaeus, 1758) was more abundant in this stratum (N = 492). PERMANOVA analysis indicated significant differences in all strata. Therefore, our study provided important information about the vertical distribution of moths, showing that their richness, abundance, and species composition are distinct between strata.

KEY WORDS. Canopy, *Erinnyis ello*, hawkmoths, sphingofauna, strata.

INTRODUCTION

The vegetation of a forest is characterized by the dominant trees that compose a continuous canopy (Veríssimo and Pereira 2014). Additionally, the forest structure can exhibit distinct layers or strata (understory, lower stratum, middle stratum, and upper stratum) depending on the phytoecological region, stage of succession, conservation status, and ecological role (Souza and Souza 2004).

Vertical stratification contributes to species diversity by offering unique microclimates regarding relative humidity, temperature, and solar radiation (Puig 2008). As well as it corroborates to generate those faunas adapted to exploit different types of resources (Campos et al. 2008), with insects as excellent distribution models since they live in almost all places and different habitats (Costa et al. 2011).

Studies of vertical distribution have shown a greater agglomeration of insects in the canopy (Amorim et al. 2022) since this stratum and the diversified environment have various ecological niches (Puig 2008). Regarding lepidopterans, especially moths, the pattern of vertical distribution in tropical forests in mountainous areas and canopy preference is confirmed for certain groups (Shulze and Fiedler 1997, Shulze et al. 2001). Nevertheless, in some cases, neither the canopy nor the understory stands out (Beck et al. 2002). However, in lowland tropical forests, the understory is richer for certain families of moths (Intachat and Holloway 2000, Brehm 2007, Campelo et al. 2020).

The moths of the Sphingidae family, also popularly known as hawkmoths, have a predominantly habit nocturnal and have a high degree of mobility, area of dispersion, and migration (Ávila-Jr et al. 2012). In addition, it happens partly due to the strong wing muscles and having the forewings larger than the hindwings allowing fast flight and displacement over long distances (Janzen 1984, Powell 2009). In addition, they have a generally long proboscis that makes them important providers of environmental services as pollinators of numerous varieties of flowering plants (Azevedo-Costa and Oliveira 2013, Oliveira et al. 2014).

The hawkmoths (Sphingidae) are formed by the subfamilies Macroglossinae, Smerinthinae, and Sphinginae (Duarte et al. 2012). They are distributed all over the world (except Greenland and Antarctica), with approximately 1,300 species and 203 genders described, even though it is possible to perceive that the tropics of America, Africa, and Asia continents concentrate the greatest biodiversity (Duarte et al. 2012). In the Neotropical region, it is estimated the occurrence of 400 species, of which 180 are found in Brazil (Duarte et al. 2012) and 128 are currently recorded for the Brazilian Amazon (Camargo et al. 2016).

Despite hawkmoths being considered one of the best inventoried and studied Lepidoptera families in the world (Kitching and Cadiou 2000), their vertical distribution still needs to be better understood. Studies of this nature are rare both for Sphingidae (Lourido et al. 2018) and for other groups of moths in the Amazon region (Lourido et al. 2008, Campelo et al. 2020), highlighting the urgent need for intensive research that will provide valuable information about the taxonomy and its functional importance in the face of the deforestation crisis that is advancing on its natural ecosystems, causing a decline in biodiversity. Therefore, a more detailed study of faunal biodiversity should be considered for a more accurate assessment of the species that exploit different profiles of the forest, since each species can have its position guaranteed in the structure and the composition, especially when it is represented in all strata (Finol 1975).

Considering that previous studies on vertical stratification of moths in tropical forests have been documented and contributed with relevant data under different environmental conditions, however the efforts have not yet been sufficient to determine a pattern of vertical distribution. Thus, the present study aimed to understand the vertical stratification of hawkmoths in an area of dense rainforest in the Tapajós National Forest, located in Pará state, Brazil; assuming that the abundance, richness and species composition of hawkmoths differ between the analyzed strata.

MATERIAL AND METHODS

The study was carried out in a tower platform (02°51'23.3"S, 54°57'31.0"W, Figs 1, 2) of 45 m high, belonging to the Large Scale Biosphere-Atmosphere in the Amazon Program (LBA). This sampling unit (SU) is located 6 km in a straight line from the inside of the Tapajós National Forest (TNF) to the federal highway BR–163 at km 67 (from the municipality of Santarém to the other city Cuiabá, located in Mato Grosso state), in the western region of Pará.

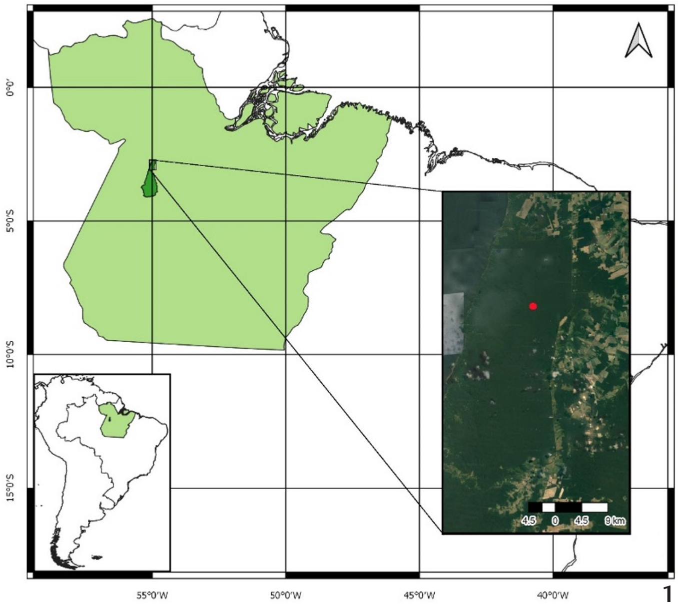
The TNF is characterized by a predominant covered vegetation of Dense Ombrophylous Forest, consisting of large trees, woody lianas, palm trees and epiphytes (Cordeiro 2005). According to the Köppen classification, its climate is of the Ami type (hot and humid), with an average annual temperature of 25.5 °C and an average annual precipitation of 1,892 mm, according to the data obtained between 1971 and 2016 from the Belterra climatological station (ICMBio 2019).

The 90 sampling events were done monthly from May 2019 to February 2020, during the first quarter or new moon period on three consecutive nights and in three vertical strata, thus totaling 30 samples per stratum. Moths were captured with light traps through the use of the Pennsylvania model (Frost 1957), which was equipped with the ultraviolet fluorescent lamps F15 T12 LN (the light has a wavelength ranging from 290 to 450 nm (Teston and Delfina 2010) that were activated at dusk (18 hours) and turned off at dawn (7 am). At the end of the trap, a funnel was placed connected to a container of 3.5 L capacity, containing 92° GL alcohol for fixing the captured insects. The traps were installed in 2 m strata (understory), 23 m (midstory), and 45 m (canopy) height.

The following day, the samples were transported to the Laboratório de Estudos de Lepidópteros Neotropicais (LELN) at the Universidade Federal do Oeste do Pará (UFOPA). After quantification, two specimens per species were mounted with entomological pins and dried in an oven at 40 °C for 48 hours, and the rest were kept in entomological envelopes. The species were identified by comparing samples with specimens from the LELN collection and consulting the specialized bibliography concerning the Sphingidae, as well as the help of a specialist to confirm them. Voucher specimens were deposited in the LELN (voucher number LELN 05.364 to LELN 05.442) collection, a part of the Museum of Zoology (MZSTM) of the UFOPA Natural Sciences Program.

The following metrics were used to analyze hawkmoth diversity: composition, abundance (N), richness (S), Shannon diversity, uniformity indexes (H' and J'), and Berger-Parker dominance (BP) (Magurran 2011). A diversity of profiles were used to assess species diversity between strata, based on the Rényi series (Tothmeresz 1995) considering the following index rates: total richness ($\alpha = 0$), Shannon-Weiner index ($\alpha = 1$) and Simpson dominance ($\alpha = 2$). Analysis of variance (ANOVA) was performed to test (t-test: LSD) whether there was a significant difference in abundance between strata (canopy, midstory and understory), for samples (30) with different variances using the BIOESTAT 5.3 program (Ayres et al. 2007).

The species richness estimates were calculated using the program "ESTIMATES" (Statistical Estimation of Species



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Figures 1–2. Map of the location of the sampling unit (red circle): (1) Tapajós National Forest, western Pará (Google Earth satellite image); (2) LBA platform tower located at Forest National Tapajós. Photo: Genilson Rego, 2009.

Richness and Shared Species from Samples) (Colwell 2013), applying the non-parametric methods Chao 2 and Jackknife 1. Moreover, it was used 100 randomizations with an abundance of classes equal to 10 (Colwell and Coddington 1994). Furthermore, rarefaction curves were made to compare richness between strata (Magurran 2011).

The Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to test for significant differences in the composition of hawkmoths between strata (30 samples per stratum), with 9,999 permutations, using the Bray-Curtis similarity index.

The Non-metric Multidimensional Scaling (NMDS) analysis was used to verify the ordering of the strata through the faunistic composition, considering it as a function of the abundance of species. Thus, applying the Bray-Curtis index, according to the dissimilarities of the patterns observed for the strata.

The PAST version 4.08 program (Hammer et al. 2001) was used for the analysis, except species richness estimations and ANOVA.

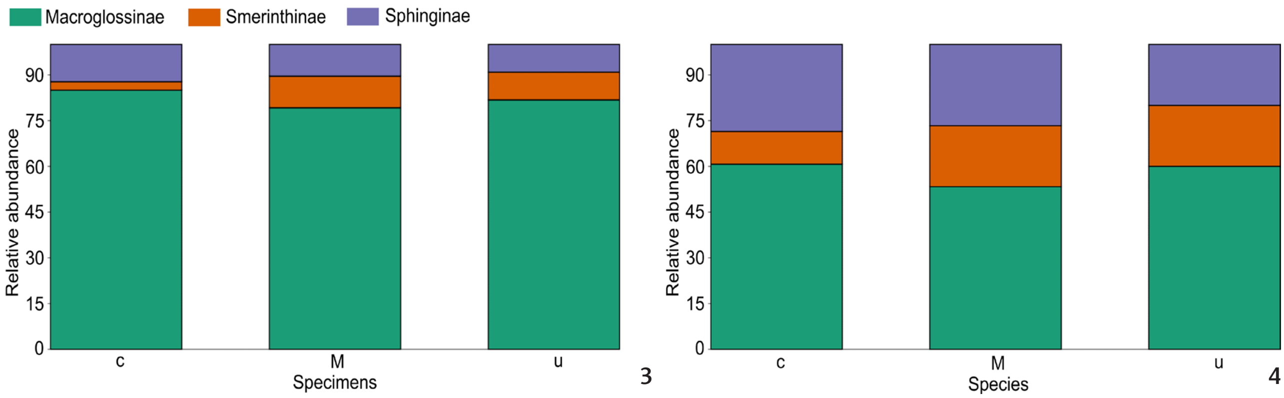
RESULTS

In this study, it was possible to register the 33 species and the 775 Sphingidae specimens belonging to the three subfamilies (Macroglossinae, Smerinthinae, and Sphinginae) (Table 1). Macroglossinae showed the highest species abundance (N = 654) and richness (S = 20) (Figs 3, 4). *Erinnyis ello* (Linnaeus, 1758) was the dominant species representing 70.8% (N = 549) of the collected specimens, followed by *Cocytius duponchel* (Poey, 1832) (N = 39), *Pseudosphinx tetrio* (Linnaeus, 1771) (N = 26) and *Erinnyis alope* (Drury, 1773) (N = 26) (see Table S1).

Table 1. Richness (S), number of specimens (N), diversity index (H), Shannon uniformity (J') and Berger-Parker dominance (BP) of Sphingidae moths collected in three vertical strata canopy (C), midstory (M) and understory (U) in the Tapajós National Forest, Pará, Brazil, from May 2019 to February 2020.

Strata	S	N	H'	J'	BP
C	28	687	1.35	0.41	0.72
M	15	77	1.51	0.56	0.65
U	5	11	1.16	0.72	0.64
Total	33	775	1.43	0.41	0.71

Moreover, Shannon's diversity (H' = 1.43) and uniformity (J' = 0.41) indexes, and Berger Parker's dominance (BP = 0.71) were determined (Table 1). The highest value observed for the diversity index (H' = 1.51) was in the midstory stratum (Table 1). Nevertheless, the maximum Shannon uniformity



Figures 3–4. Faunal composition of Sphingidae from canopy (C), midstory (M) and understory (U) samples of the Forest National Tapajós, Pará, Brazil, from May 2019 to February 2020. Analyzes were based on (3) abundance and (4) richness.

value (J' = 0.72) and the lowest value for Berger Parker dominance (BP = 0.64) were assigned for the understory (Table 1).

Furthermore, the values of the diversity as mentioned above, the index rates corroborate to the results which indicates that the species diversity profiles at the beginning of the α scale (α = 0) the canopy was richer than the other strata (Fig. 5). However, as the scale had increased, the curves intersected (α = 0.72) and the greatest diversity and dominance was observed for the midstory stratum (Fig. 5).

The canopy concentrated 84% of the species (S = 28) and 88% of the specimens (N = 687) with a decrease of both parameters in the strata below the canopy (Table 1). The exclusive species were significant in the canopy (17), which, together with the midstory (four) and the understory (one), totalized 22. Between the strata, four species were shared *Agrius cingulata* (Fabricius, 1775), *Adhemarius palmeri* (Boisduval, 1875), *E. ello*, and *Erinnyis oenotrus* (Cramer, 1780) (see Table S1).

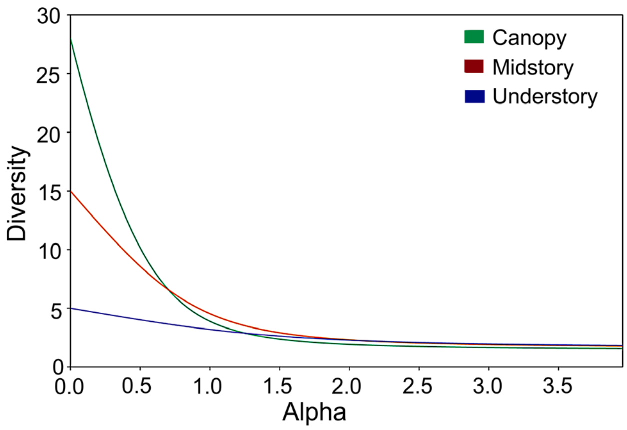


Figure 5. Species diversity profiles in the Rényi series samples in the three strata canopy, midstor and understory, in the Forest National Tapajós, Pará, Brazil, from May 2019 to February 2020.

Species composition and observed values for richness and abundance were different. ANOVA confirmed that there was a significant difference between abundance and strata (F = 5.263; GL = 2; p = 0.0072): canopy (mean = 22.9) and midstory (mean = 2.5) (t = 2.655; p < 0.01); canopy and understory (mean = 0.3) (t = 2.942; p < 0.01); while the difference was not significant between midstory and understory (t = 0.287; p > 0.01).

The "Chao 2" and "Jackknife 1" richness estimator assumes a richness of 42 (± 8.11 and ± 3.21, respectively). Moreover, about 78.57% of the species expected were captured. In terms of comparison between the strata, these estimators agree with the species rarefaction curve in that when the samples in the canopy are rarefied to 11 specimens, the abundance still exceeds what was registered for the midstory and understory. This indicates that they are promising for capturing more species (Fig. 6).

The PERMANOVA results showed significant differences in the composition of the hawkmoth between the strata (F = 12.86; p < 0.01), being proven by the pairwise test that identified such differences between the canopy and the other strata (canopy x midstory, p = 0.0003; canopy x understory, p = 0.0003; midstory x understory, p = 0.0021). However, the ordination analysis (NMDS) showed that the species composition of the canopy has less similarity with the understory, while the fauna of the midstory was more similar to that of the other strata (Fig. 7) and presented a stress level of 0.54.

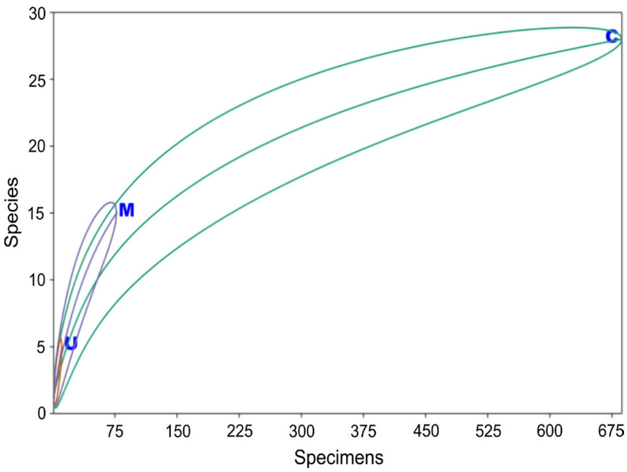


Figure 6. Rarefaction curves of the observed species richness of Sphingidae based on the number of specimens, collected with light traps, in the three strata canopy (C), midstory (M) and understory (U), in the Forest National Tapajós, Pará, Brazil, from May 2019 to February 2020.

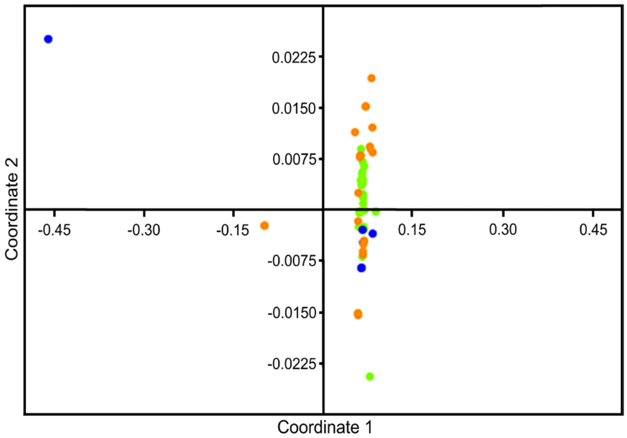


Figure 7. Non-metric Multidimensional Scaling analysis (NMDS) based on the Bray-Curtis index for Sphingidae species collected with a light trap in Forest National Tapajós, Pará, Brazil, from May 2019 to February 2020. Canopy (green dots), midstory (orange dots) and understory (blue dots).

DISCUSSION

Hawkmoth diversity can be found in an area of dense rainforest in the TNF, which it corresponds to 25% of the richness recorded for the Brazilian Amazon (Camargo et al. 2016). However, related works on this family report several species, which was superior to the present study in Amazonian forests (Motta et al. 1991, 1998, Motta and Andreazze 2001, 2002, Motta and Xavier-Filho 2005, Hawes et al. 2009, Camargo et al. 2016). In qualitative and quantitative terms of species, Macroglossinae contributed considerably, configuring as the main subfamily as it occurs with the highest incidence of richness in inventories and faunal studies (Motta et al. 1991, 1998, Motta and Andreazze 2001, 2002, Motta and Xavier-Filho 2005, Lourido et al. 2018, Conceição and Teston 2020). Regarding the discrepancy in the abundance of species observed for *E. ello* relating to the others, that can be explained by the large number of specimens collected in the three samples of February 2020 (N = 461), which may be associated with environmental factors such as precipitation and the phase of the moon (Brehm 2007).

The diversity and uniformity of hawkmoths were low due to the high dominance of the *E. ello* species, which corresponded to most specimens collected in the general analysis and between strata. However, the greater diversity of species found in the midstory can be explained by the high dominance of *E. ello* in the canopy. *Erinnyis ello* has been mentioned in the literature as being among the most abundant species (Motta et al. 1998, Lourido et al. 2018, Conceição and Teston 2020). Motta et al. (1998) highlight its ability to adapt to different environments, both in terms of food supply and the decline in humidity in less rainy periods. In addition, they have great economic importance since this species is polyphagous and one of the main causes of damage to Brazil's rubber tree and cassava crops (Santos et al. 2021).

Hawkmoth abundance massively intensified in the higher strata with more than half of the species occurring only in the canopy and differed in their composition between strata. According to Lourido et al. (2018), these species fly over the treetops, possibly for dispersal, foraging, and mating, due to the physiological flight characteristics of the group (Beck and Linsenmair 2006). However, although hawkmoths are quite active and quick to travel long distances, this allows us to infer a more representative local fauna (Beck and Linsenmair 2006, Merckx and Slade 2014) which we assume to be attributed to the strong tendency of the vegetation type (Niermann and Brehm 2022) or the efficiency of the type of trap used (Brehm et al. 2021). This preference for the canopy was also highlighted in a study that only analyzed the canopy of a Dense Ombrophylous Forest in Central Amazonia, inventorying 52 species and 1,748 specimens of hawkmoths (Lourido et al. 2018), as well as other research reinforces this distribution pattern (Schulze and Fiedler 1997).

The sphingofauna in the TNF may be richer, considering that the species richness estimates indicated such an increase with the introduction of more samples. This can indeed be considered valid since 20 species were reported (Jakeline Arcanjo de Arcanjo, unpublished data) for this conservation unit and, bearing in mind that the species richness in areas of Amazonian forests has been quite expressive in other works (Motta et al.1991, 1998, Motta and Andreazze 2001, 2002, Motta and Xavier-Filho 2005, Hawes et al. 2009, Camargo et al. 2016, Lourido et al. 2018).

The faunal composition between strata differed considerably, with a canopy trend different from the others. This peculiarity is due to the entire fauna, with almost half of the species occurring only in the canopy, and the rest were shared with the midstory. The canopy possesses unique kinds of microclimatic characteristics (light, wind, temperature, and relative humidity variation), inherent structure, and dynamics that attract a variety of animals drawn to the numerous and varied habitats (foliage, epiphytes vines, cavities of branches, hollow trunks, and branches), diversified and abundant food resources (leaves, flowers, and fruits) (Puig 2008). Furthermore, the aerodynamic body and wings of hawkmoths make them excellent fliers capable of hovering in the air (Grimaldi and Engel 2005), constituting important attributes to withstand microclimatic instability in the higher strata.

Considering that most studies only prioritize one stratum, our study provided important information about the vertical distribution of hawkmoths, showing that species richness, abundance, and composition are different between strata. Among them, the canopy stood out in quantitative and qualitative terms of species, showing the preference of hawkmoths for this stratum. This contribution can support answering gaps in the structure and complexity of tropical forest fauna, especially with the addition of a stratum that connects the extremities. However, we emphasize that the vertical distribution of hawkmoths needs a better understanding under the influence of other variables, such as, for example, the interaction with its host plant and food resource.

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The authors have declared that no competing interests exist.

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Supplementary material S1

Table S1. Richness and abundance of Sphingidae collected in three vertical strata canopy (C), midstory (M) and understory (U) in FLONA do Tapajós, Pará, Brazil, from May 2019 to February 2020.

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