Moth communities are more diverse in the understory than in the canopy of a tropical lowland rainforest in NW Ecuador

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Abstract

Tropical rainforests are the most species-rich terrestrial habitats and provide distinct niches for specialization and speciation, in part due to their vertical stratification. Stratification is observed in many insect orders as a result of abiotic factors, resource availability, and insect behavior. Here, we investigate the stratification of five clades of Lepidoptera: Erebidae-Arctiinae, Geometridae, Hedylidae, Saturniidae and Sphingidae, which differ in many aspects of their ecology and traits. The study was carried out in a tropical rain forest of the Chocó region in NW Ecuador. We used funnel traps equipped with weak UV LED lamps to sample moths simultaneously in the canopy and understory in four forest habitats. We identified species using reference collections and with the aid of DNA barcoding and present a qualitatively unique data set for Neotropical rainforests, with 12,472 individuals of 676 species collected in 48 nightly catches. Species richness was on average higher in the understory (73.54 ± 22.58) than in the canopy (59.09 ± 17.24), and median sample sizes were similar (understory: 217.5 (160.5 - 336), canopy: 187.5 (138 - 328.5)). We found taxon-specific patterns: Arctiinae and Sphingidae – the stronger flyers – were more species-rich and abundant in the canopy, and weaker flyers Geometridae and Saturniidae were more species-rich and abundant in the understory. We assume that predation pressure, availability of nectar and host plants shape the vertical distribution of moth assemblages. Communities largely overlapped and were highly nested in each stratum and between habitat types, and differences in composition among habitats were mainly driven by elevation. We found more species in regenerating forests compared to old growth forests, while sample size was independent of abiotic factors like elevation, temperature, or humidity. Our results allow a comprehensive insight into differences in stratification of five moth clades in a tropical rainforest at high taxonomic resolution with respect to habitat types and influences of environmental factors.

Keywords: Chocó, stratification, light trapping, spatial distribution, regeneration, old growth forest

Introduction

Tropical rainforests the most species rich habitats on earth (Plotkin et al., 2000) and the species richness of many taxa in forests can be explained by structural parameters (Storch et al., 2023). One of these variables is the vertical stratification of forests, as the biodiversity of a forest can be predicted by its vertical structural complexity (Gámez & Harris, 2022). A stratified habitat creates multiple spaces for specialization and speciation and provides distinct niches as a result of interactions of microhabitats and microclimatic conditions (Shaw, 2004). The canopy acts as an interface between the terrestrial biomass and the atmosphere above the vegetation (Ozanne et al., 2003) and is considered as one of the most important habitats for insects (e.g. Basset et al., 2003; Intachat & Holloway, 2000; Punthuwat et al., 2024; Schulze et al., 2001). Despite the importance of the canopy, it has often been neglected in research because it is difficult to access and poses logistical challenges (Barker & Pinard, 2001). Some of these challenges can be overcome by using different techniques such as cranes (Parker et al., 1992), towers (Böttger et al., 2025) or ropes (Brehm, 2007; Diniz et al., 2025).

Insects play a crucial role in ecosystems and their functions (Verma et al., 2023), they are the most important and efficient pollinators (Cock et al., 2013) and contribute to physical and chemical decomposition (Singh et al., 2023). Insects serve as predators and prey, thereby influencing biodiversity and controlling populations (Waldbauer, 2006) and influence soil structure and biological networks in the soil. The Neotropical region harbors almost a third of all insect species (Stork, 2018). It is estimated that the insect fauna in tropical canopies is twice as diverse as in the understory (Erwin, 1982), but this estimate is debated controversially (García-Robledo et al., 2020; Ødegaard, 2000). The stratification of arthropods is determined by abiotic factors such as solar radiation, forest physiognomy, resource availability and arthropod behavior (Basset, 1991; Basset et al., 2003). In addition, herbivorous insects might also be differently adapted to the nitrogen content of leaves (Le Corff & Marquis, 1999) and microclimatic conditions (Rytteri et al., 2021). Insect stratification in tropical rainforests has been demonstrated in all major insect orders(Punthuwat et al., 2024 , Punthuwat et al., 2024; Ruchin, 2023).

In Lepidoptera, stratification has been shown for a wide range of elevations for rainforest sites in many regions (Ashton et al., 2016). For example, in temperate deciduous forests, moth diversity was higher in the understory than in the canopy (Böttger et al., 2025; Hirao et al., 2009; Seifert et al., 2020). Geometridae were consistently more abundant in the understory, Erebidae more common in the canopy and Noctuidae were either also more common in the canopy or had no preferred stratum. (Böttger et al., 2025; De Smedt et al., 2019).

Lepidoptera are well suited for comparative studies as they are a diverse group with ca. 180,000 known species (Stork, 2018) and their populations are sensitive to environmental changes (Thomas & Hanski, 2004). They are among the most important nocturnal pollinators of a wide range of plants globally (Macgregor et al., 2015, Hahn & Brühl, 2016). Using artificial light sources during the night, moths can easily be collected in high numbers in a short time (Brehm, 2007; De Smedt et al., 2019; Fabian et al., 2024). Lightweight small lamps are available (Brehm, 2017) and allow automated collection combined with vane traps (Singh et al., 2022).

Because species identification of tropical species is a major challenge, we focused on five groups of Lepidoptera in order to cover a large range of life histories and morphological characteristics. These were the two extremely species-rich clades Erebidae-Arctiinae and Geometridae, both of which have been extensively studied in various Neotropical regions (e.g. Brehm, 2007; Brehm et al., 2003; Hilt, 2005; Jaimes Nino et al., 2019). We added two, less speciose but taxonomically well-known groups, the Saturniidae and the Sphingidae, which have a significantly larger body size, and a significantly different ecology. The small and ecologically interesting group of moth-like butterflies (Hedylidae) was also included.

Previous studies in the tropics indicate taxon-specific patterns: For instance, Arctiinae were more diverse in the canopy, whereas Geometridae were more diverse in the understory of lowland rainforests (Brehm, 2007; Schulze et al., 2001). Sphingidae were more species rich and abundant in the canopy (Schulze et al., 2001; Valente & Teston, 2024) and possess a flight machinery to cover long distance flights for finding larval hosts plants (Janzen, 1984). Saturniidae on the other hand also have very large bodies, but only have rudimentary mouth parts and are capital breeders (Janzen, 1984; Tammaru & Haukioja, 1996).

While stratification plays a major role in shaping local insect communities, they are also highly influenced by different forest habitats and land use. Moth communities in secondary forests also differ in their response in terms of species richness and abundance (Taki et al., 2010). Arctiinae, Saturniidae and Sphingidae responded evenly in abundance and community structure but varied in species richness following disturbance (Hawes et al., 2009).

We sampled moths of the five clades both in the canopy and the understory in a chronosequence of regenerating cacao plantations and pastures and old growth forests. Given results from previous studies and the different ecology of the clades, we expected contrasting patterns of diversity in the five taxa between canopy and understory, with higher abundance and diversity of Arctiinae and Sphingidae in the canopy and the inverse pattern in Geometridae and Saturniidae, because of their respective flight capabilities (Brehm, 2007; Intachat & Holloway, 2000; Valente & Teston, 2024). For Saturniidae, we expect a higher abundance and diversity in the understory because of predator avoidance such as bats (Bernard, 2001; Campelo et al., 2020). Overall, we expected an influence of elevation and temperature on moths because these are well known to shape the communities (Brehm et al. 2007). We expected a similar diversity of moth communities between regenerating and old growth forests (in a mosaic of habitats) beause plant species composition – important for both caterpillars and most adult moths – in regenerating forests is often as diverse as in old forests (Saldarriaga et al., 1988).

Materials and methods

Study area

We conducted our study in the Río Canandé reserve (0.5263°N, -79.2130°E), in Esmeraldas Province, NW Ecuador. The reserve was created in 2000 and includes around 84.9km^2 of protected area (Fundación Jocotoco - Jocotours, 2024, Fig. 1).

Its elevation ranges between 100–500m a.s.l. and it is part of the tropical forest of the Chocó-Darien eco-region with lowland evergreen forest on the western side of the Andes. Between 1938 and 1988, the Ecuadorian Chocó below 900m asl was deforested by 95%. In the lowlands, deforestation is still ongoing and only 3% of the rain forest have remained. The topography of the reserve and its surrounding areas is hilly and is traversed by several streams (Escobar et al., 2025). It consists of a mosaic of old-growth forests, pastures, cacao plantations as well as regenerating forests (Hoenle et al., 2022). The cultivation of land usually dates back less than 50 years.

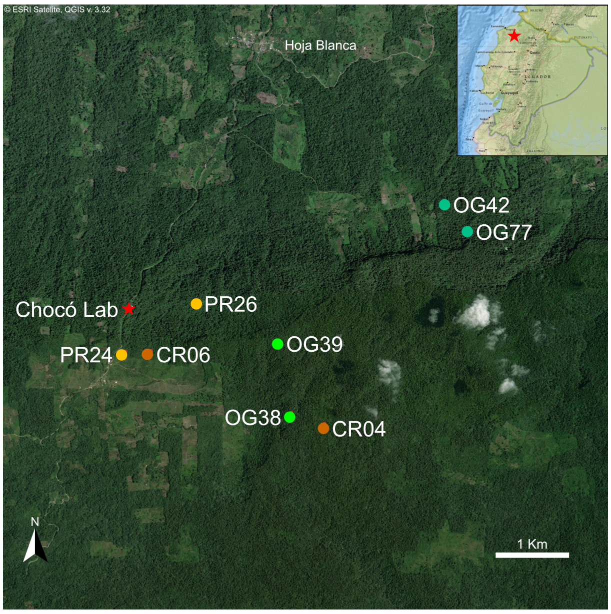

Fig. 1: Satellite image of the study area in the Chocó Forest in Esmeralda province, NW Ecuador. Points mark the positions of the sites. Light brown = cacao regeneration, bright green = old growth forest

at high elevations, dark green = old growth forest at low elevations, yellow = pasture regeneration, numbers = site ID. Red star = position of the research station. © ESRI satellite, QGIS.

The Chocó rainforest is one of the rainiest places on earth (Poveda & Mesa, 2000) with an annual precipitation of 3000–5000mm (Plan de Manejo del Refugio de Vida Silvestre El Pambilar, 2011). The region has average temperatures between 25–26°C and has one of the most plant diverse communities in the world with high levels of local and regional endemism (Gentry, 1986). When compared to other Neotropical forests, the understory of Chocó forests varies with a higher diversity and density of fertile species, even on poor soils. We chose a total of eight plots for our study: two were in cacao regeneration sites (CR), two in were pasture regeneration sites (PR), and four were old growth forest sites (OG). These latter are divided into two sites each with a higher (OG-high) and a lower elevation (OG-low, Fig. 1). See Fig. S1 for photographs of understories of the habitat types. The elevation of the sites ranged from 325m asl to 576m asl (Tab. S1). CR and PR varied slightly in their age of regeneration. Seven plots were chosen from plots established by the DFG-funded Research Unit Reassembly FOR 5207 (Escobar et al., 2025).

Traps and sampling

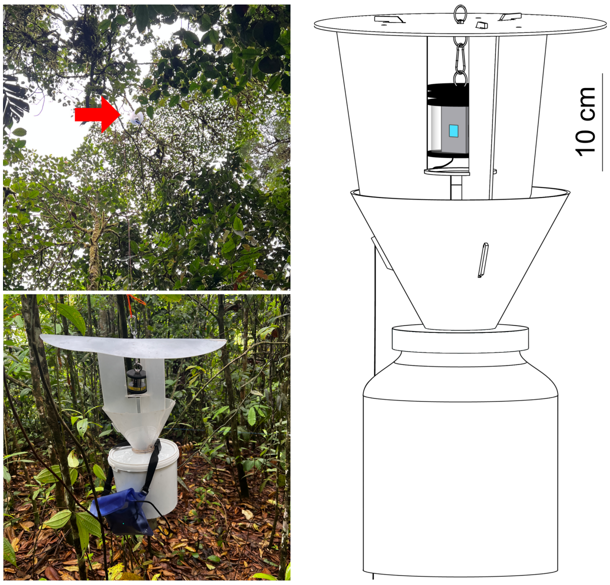

Fig. 2: Photographs of the funnel trap set up in the canopy (red arrow) and understory, and 3D model of a trap. Egg cartons and chloroform supply are placed inside the bucket. The blue bag stores the battery. On top of the trap is a roof extension (not shown in the 3D model).

The basic trap design was described by Brehm (2007) and Singh et al. (2022). The traps consisted of a roof (diameter 50cm), three vanes (length 30cm) and a funnel of white polypropylene (Fig. 2). This chosen design proved to be most efficient in attracting the most moth species and individuals (Singh et al., 2022). We used LepiLED *mini* lamps (Insects & Light, Jena) to attract moths (Böttger et al., 2025; Niermann & Brehm, 2022), equipped with eight power LEDs with mixed radiation (Brehm, 2017). Power bank batteries (26 Ah) were used to supply electricity**.**

We conducted trapping from October to December 2021 and March to May 2022. All trapping events took place in phases around new moon in the lunar cycle, thus minimizing the negative effect of full moon on catches (Nag & Nath, 1991). A catch started at dusk at around 18:00 and lasted 12 hours. The on / off switching of the lamps was controlled by USB-timers (Lucstar, China). We collected during two time periods in 2021 and one period in 2022 at each site in the canopy and understory in parallel, resulting in 48 pairwise collected samples. The traps in the canopy were pulled upwards using the bow and arrow method (Diniz et al., 2025). We always collected at the exact same location in the understory. In the canopy, however, the position differed between 2021 and 2022 by a few meters because some of the hauling ropes had to be replaced in order to pull up the traps. Understory traps hung at 1.7m in height above ground level. The height of the canopy traps ranged between 12.4m and 20.9m (Tab. S. 2) as it was not possible to specify an exact height with the bow/arrow method. Additionally, canopy trap height was also limited by the height of the canopy itself. All sites were equipped with environmental sensors in April 2022. These loggers recorded temperature and humidity every 15 minutes from April 2022 to December 2022, April 2023 – June 2023 and from September 2023 – October 2023.

Specimen handling and identification

We picked up the traps on the next day and processed the samples in the nearby research station. Since identification was usually not possible in the field, we put most of the material into glassine bags and froze the samples. For common species, we took at least three voucher specimens per species and sample and photographed the remaining individuals. The prepared specimens are permanently stored in the entomological collection of the Phyletisches Museum Jena (PMJ) and are accessible for further investigation and taxonomic work. The Herbario Instituto Nacional de Biodiversidad and Museo de Zoología de la Universidad Technológica Indoamérica issued the mobilisation permits MAAE-CMARG-2021-0284 and MAATE-DZ2-OTQ-006-2021, respectively. The Museo de Historia Natural "Gustavo Orcés V." issued the export permit 16-VS-OTO-D22E-MAATE-2021.

After preparation, we sorted specimens morphologically. Species were identified to the lowest possible level using refence collections in the PMJ, the research collection of G. Brehm and photographs taken by him in the Natural History Museum (London). Electronic species catalogues are being prepared (Brehm et al., in prep.). All morphospecies were assigned with unique species numbers within each family. 505 individuals were DNA barcoded in the Canadian Centre for DNA Barcoding, using a standardized protocol for amplifying, and analyzing a 658 base pair region of the CO1 gene (deWaard et al., 2008). The DNA barcoding assigned 483 individuals to Barcode Index Numbers (BINs) in the BOLD Database. This DNA analysis further supported and refined the assignment of the material to at least subfamily level, often to genera and less frequently to species level (Brehm et al. in preparation). Each individual was assigned with unique species number. These numbers which are cross-comparable to individuals in the PMJ collected during other campaigns in the Neotropical region.

As the focal taxa differ significantly in their respective species richness, we also carried out some of our analyses at a lower taxonomic level. This was the case in Geometridae (subfamilies Desmobathrinae, Ennominae, Geometrinae, Larentiinae, and Sterrhinae) and in Arctiinae (tribe

Lithosiini, the tribe Arctiini with subtribes Arctiina, Phaegopterina, Pericopina, and the sister clades Ctenuchina+Euchromiina combined) (see Jacobson & Weller, 2002; Pinheiro & Duarte, 2013).

Statistical analyses

We performed all statistical analyses in R (version 4.4.2, R Core Team, 2024) and R Studio (version 2022.10.0 RStudio Team, 2024). We calculated species accumulation curves as well as sample coverage using the *iNEXT* package (Hsieh et al., 2016) with both the Hill numbers q = 0 and q = 1 (Hill, 1973). For analyses of the species diversity, we combined all samples for strata (n = 2 strata x 4 habitats = 8) and for habitats (n=4). We applied the *vegan* package (Oksanen et al., 2020) and calculated observed species richness by strata (canopy vs. understory) and by habitat (CR vs. OG. vs. PR). Furthermore, we calculated four richness estimators: Fisher's α (Fisher et al., 1943), Chao- estimator (Chao, 1987), Jackknife 1- index (Zahl, 1977) and bootstrap estimator (Burnham & Overton, 1979). Furthermore, we calculated Fisher's α for each sample individually and checked for normal distribution of these values in each stratum with a Shapiro test (Shapiro & Wilk, 1965). We calculated the means for normal distributed data and tested for differences using a t test for paired data. In addition, we used rarefied diversity of each sample within each focal group to access strata specific diversity patterns. We calculated the subsample size of each species by site matrix as the minimum of all row sums and applied this within the *rrarefy* function of the *vegan* package (Oksanen et al., 2020). For Hedylidae, Saturniidae and Sphingidae, this resulted in empty vectors due to the low sample size. For Erebidae-Arctiinae and Geometridae, we generated paired boxplots and tested for differences with a t-test for normal distributed data (Arctiinae) and Mann-Whitney-U-Test for non-normal distributed data (Geometridae).

We analysed species strongly associated with each stratum and habitat with the *indicspecies* package (De Cáceres & Legendre, 2009). We tested for similarity among all focus taxa across strata and habitats for non-metric multidimensional scaling (NMDS) for ordination analyses of our samples, based on the Bray-Curtis distance (Bray & Curtis, 1957). We tested these differences with analyses of similarity (ANOSIM) and adjusted the p-values for multiple testing using a false-discovery rate control (Benjamini & Hochberg, 1995). Hedylidae and Sphingidae were not included because of low species numbers and rare species. We used the *adespatial* package (Dray et al., 2022) for calculations of beta diversity between the strata and habitats for the focal groups. Beta diversity is composed of "nestedness" and "turnover" (Baselga, 2010) and usually refers to the Sørensen index of dissimilarity (Sørensen, 1948). We applied generalized linear mixed models to check for the influence of environmental factors on sample sizes. We rescaled the variables average humidity, average temperature, and canopy height (Tab. S2). We choose site id as random effect and a poisson error distribution for count data. We set up three models, two of which failed due to large eigenvalues (Tab. S3). Furthermore, we checked for overall differences in sample size between strata. We checked for normal distribution between both strata with a Shapiro test (Shapiro & Wilk, 1965) and conducted a paired Wilcoxon test (Wilcoxon, 1945) for non-normal data.We visualized our data by using the *ggplot2* package (Wickham, 2016) and Affinity Designer (v. 2.0.3).

Results

Diversity patterns

We captured a total of 12,472 individuals of 676 species belonging to our five focal groups in 48 nightly catches (Tab. 1). Of these, we exported, prepared, and labelled 9,897 individuals (79.4 %) and stored them in the collection of the PMJ. We collected 6,328 individuals (521 species) in the canopy and 6,144 individuals (586 species) in the understory (Tab. 1). Arctiinae represent nearly two thirds of all collected individuals with two thirds of these from regenerating plots. Arctiinae also had most exclusive species in the canopy (48) whereas Geometridae had most exclusive species in the understory (90). For all habitats, the number of exclusive species per focal group was mostly equally distributed. Canopy and understory shared 431 species and all habitats had 191 species in common. A complete list of all individuals and species can be found in the supplementary material (S2).

Tab.1) Observed, exclusive and shared species numbers as well as individuals per family and combined, separated by strata and habitats. Note that the species numbers do not add up to its total sum as some are shared. Hedylidae are not listed because they only contributed with a total of 61 individuals, but these are included in the total sum. Details are shown in Tab. S4. **Bold face**: highest number.





	Arctiinae			Geometridae			Saturniidae			Sphingidae			All		
	sp.	exc.	ind.	sp.	exc.	ind.	sp.	exc.	ind.	sp.	exc.	ind.	sp.	exc.	ind.
STRATUM															
Canopy	**243**	**48**	**4605**	208	31	1463	41	4	130	**22**	**6**	**90**	521	90	**6328**
Understory	235	40	3585	**267**	**90**	**1996**	**57**	**20**	**490**	21	5	52	**586**	**155**	6144
shared	195	--	--	177	--	--	37	--	--	16	--		431	--	--
HABITAT															
CR	**208**	18	2308	195	26	933	38	4	165	15	2	31	**462**	50	3450
OG-high	190	17	1659	176	23	884	42	5	**239**	**19**	4	**63**	431	49	2868
OG-low	162	5	1401	151	9	580	26	4	72	9	1	16	352	19	2079
PR	196	**22**	**2822**	**196**	**34**	**1062**	**43**	**6**	144	12	4	32	454	**66**	**4075**
shared	95	--	--	78	--	--	15	--	--	3	--	--	191	--	--

TOTAL	283	--	8190	298	--	3459	61	--	620	27	--	142	676	--	12472

Legend: CR = cacao regeneration, exc. = number of exclusive species, ind. = individuals, OG-high = old growth forest high elevation, OG-low = old growth forest low elevation, PR = pasture regeneration, sp. = number of species.

The species accumulation curves (Fig. 3) indicate significant differences when comparing all focal groups combined between strata. Both strata had a high sample coverage above 97% (Tab. S5). The understory was generally more species rich than the canopy (Fig. 3). This is true for the Hill numbers q = 0 and q = 1 (Hill, 1973). The least species rich habitat across all Lepidoptera groups were OG-low sites; PR sites were intermediate (Fig. 3). Species richness was highest between CR and OG-high (confidence intervals do not overlap). Sample coverage ranged between 93% and 96%.

At family level, only Geometridae were significantly more species rich in the understory for both Hill numbers (Fig. S2). Both strata had a sample coverage of 96% (Tab. S5). When comparing the habitats, Arctiinae showed a significant difference with the CR plots being more species rich than OG-low plots for q = 0 (Fig. S2). For q = 1, which gives less weight to singleton species, species richness was highest in CR and OG-high plots, intermediate in PR and lowest OG-low plots. Sample coverage was between 96–98% (Tab. S5). Saturniidae were more species rich in PR plots compared to all other (q = 0, sample coverage 89%). The species accumulation curves for Hedylidae and Sphingidae show dispersed confidence intervals.

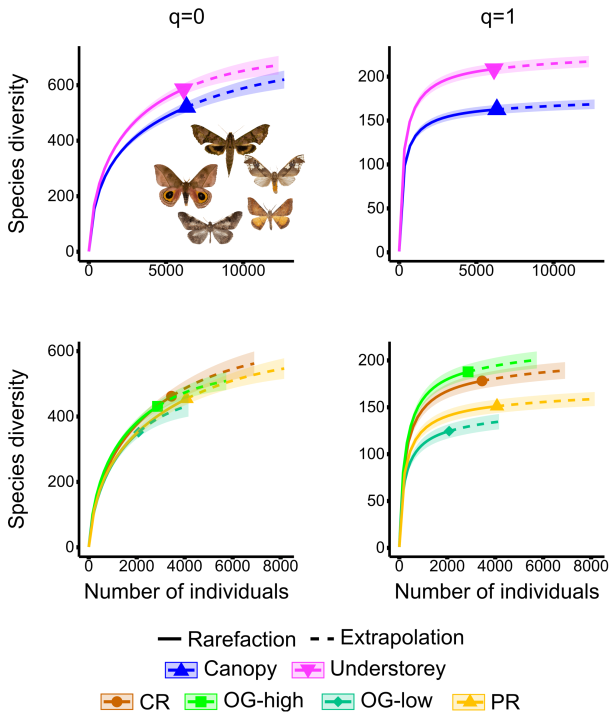

Fig 3: Species accumulation curves for all Lepidoptera, separated by strata and habitat based on species richness (q = 0) and exponential Shannon index (q = 1). The curve represents sample size (solid line) and extrapolated species numbers (dashed line) with 95% confidence interval (shade).

Fisher's α values for each sample, separated by strata, followed a normal distribution (p: canopy = 0.719; understorey = 0.848). The means of Fischer's α indicate a higher diversity in the understorey (73.54 ± 22.58) compared to the canopy (59.09 ± 17.24). A t-test for paired data showed significant differences between both strata (t = -3.5179, df = 23, p = 0.001846) Species number estimators suggested around 80–90 more species in the understory compared to the canopy (Tab. S6). For Arctiinae, Fisher's α and estimators were similar in both strata. Geometridae were more diverse in the understory (Fisher's α 82.9 vs. 66.3) and species estimators suggest 70 more species in the understory than in the canopy.

For both groups, rarefied diversity (q = 1) of each sample did not indicate significant differences between strata (Fig. 4). However, in Geometridae, many plots showed the same rarefied diversity, resulting in many ties and the median being the same value as the lower 25% Quartile (canopy) or higher 25% quartile (understory). For Geometridae, a Mann-Whitney-U-Test showed no differences between the strata (W = 323.5; p = 0.42). A t-test for the normal distributed rarefied diversity data of Arctiinae did not show significant results between the strata (t = -0.085; df = 38.7; p = 0.93).

Saturniidae are consistently estimated to be more species rich, however Fisher's α suggests a slightly higher diversity in the canopy (20.6 vs. 16.7, Tab. S6). Sphingidae species numbers between strata is quite similar and all the estimators suggest a similar species number, as the standard errors overlap. Furthermore, they showed the lowest alpha diversity of all groups with the understory being more diverse than the canopy (13.1 vs. 9.3).

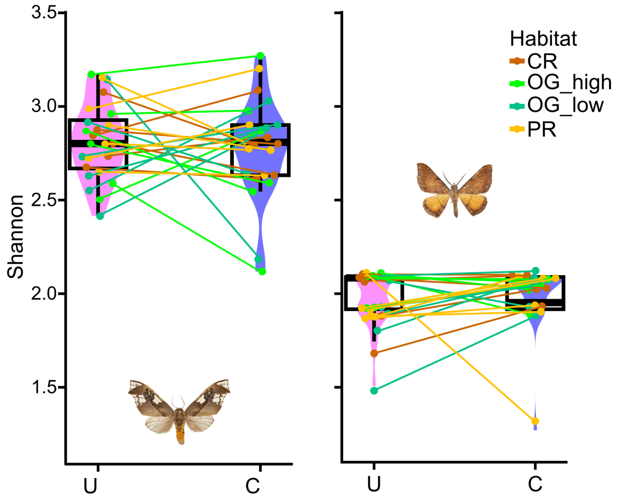

Fig 4: Rarefied diversity (q = 1) of Arctiinae (left) and Geometridae (right) of all samples (n=48), separated by strata (U = understory; C = canopy). Thick horizontal lines indicate the distribution's median. Shaded areas represent data point density. Colorful lines connect corresponding samples from both strata. Note that a t test for Arctiinae and a Mann-Whitney-U-Test for Geometridae did not show any significant differences between strata.

Among habitats, CR and OG-high sites showed higher alpha diversity (Fisher's α 143.4 and 140.7, Tab. S6) compared to OG-low and PR sites (121.5 and 130.8). All estimators suggest most species in CR, followed by PR and least species in OG sites. However, the observed species number was roughly the same between CR, OG-high and PR. Arctiinae diversity was similar on CR and OG-high sites (Fisher's α 55.4 and 55.3) but lower at OG-low and PR sites (47.4 and 47.9). Geometridae were more diverse in regeneration sites (Fisher's α 75.1 and 70.6, respectively) compared to OG sites (high: 66.0 low: 66.3). Saturniidae showed their highest α diversity in PR sites (20.8) while the other three habitats were roughly similar. For Sphingidae, Fisher's α was highest in CR (11.4), roughly similar in both Ogs and lowest in PR (7.0).

Indicator species and community patterns

We detected a total of 80 indicator species: 32 Arctiinae, 30 Geometridae, 15 Saturniidae and three Sphingidae (Tab. S7). There were 51 indicator species for both strata (12 for the canopy and 39 for the understory). The numbers of indicator species in Arctiinae between canopy and understory were similar (8 vs. 6, respectively.) Only three Geometridae species were indicators for the canopy, but 19 for the understory. No Saturniidae species was an indicator species for the canopy, but 13 species for the understory. For habitats, we detected 29 indicator species (2 for CR, 14 for OG-high and 13 for PR).

In the NMDS ordinations, one point represents all samples at one site from one stratum (Fig. 5, 16 datapoints per graph). These ordinations are split according to moth groups. The community composition of Arctiinae, Geometridae and Saturniidae was explained by average temperature and elevation (both $p < 0.05$) (Fig. 5). Average humidity and regeneration time did not explain data separation.

There was an overlap for all focal taxa combined between canopy and understory samples which was mostly driven by the overlap of Arctiinae. Arctiinae canopy communities were not different from the understory ones (ANOSIM p_adjust = 0.1023, Tab. S8). For Geometridae, understory samples appeared to be well nested within the canopy (Fig. 5), however ANOSIM showed significant differences (p_adjust = 0.0112, Tab.5). Saturniidae showed a clear separation in communities across the strata and in the opposite direction of the environmental factors (ANOSIM p_adjust = 0).

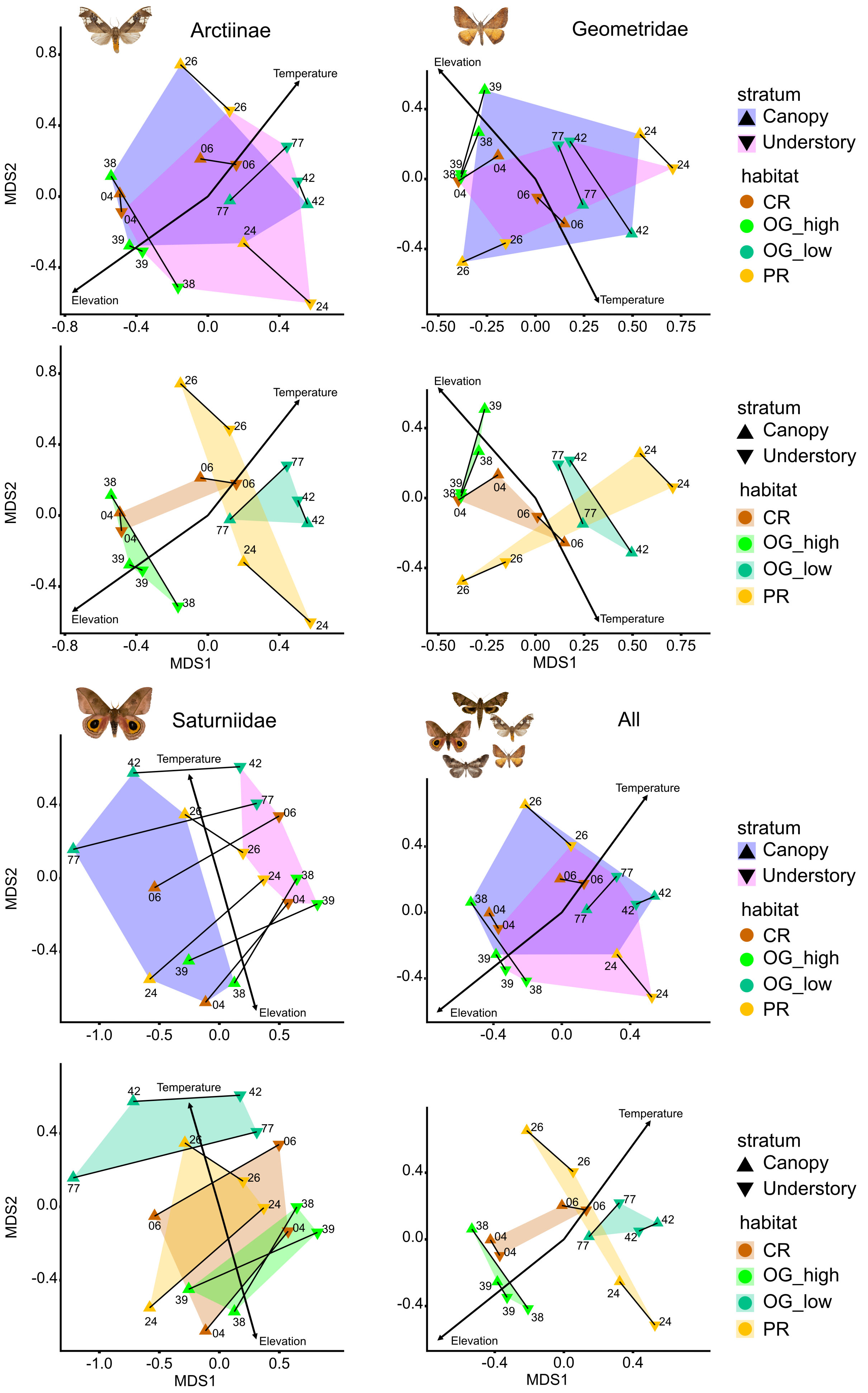
Arctiinae
Geometridae
Saturniidae
All
MDS1
MDS2
Temperature
Elevation
0.8
0.4
0.0
-0.4
-0.8
-0.50
-0.25
0.00
0.25
0.50
0.75
-1.0
-0.5
0.5
stratum
Canopy
Understory
habitat
CR
OG_high
OG_low
PR
04
06
24
26
38
39
42
77

Fig. 5: NMDS ordinations for three species-rich Lepidoptera taxa Arctiiane (A, B); Geometridae (C, D); Saturniidae (E, F) and all Lepidoptera combined (G, H). Polygons show the area covered by one stratum (A, C, E, G) or habitat (B, D, F, H). A triangle represents three repeated catches at each side. Connecting lines between triangles visualize corresponding data from canopy and understory. Numbers show site identity. Arrows show the significant post-hoc vectors of environmental factors. Note that Hedylidae and Sphingidae are not included due to their low sample sizes and high stress values.

All samples from old growth forest sites appeared quite similar (Fig. 5). Both high and low sites clustered closely together but there was a difference between high and low, which was well explained by the environmental gradients. Regenerating sites appeared far less homogeneous as they spread along the axes of the NMDS plots. Arctiinae, Geometridae and all groups combined showed significant differences along the habitats (Tab. S8). Only Saturniidae did not show any difference (ANOSIM p_adjust = 0.1023).

The GLMMs (Tab. S3) did not detect any influence of environmental factors on sample sizes. This is true for average humidity and temperature, plot elevation above sea level and trap elevation above ground as well as habitat type. Sample sizes followed a non-normal distribution (p: Canopy < 0.05, Understorey = 0.0362). A Wilcoxon test for paired data did not show any differences in sample sizes between strata (V = 151, p = 0.9886)

All values for beta diversity (Sørensen, 1948), ranged from 0.077 for Hedylidae between strata to 0.466 for Geometridae between habitats (Fig. 6). The beta diversity of Geometridae, Saturniidae and Sphingidae was nearly identical for both strata and habitats, but Saturniidae showed a much larger species turnover. Beta diversity for Sphingidae between habitats was driven by nestedness, while Hedylidae beta diversity was driven by species turnover.

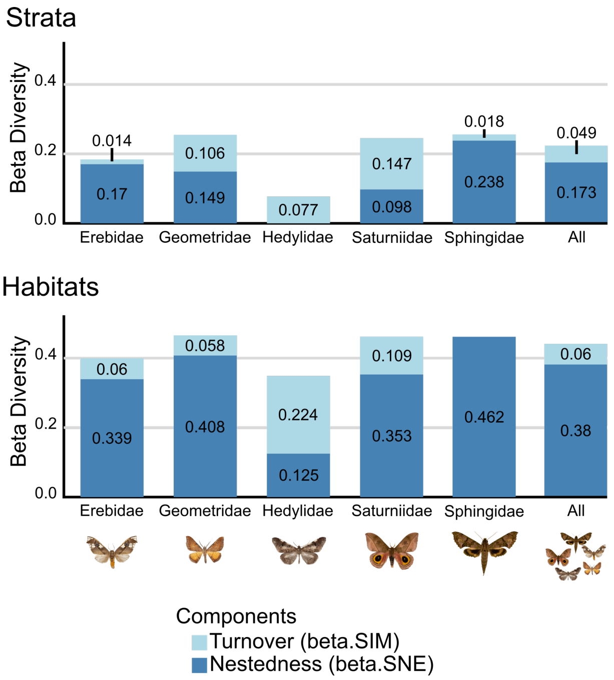

Fig. 6: Beta diversity, composed by nestedness and turnover, as index of dissimilarities for all samples, separated by focal groups and strata as well as habitats.

Community composition showed only small variation when focusing on individuals (Fig. 7). Arctiinae dominated both strata and all habitats above 50%. Lithosiini were the most dominant group, with *Agylla* and *Nodozana* being the most dominant genera with 1067 and 591 individuals, respectively. Saturniidae were more abundant in the understory and in the OG-high sites. The proportion of Phaegopterina (Arctiinae), Geometrinae, Larentiinae and Sterrhinae (all Geometridae) shows only small variation across the strata and habitats.

When focusing on species numbers, Arctiinae are still a dominant group, but its dominance is never higher than 50 %. The most species rich group across strata and all habitats is Ennominae with *Macaria* and *Pero* being the most species rich genera with 17 and 12 species, respectively. Lithosinii had disproportionately few species compared to their high specimen counts. The proportion of Saturniidae and Sphingidae species between strata is quite similar and as high as among the habitats, but both groups were represented only with a few specimens.

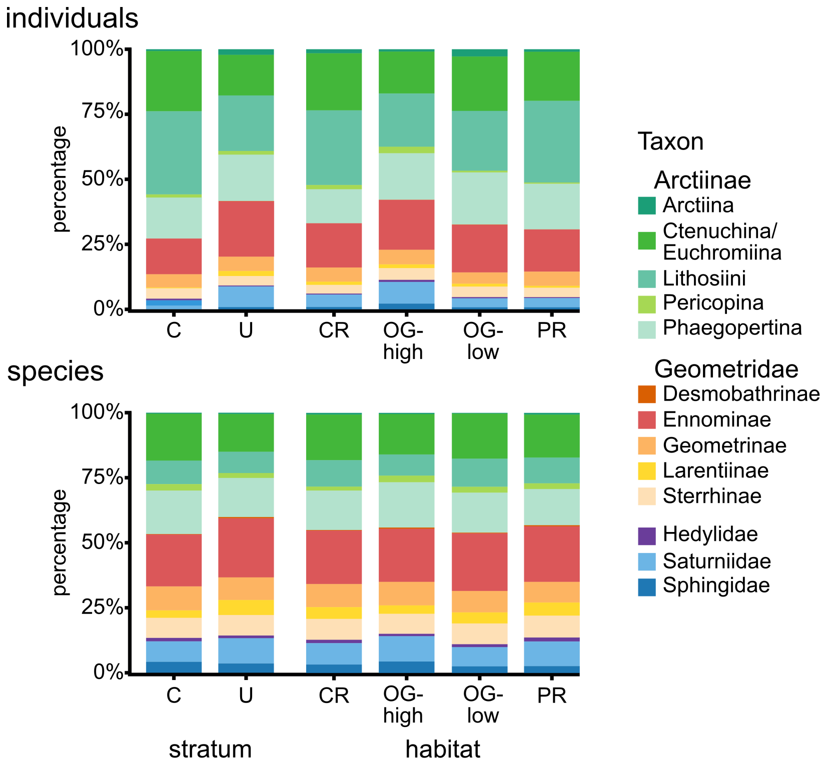

Fig. 7 Community composition at the level of focal groups between the strata and habitats, separated by individuals and species. C = canopy, CR = cacao regeneration, OG = old growth forest, PR = pasture regeneration, U = understory.

Discussion

Group-specific stratification of moths

Our study represents a qualitatively unique data set not only for the Chocó region but for Neotropical rainforests generally. We got a more comprehensive insight into moth stratification in a tropical rainforest as compared to previous studies that focused on fewer groups (e. g. Brehm, 2007; Diniz et al., 2025; Valente & Teston, 2024). Using several light-weight UV traps at once, we applied an innovative and efficient sampling method (Brehm, 2007; Diniz et al., 2025; Singh et al., 2022). This approach allowed a simultaneous sampling in two strata, which is strongly recommended (Spalding, 2024). A broader sampling approach might allow for further insights in moth community responses to habitat changes (Correa-Carmona et al., 2022; Diniz et al., 2025), but this results in less repetitions within the constraints of available resources.

For all five moth clades combined, we found a higher species number in the understory and diversity, and overall similar numbers of individuals. Our expectations of Geometridae and Saturniidae being more abundant and species rich in the understory and Arctiinae being more diverse in the canopy, even if only slightly, were met. Only with Sphingidae did we find a slightly different pattern than we had expected.

Canopies are fundamentally different in terms of many parameters such as UV radiation, evaporation rate and wind speed as compared to the understory (Lowman & Rinker, 2004; Ozanne et al., 2003). Their arthropod communities are supposed to be twice as diverse as in understories (Basset et al., 2003; Erwin, 1982; Ødegaard, 2000). Many insect orders show stratification patterns in different habitat types around the globe (e.g. Ashton et al., 2016; Brehm, 2007; Hirao et al., 2009; Punthuwat et al., 2024; Ruchin, 2023). Diniz et al. (2025) could only explain little variation in abundance and diversity of arctiinae moths between both strata by canopy height, legacy, and proportion of forest.

Predation is a major candidate as a potential driver of vertical stratification in moths. Insectivorous bats forage with the onset of dusk during night and are more active in tropical canopies (Bernard, 2001; Carr et al., 2020). Certain moth groups (such as Sphingidae) are fast flyers and thus often easily able to escape predators (Janzen, 1984). We found indeed more Sphingidae individuals in the canopy (although a higher diversity in the understory). On the other hand, Saturniidae – with equally large bodies as Sphingidae – are more threatened by bats due to their low flight capabilities. The canopy is probably a particularly dangerous place for rather poorly defended large flying insects, and our results show significantly more species and individuals in the understory. Several species of Saturniidae have evolved a bat-irritation strategy such as using folded structures in the wingtips that reflect ultrasound particularly effectively or hindwing decoy (Lee & Moss, 2016; Neil et al., 2021). A common defense mechanism of moths is hearing with tympanal organs – being present in Arctiinae, Geometridae and Sphingidae (Kawahara & Barber, 2015; Zha et al., 2009). La Cava et al. (2024) showed that 21ympanite moth species can actively avoid predation by bats and also choose denser forests with less bat activity. Geometridae show indeed a clear stratification with more species and individuals being present in the understory, probably avoiding bat predation. Lastly, Arctiinae might yet have another strategy with regard to bats: Many species possess chemical defense systems (Weller et al., 1999; Zaspel et al., 2014) and are able to emit ultrasonic clicks as aposematic signals to bats (Dunning et al., 1992). Insectivorous birds, ants and spiders could also contribute to the shaping of moth communities since the activity could vary between the strata (Walther, 2002a). Especially birds are likely to play a major role as predators, and most signals displayed on moth wings are addressed to birds, such as false eyespots in Saturniidae or hymenopteran mimics in Arctiinae (Weller et al. 1999).

Resource availability is another potentially major driver for shaping arthropod stratification (Basset et al., 2003). Overall, knowledge on host plants of lepidopterans is sparse (Diniz et al., 2001). For Geometridae, species accumulation curves strengthen the impression of an understory group; we found 19 indicator species, four of these were *Eois*. *Eois* caterpillars are associated with understory *Piper* bushes and treelets (Bodner et al., 2012). Except for Desmobatrinae, all other Geometridae subfamilies are represented as indicator species of the understory. In Arctiinae, it is assumed that Poacaceae and Asteraceae are important plant families (Rab Green et al., 2011) but so far, their survey was exclusively conducted in the understory. However, genera such as *Macrocneme* or *Poliopastea* caterpillars were reported feeding on Apocynaceae and Asclepiadaceae (see Brehm, 2007; Janzen & Hallwachs, 2005), both plant families represented with lianas flowering in the canopy. We found three *Agylla* species as indicators of the canopy; it is assumed that such Lithosinii species feed on lichens (Kawagoe et al., 2022).

The availability of flowering plants as nectar source might also have an important impact on the vertical distribution of moths. For instance, tree flowering intensity increases the number of species and individuals of Geometridae with a short delay (Intachat et al., 2001). Among our focal groups, Sphingidae are likely to have the longest proboscises, allowing them to pollinate flowers that cannot be reached by other insects, e.g., they pollinate epiphytic orchids with long tubes (Danaher et al., 2020). The understory mainly composes of aroids and piperoids, while orchids and ferns are more present in the canopy. Additionally, hawkmoths also pollinate a variety of tree species, shrubs, herbs, and lianas (Haber & Frankie, 1989). This distribution might explain why we found a higher diversity of Sphingidae in the understory but more individuals in the canopy. Hawkmoths are able to fly long distances, so they can easily reach this wide range of hosts plants, which enables their life strategy as income breeders (Janzen, 1984; Tammaru & Haukioja, 1996). In contrast, the capital breeders Saturniidae lack functional mouthparts, so they cannot make use of the flower rich canopy (Janzen, 1984).

Higher moth diversity in regenerating forests

We observed different communities for all moth clades when comparing old growth forest sites to regenerating forest sites. This differentiation was mostly driven by abundance shifts. At focal group level, species numbers were similar between habitats. There was also a shift in community composition in Arctiinae and Geometridae, but not in Saturniidae. This shift followed an increase in elevation of the sampling sites. Regenerating sites were less homogeneous compared to old growth sites. This results are in line with diversity patterns along elevational gradients for Sphingidae and Geometridae, which showed a peak at mid elevations and are supposed to reflect floristic assemblages along these gradients (Beck et al., 2017; Ignatov et al., 2011).

We did not detect any influence of environmental factors such as elevation, humidity, and temperature on sample size. The same was observed for Arctiinae with a wider sampling scheme covering more habitats and sites (Diniz et al., 2025). However, there is evidence that different moth taxa can be used as indicators for environmental factors and habitats. Arctiinae respond with decreasing abundance, whereas abundance of species in certain Geometridae increased with disturbance (Kitching et al., 2000). These patterns can be explained by food plant preferences: Species in disturbed habitats tend to prefer herbaceous and weedy plants, whereas species in undisturbed habitats tend to feed on woody plants, tress, or vines (Common, 1990; Kitching et al., 2000).

We found more moth species in regenerating sites as compared to old growth forests. Diniz et al. (2025) did not detect such differences in diversity of late regenerating forests and old growth forests. The regenerating habitats in our study have regenerated for 20–32 years and are located in a matrix of old growth habitats as well as actively farmed areas. The plant species composition in regenerating forests is often as diverse as in old forests but with plant species that are more abundant compared to old forests (Saldarriaga et al., 1988), so they fit in the disturbance regime described by the intermediate disturbance hypothesis (Connell, 1978).We found a high nestedness for all groups between sampling sites, which peaked for Sphingidae making up the complete beta diversity. They are able to cover long distance flight between habitats (Janzen, 1984), thus, their communities do not show landscape-related patterns at small spatial scales (Correa-Carmona et al., 2022).

Light trapping and the role of museum collections

Light trapping was used in a broad range of similar ecological studies comparing moth communities and has proven to be an extremely effective method (e.g. Holzhauer et al., 2025; Niermann & Brehm, 2022). UV LEDs are well suited to attract a representative number of Lepidoptera while keeping energy consumption manageable, which is crucial in remote areas (Brehm, 2017). However, there are also minor methodological imbalances in light trapping because some macromoth families show differences in their responses to artificial light; for instance, Erebidae are attracted from slightly further away as compared to Geometridae (Merckx & Slade, 2014). We processed our samples at a high taxonomic resolution and store most specimens (9,897) in a permanent scientific collection. This collection allowed the efficient and targeted selection of individuals for a comprehensive DNA barcoding analysis, which provides the base for species determination at a high taxonomic resolution. It will also be essential for the production catalogue of moths of the Canandé Reserve and it comprises a large number of species new to science that are accessible for taxonomic work in the future (Brehm et al. submitted). Collections generally allow long-term verification of all results and incorporation of new findings in the future.

Conclusions

Our study provides clear evidence for group-specific patterns of vertical stratification in moths that has rarely been shown before in a tropical rainforest. So far, we do not know the underlying mechanisms in detail. However, the study of moths with such different traits as present in the investigated families allows conclusions about probable causes of stratification. These include for instance traits of body shape and body size (Böttger et al., 2025; Graça et al., 2017), wing shape (see DeVries et al., 2010) and coloration (Diniz et al., 2025). The required tools for capturing and automatically analyzing of multispectral images are currently under development and will be available soon (Brehm 2025; Correa-Carmona, Böttger, Brehm, unpublished data).

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Conflict of interest statement

The authors declare no conflict of interest

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Author contributions

D.B., D.U.M., A.K., S.D.L. and G.B. conceived the research project. A.K., S.D.L. and GB acquired and managed the funding. Fieldwork was conducted by D. B, D.U.M. and G.B. Databasing was managed by D.B. and G.B. G.B. managed the curation and identification of specimens. D.B. analyzed the data and conducted the statistical analyses. D.B. and G.B. drafted the manuscript together, and D.U.M., A.K. and S.D.L reviewed it. All authors read and approved the manuscript.

Appendix

CR06, 03.11.2021 OG42, 05.11.2021 PR26, 29.10.2023

Fig. S1: Understory vegetation composition at three plots representing the different habitats. CR = cacao regeneration, OG = old growth forest, PR = pasture regeneration. All photographs: Dennis Böttger

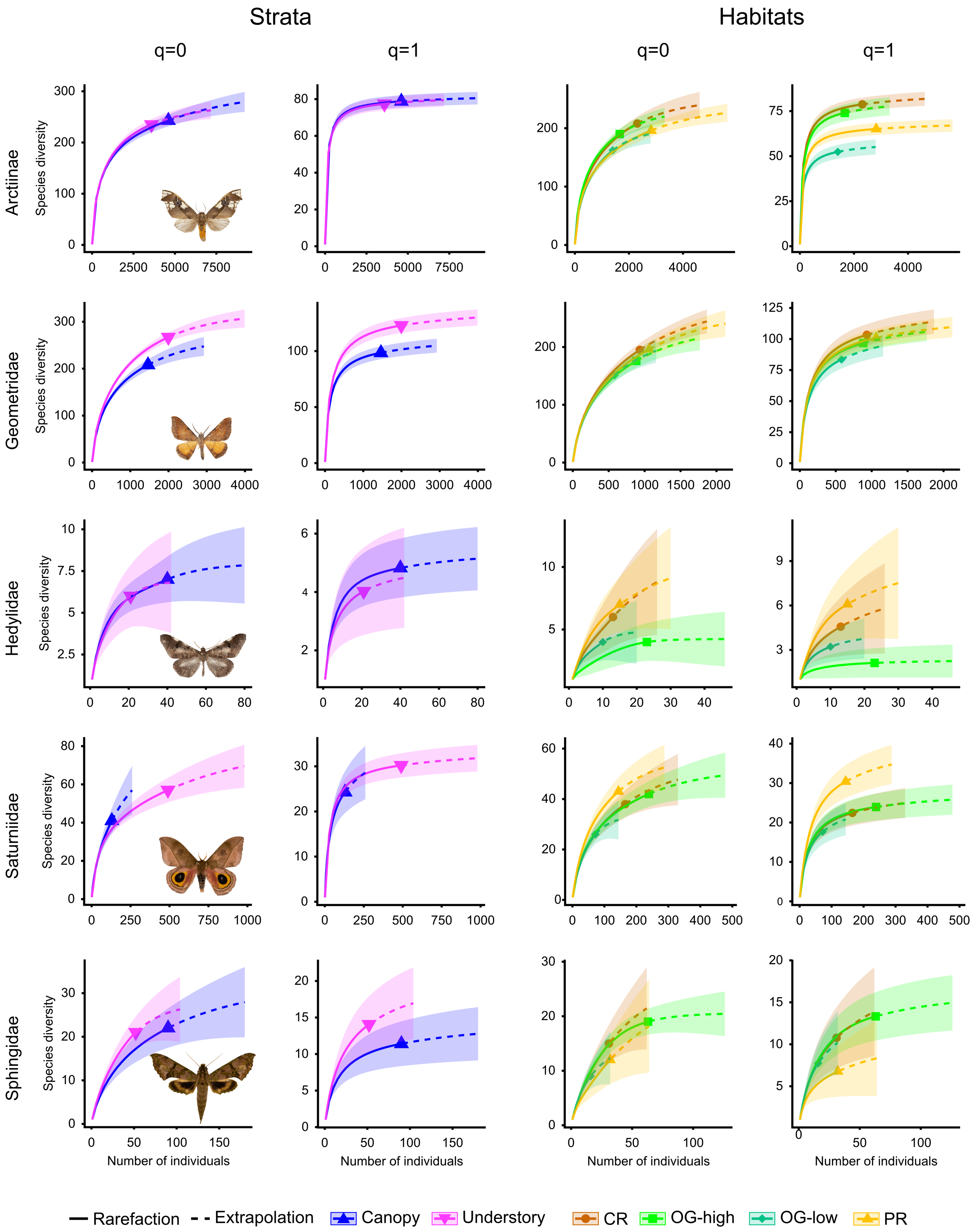

Fig. S2: Species accumulation curves for five groups of Lepidoptera, separated by strata and habitats based on species richness (q = 0) and exponential Shannon index (q = 1). The curve represents sample size (solid line) and extrapolated species numbers (dashed line) with 95% confidence interval (shade).

Tab. S1: Coordinates and elevation of the study sites.

Plot		Latitude	Longitude	Elevation (m asl)	Regeneration year	Average Temperature	Average Humidity
CACAO REGENERATION							
CR04		0.511733210	-79.18950979	560	2002	22.3°C	99.5%
CR06		0.520721963	-79.21059304	397	1990	23.0°C	99.8%
OLD GROWTH FOREST							
OG38	high	0.513320000	-79.19337000	535	--	21.6°C	99.9%
OG39	high	0.521800000	-79.19516000	576	--	21.5°C	97.5%
OG42	low	0.538493693	-79.17462629	374	--	22.6°C	97.9%
OG77	low	0.535481000	-79.17220400	370	--	22.6°C	97.9%
PASTURE REGENERATION							
PR24		0.520523982	-79.21374598	381	2002	22.7°C	98.5%
PR26		0.526453592	-79.20466318	325	1995	23.3°C	97.6%

Tab. S2: Trapping dates and elevation of all traps as well as sample sizes.

Samplecode	Date	Stratum	Trap height (m above ground)	Individuals
CR04				
0401	08.11.21	Understory	1.7	493
0402	24.11.21	Understory	1.7	184
0403	29.03.22	Understory	1.7	287
0411	08.11.21	Canopy	17.0	336
0412	24.11.21	Canopy	17.0	135
0413	29.03.22	Canopy	17.0	288
CR06				
0601	10.11.21	Understory	1.7	206
0602	25.11.21	Understory	1.7	524
0603	23.03.22	Understory	1.7	144
0611	08.11.21	Canopy	18.3	326
0612	25.11.21	Canopy	18.3	190
0613	23.03.22	Canopy	16.1	337
OG38				
3801	04.11.21	Understory	1.7	201
3802	09.11.21	Understory	1.7	229
3803	28.03.22	Understory	1.7	250
3811	02.11.21	Canopy	20.9	449
3812	09.11.21	Canopy	20.9	185
3814	23.05.22	Canopy	20.9	157
OG39				

	3901	08.11.21	Understory	1.7	364
	3902	24.11.21	Understory	1.7	178
	3904	26.03.22	Understory	1.7	350
	3911	09.11.21	Canopy	17.7	126
	3913	24.11.21	Canopy	17.7	73
	3915	10.04.22	Canopy	17.7	306
OG42					
	4201	05.11.21	Understory	1.7	236
	4202	11.11.21	Understory	1.7	120
	4204	26.04.22	Understory	1.7	133
	4211	05.11.21	Canopy	12.7	139
	4212	11.11.21	Canopy	12.7	92
	4214	26.04.22	Canopy	20.0	181
OG77					
	7701	05.11.21	Understory	1.7	288
	7702	11.11.21	Understory	1.7	138
	7703	05.04.22	Understory	1.7	199
	7711	05.11.21	Canopy	13.5	216
	7712	11.11.21	Canopy	13.5	94
	7713	26.04.22	Canopy	18.9	243
PR24					
	2401	28.10.21	Understory	1.7	166
	2402	12.11.21	Understory	1.7	67
	2404	23.03.22	Understory	1.7	88
	2411	28.10.21	Canopy	15.5	171
	2412	12.11.21	Canopy	15.5	98
	2414	23.03.22	Canopy	15.5	169
PR26					
	2601	30.10.21	Understory	1.7	627
	2602	26.11.21	Understory	1.7	336
	2603	26.04.22	Understory	1.7	336
	2611	29.10.21	Canopy	12.4	831
	2612	26.11.21	Canopy	12.4	433
	2613	10.04.22	Canopy	12.4	753

Tab. S3: Generalized linear mixed models for analyses of influences of environmental factors of sample size.

Model_1 ß glmer(N ~ scale(Average_Temp, scale = F) * scale(Average_Hum, scale = F) + (1|Plotnumber), data = Sizes, family = "poisson")	
Model_2 ß glmer(N ~ scale(Average_Temp, scale = F) * scale(Average_Hum, scale = F) + (Habitat) + (scale(Canopy_height, scale = F)) + (1|Plotnumber), data = Sizes, family = "poisson")	x
Model_3 ß glmer(N ~ (scale(Canopy_height)) + (Habitat) + scale(Elevation_plot, scale = F) + (1|Plotnumber), data = Sizes, family = "poisson")	x

Legend: x = failed due to large Eigenvalue.

Tab. S4: Observed, exclusive and shared species numbers as well as individuals for Hedylidae, separated by strata and habitats. Note that the species numbers do not add up to its total sum as some are shared. **Bold face**: highest number.

	Hedylidae		
	sp.	exc.	ind.
STRATA			
Canopy	**7**	**1**	**40**
Understory	6	0	21
shared	6	--	--
HABITATS			
CR	6	0	13
OG-high	4	0	**23**
OG-low	4	0	10
PR	**7**	0	15
shared	3	--	--
TOTAL	7	--	61

Tab. S5: Sample coverage for five Lepidoptera groups and combined, separated by strata and habitat.

	C	U	CR	OG-high	OG-low	PR
Arctiinae	99%	99%	98%	97%	96%	98%
Geometridae	96%	96%	92%	93%	89%	93%
Saturniidae	84%	96%	91%	95%	85%	89%
Spingidae	90%	81%	72%	94%	70%	75%
Hedylidae	95%	91%	71%	96%	84%	81%
All	98%	98%	95%	95%	94%	96%

Legend: C = canopy, CR = cacao regeneration, OG = Old growth forest, PR = pasture regeneration, U = understory.

Tab. S6: Species richness (observed and estimated) and diversity measures of moth communities, separated by focal taxa, strata and habitats. Note that Hedylidae are not included due to their low overall species number of 7. **Bold face**: higher number.

STRATA	**sp. obs**	**Chao ± SE**	**Jackknife ± SE**	**Bootstrap ± SE**	**Fisher's α**	**Shannon-Wiener**
ARCTIINAE						
Canopy	**243**	**286.7** ± 14.5	**299.0** ± 25.5	**270.1** ± 14.6	54.7	**4.4**
Understory	235	271.2 ± 12.1	290.1 ± 21.9	262.4 ± 13.7	**56.4**	4.3
GEOMETRIDAE						
Canopy	208	255.6 ± 14.8	271.9 ± 29.7	238.7 ± 17.2	66.3	4.6
Understory	**267**	**335.1** ± 18.5	**350.1** ± 35.1	**306.4** ± 19.6	**82.9**	**4.8**
SATURNIIDAE						
Canopy	41	60.2 ± 11.0	60.2 ± 8.3	49.8 ± 4.5	**20.6**	3.2
Understory	**57**	**82.0** ± 15.5	**74.5** ± 7.6	**64.8** ± 3.7	16.7	3.4
SPHINGIDAE						
Canopy	**22**	35.2 ± 11.0	31.6 ± 4.9	**26.3** ± 2.8	9.3	2.4
Understory	21	**42.4** ± 16.4	**33.2** ± 6.8	26.2 ± 3.6	**13.1**	**2.6**
ALL						
Canopy	521	643.1 ± 24.7	671.5 ± 66.7	592.7 ± 37.7	134.6	5.1
Understory	**586**	**724.4** ± 26.3	**755.8** ± 68.8	**666.**8 ± 38.4	**159.3**	**5.3**
HABITATS						
ARCTIINAE						
CR	**208**	**268.5 ± 17.4**	**274.0 ± 38.1**	**239.0 ± 19.1**	**55.4**	4.4
OG_high	190	220.6 ± 10.2	240.2 ± 29.6	214.8 ± 17.1	55.3	4.3
OG_low	162	199.7 ± 12.3	213.0 ± 29.6	186.5 ± 15.5	47.4	4.0
PR	196	245.1 ± 15.3	252.2 ± 36.4	222.6 ± 21.1	47.9	4.2
GEOMETRIDAE						
CR	195	**274.8 ± 21.7**	**270.0 ± 44.6**	**229.7 ± 22.1**	**75.1**	**4.6**
OG_high	176	248.8 ± 21.3	241.2 ± 40.6	206.1 ± 21.2	66.0	**4.6**
OG_low	151	226.3 ± 22.3	214.8 ± 37.2	180.2 ± 17.6	66.3	4.4
PR	**196**	249.5 ± 15.1	264.2 ± 43.1	228.5 ± 24.7	70.6	**4.6**
SATURNIIDAE						
CR	38	54.5 ± 9.8	53.8 ± 12.4	45.3 ± 7.3	15.5	3.1
OG_high	42	53.3 ± 7.0	56.2 ± 9.2	48.8 ± 5.6	14.8	3.2
OG_low	26	29.5 ± 3.0	34.2 ± 5.1	30.3 ± 3.9	14.6	2.9
PR	**43**	**56.0 ± 7.5**	**59.5 ± 10.1**	**50.9 ± 5.8**	**20.8**	**3.4**
SPHINGIDAE						
CR	15	24.4 ± 8.2	22.5 ± 5.0	18.4 ± 2.7	**11.4**	2.4
OG_high	**19**	20.2 ± 1.5	**23.5 ± 3.1**	**21.6 ± 2.6**	9.2	**2.6**
OG_low	9	27.4 ± 23.4	14.2 ± 2.9	11.3 ± 1.3	8.5	2.0
PR	12	**49.5 ± 44.8**	19.5 ± 6.2	15.2 ± 3.3	7.0	1.9
ALL						
CR	**462**	**630.0 ± 30.5**	**629.2 ± 98.3**	**539.8 ± 48.4**	**143.4**	**5.2**
OG_high	431	533.1 ± 20.5	566.0 ± 79.7	495.7 ± 42.6	140.7	**5.2**
OG_low	352	470.3 ± 24.2	482.5 ± 75.5	413.2 ± 37.5	121.5	4.8
PR	454	586.1 ± 25.0	606.2 ± 96.5	525.8 ± 53.7	130.8	5.0

Tab. S7: Indicator species for strata and habitats. All samples combined.

	Family	Sp. nr.	Taxon	species	stat.	p
STRATA						
C	Arctiinae	792	Ctenuchina/Euchromiina	*Sphecosoma* sp.	0.724	0.006
		831	Ctenuchina/Euchromiina	*Isanthrene basifera*	0.709	0.001
		1125	Ctenuchina/Euchromiina	*Saurita* nr. *temenus*	0.666	0.028
		804	Ctenuchina/Euchromiina	*Episcepsis hypoleuca* group	0.637	0.014
		856	Lithosiini	*Agylla* sp.	0.635	0.007
		858	Lithosiini	*Agylla* sp.	0.592	0.021
		1336	Lithosiini	*Talara* sp.	0.581	0.030
		956	Phaegopertina	*Phaeomolis* near *polystria*	0.556	0.023
	Geometridae	3694	Sterrhinae	gen. sp.	0.565	0.041
		1612	Sterrhinae	*Semaeopus illimitata illimitata*	0.509	0.034
		3590	Ennominae	*Macaria arenisca*	0.493	0.034
	Sphingidae	113	Sphingidae	*Pachylia darceta*	0.500	0.017
U	Arctiinae	1067	Phaegopertina	*Pelochyta* sp.	0.851	0.001
		917	Phaegopertina	*Baritius* near *eleuthera*	0.683	0.020
		1409	Phaegopertina	*Ochrodota* sp.	0.559	0.039
		923	Phaegopertina	*Elysius* nearr *pyrosticta*	0.559	0.023
		828	Ctenuchina/Euchromiina	*Heliura* sp.	0.554	0.035
		1260	Phaegopertina	*Symphlebia tesselata*	0.523	0.026
	Geometridae	3632	Ennominae	*Physocleora* sp.	0.782	0.001
		3569	Ennominae	*Glena* near *juga*	0.766	0.006
		1164	Ennominae	*Paragonia* near *cruraria*	0.752	0.002
		1374	Ennominae	"*Eutomopepla*" *artena*	0.733	0.002
		64	Ennominae	*Oxydia agliata* group	0.723	0.002
		3686	Sterrhinae	*Semaeopus* sp.	0.719	0.001
		1914	Geometrinae	*Athena* group sp.	0.709	0.001
		2002	Ennominae	*Eusarca nemora* group	0.645	0.008
		1334	Ennominae	*Hymenomima seriata*	0.598	0.016
		3651	Ennominae	"*Isochromodes*" sp.	0.593	0.008
		3600	Ennominae	*Melanolophia* sp.	0.559	0.034
		1956	Larentiinae	*Eois* sp.	0.546	0.029
		2562	Ennominae	*Herbita* sp.	0.544	0.042
		4417	Larentiinae	*Euphyia* sp.	0.540	0.008
		1957	Larentiinae	*Eois* sp.	0.524	0.020
		1941	Geometrinae	*Rhodochlora* near *brunneipalpis*	0.515	0.024
		1961	Larentiinae	*Eois apyraria* group	0.500	0.013
		3654	Sterrhinae	*Cyclophora* sp.	0.456	0.050
		3703	Larentiinae	*Eois undulosata* group	0.456	0.048
	Saturniidae	151	Saturniidae	*Rhescynthis hippodamia*	0.753	0.001
		133	Saturniidae	*Grammopelta lineata*	0.724	0.001
		120	Saturniidae	*Dirphia durangensis*	0.694	0.001
		149	Saturniidae	*Pseudodirphia menander reducta*	0.675	0.001

		144	Saturniidae	*Oxytenis nubila nuboroiana*	0.657	0.003
		129	Saturniidae	*Eacles tyrannus*	0.653	0.004
		150	Saturniidae	*Pseudodirphia* sp.	0.645	0.001
		107	Saturniidae	*Automeris niepelti*	0.577	0.004
		148	Saturniidae	*Oxytenis espichinchensis*	0.577	0.004
		126	Saturniidae	*Titaea tamerlan amazonensis*	0.500	0.023
		108	Saturniidae	*Automeris exigua*	0.487	0.049
		106	Saturniidae	*Automeris zaruma*	0.456	0.050
		109	Saturniidae	*Automeris banus* or *argentifera*	0.456	0.043
	Sphingidae	118	Sphingidae	*Xylophane*s sp.	0.456	0.045
HABITATS						
CR	Arctiinae	825	Ctenuchina/Euchromiina	*Galethalea* (*Eucereon*) near *exile*	0.604	0.010
	Geometridae	3628	Geometrinae	*Synchlora astraeoides* group	0.598	0.014
OG-high	Arctiinae	982	Phaegopertina	*Watsonidia reimona*	0.757	0.001
		983	Phaegopertina	*Zatrephes* sp.	0.736	0.003
		903	Pericopina	*Hypocrita* near *chalybea*	0.707	0.003
		1131	Ctenuchina/Euchromiina	*Cacostatia* near *germana*	0.624	0.007
		928	Phaegopertina	*Gorgonidia buckleyi* group	0.612	0.006
		946	Phaegopertina	*Melese* sp.	0.594	0.008
		921	Phaegopertina	*Cresera annulata*	0.577	0.009
		1181	Phaegopertina	*Amphelarctia priscilla* group	0.535	0.022
	Geometridae	3686	Sterrhinae	*Semaeopus* sp.	0.704	0.001
		1941	Geometrinae	*Rhodochlora* near *brunneipalpis*	0.550	0.028
		1957	Larentiinae	*Eois* sp.	0.542	0.032
		3683	Sterrhinae	Semaeopus sp.	0.535	0.034
	Saturniidae	122	Saturniidae	*Dirphia somoccidentalis*	0.605	0.016
	Sphingidae	119	Sphingidae	*Xylophanes kiefferi*	0.500	0.041
PR	Arctiinae	1315	Lithosiini	*Euthyone grisescens* group	0.622	0.007
		807	Ctenuchina/Euchromiina	*Eucereon* cf. sp.	0.604	0.012
		970	Phaegopertina	*Trichromia* cf. *atta*	0.601	0.010
		2013	Phaegopertina	*Ormetica sypilus*	0.584	0.008
		1124	Ctenuchina/Euchromiina	*Cosmosoma saron*	0.577	0.037
		954	Phaegopertina	*Parathyris cedonulli* group	0.577	0.015
		869	Lithosiini	*Cisthene croesus*	0.566	0.013
		1280	Phaegopertina	*Pseudepimolis* sp.	0.563	0.047
		1322	Lithosiini	*Talara rufibasis* group	0.471	0.037
	Geometridae	1158	Ennominae	*Perigramma* near *vicina*	0.516	0.037
		1940	Geometrinae	*Pyrochlora rhanis* group	0.516	0.047
		4222	Geometrinae	*Chloropteryx* near *dalica*	0.488	0.050
	Saturniidae	141	Saturniidae	*Hyperchiria* cf. *volcana*	0.546	0.028

Legend: C = canopy, CR = cacao regeneration, OG = old growth forest, PR = pasture regeneration, Sp. nr. = Species number for discrimination, stat. = statistical value, U = understory.

Tab. S8) Results of the analysis of similarity (ANOSIM) for all focal groups and strata as well as habitats. P values are corrected by using the false-discovery rate control from Benjamini & Hochberg (1995). Note that Hedylidae and Sphingidae are not represented as their analyses is not representative due to low sample sizes.

Familiy	Comparison	R_value	p_values	p_adjust
Arctiinae	Strata	0.1272	0.1023	0.1023
	Habitat	0.4306	0.0022	0.0050*
Geometridae	Strata	0.2877	0.0093	0.0148*
	Habitat	0.3273	0.0056	0.0112*
Saturniidae	Strata	0.6127	0.0	0.0*
	Habitat	0.161	0.0933	0.1023
All	Strata	0.2533	0.0169	0.0225*
	Habitat	0.4227	0.0013	0.0052*

Legend: * = significant result