



Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest

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Summary

The vertical stratification of two species-rich moth families (Lepidoptera: Arctiidae, Geometridae) was analysed in a lowland rain forest in Costa Rica. Moths were trapped with automatic 8 W ultraviolet light traps at three sites in the understorey and canopy of a primary forest at the La Selva Biological Station (10.4° N, 84.0° W). A total of 846 arctiid moths (148 species) and 946 geometrid moths (140 species) were analysed. Species richness and diversity of arctiid moths was significantly lower in the understorey than in the canopy (Fisher's alpha: 24 vs. 49) whereas geometrid moths showed an inverse pattern (Fisher's alpha: 44 vs. 27). This resulted in an overall increase in the proportion of conspicuously coloured species towards the canopy. Moth ensembles were clearly separated in multidimensional scaling ordinations, and differed significantly in their faunal composition and dominance between the strata. The available host plant data suggest that the flight height of moths was determined by larval resource availability. Examples include understorey flyers such as the geometrid genus *Eois* feeding on *Piper*, and canopy flyers such as the arctiid moth genera *Aclytia*, *Macrocne* and *Poliopastea* which feed on lianas. © 2006 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Zusammenfassung

Die vertikale Stratifizierung von zwei artenreichen Nachtfalterfamilien (Lepidoptera: Arctiidae, Geometridae) wurde in einem Tieflandregenwald in Costa Rica untersucht. Die Falter wurden mit automatischen 8 W Ultraviolett-Lichtfallen an drei Standorten im Unterwuchs und im Kronenraum eines Primärwaldes der Station La Selva (10.4° N, 84.0° W) gefangen. Insgesamt wurden 846 Arctiiden (148 Arten) und 946 Geometriden (140 Arten) analysiert. Artenreichtum und Diversität der Arctiidae waren im Unterwuchs signifikant geringer als im Kronenraum (Fishers alpha: 24 bzw. 49). Geometriden zeigten dagegen ein umgekehrtes Muster (Fishers alpha: 44 bzw. 27).

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27). Insgesamt nahm hierdurch der Anteil auffallend gefärbter Arten zum Kronenraum hin zu. Die Faltergemeinschaften der beiden Schichten wurden klar durch Ordinierungen (Multidimensionale Skalierung) aufgetrennt. Sie unterschieden sich deutlich in ihrer faunistischen Zusammensetzung und Dominanzstruktur. Die verfügbaren Angaben zu Wirtspflanzen weisen darauf hin, dass die Flughöhe der Falter von der Verfügbarkeit von Ressourcen für die Raupen abhängt. Typische Falter des Unterwuchses sind z.B. Vertreter der Gattung *Eois* (Geometridae), die *Piper* fressen, während die Arctiiden *Aclytia*, *Macrocneme* und *Poliopastea* vorwiegend im Kronenraum fliegen und sich von Lianen ernähren.

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Introduction

Tropical canopy ecology is a young discipline which has expanded as new access techniques and sampling methodologies have become available. These facilitate research on a type of habitat that has been regarded as the 'last biotic frontier' and a biodiversity hotspot (Basset, Novotny, Miller, & Kitching, 2003b; Erwin, 1983). Arthropods in tropical rain forests are the dominant group in terms of the number of species, and they also play an important role in many ecological processes (Schowalter, 1995). So far, little is known about the stratification of most arthropods within rain forests. A better knowledge of their spatial distribution could help to understand how high species richness can be maintained in such ecosystems. Many studies on arthropods have focused on the canopies themselves, without taking account of other forest strata (e.g. most studies using fogging techniques, Basset et al., 2003b). The present study includes an investigation of the understory and compares the diversity and abundance of insects between the two strata.

Moths were chosen as model organisms within a lowland rain forest in Costa Rica. The Lepidoptera are one of the four most species rich insect orders, and caterpillars are important insect herbivores in neotropical rain forests (Barone, 1998). Two families, Arctiidae and Geometridae, were selected for study and identified to species level. Geometridae and Arctiidae are two of the largest four lepidopteran families (species number worldwide: ca. 21,000 and 11,000, respectively, Scoble, 1999; Watson & Goodger, 1986) that are particularly species-rich in the Neotropical region (Brehm, Pitkin, Hilt, & Fiedler 2005; Hilt & Fiedler, 2005). They represent useful units for ecological analyses because they both form monophyletic clades, a relatively high proportion can be assigned to named species, and host plant data are available for some of them (e.g. Janzen & Hallwachs, 2005).

Can we expect to find a vertical stratification of adult flying insects such as geometrid and arctiid

moths? At first sight, an equal distribution of mobile flying insects in the canopy and the understory of a rain forest (the null-hypothesis) appears to be plausible because the direct flight distance between the understory and the canopy (less than 40m) can be covered even by a small insect. However, previous studies have shown that many groups of arthropods, including flying insects, are not equally distributed along vertical gradients in tropical rain forests (e.g. De Dijn, 2003; DeVries, Murray, & Lande, 1997; DeVries & Walla, 2001; DeVries, Walla, & Greeney, 1999; Intachat & Holloway, 2000; Kato et al., 1995; Schulze & Fiedler, 2003; Tanabe, 2002).

The potential determinants for vertical stratification of arthropods in rain forests were grouped by Basset, Hammond, Barrios, Holloway, and Miller (2003a) into four categories: (1) abiotic factors, (2) forest physiognomy and tree architecture, (3) resource availability, and (4) arthropod behaviour per se. Knowledge of the biology of tropical arthropod species is usually poor, and it is often difficult to decide which determinant is decisive. Several studies of the vertical stratification of butterflies have regarded the third point, resource availability, as the best explanation for the observed distribution patterns (e.g. Beccaloni, 1997; DeVries et al., 1999; Schulze, Linsenmair, & Fiedler, 2001). So far, a lack of knowledge of the life histories of nocturnal Lepidoptera has prevented such an interpretation (Beck, Linsenmair, & Fiedler, 2002; Schulze & Fiedler, 2003).

Few studies have investigated the vertical stratification of arctiid and geometrid moths in tropical forests, and none have been performed in the neotropical region. Studies undertaken in SE Asia have shown that there was a similar diversity of geometrid moths in the canopy and the understory (Beck et al., 2002), or a higher diversity in the understory compared with higher strata (Intachat & Holloway, 2000; Schulze, 2000). Schulze et al. (2001) found no significant differences in the diversity of Arctiinae (a subfamily of

the Arctiidae) between the two strata in a rain forest in Borneo, but demonstrated that more individuals and a higher proportion of nectar-feeding species occurred in the canopy.

In this study, the null hypothesis of equal abundance and diversity of Geometridae and Arctiidae in the canopy and the understorey of a Costa Rican lowland rain forest was examined. In addition, beta diversity and faunal differences between the two strata were investigated, and a relationship between host plant growth form and flight height was tested.

Methods

Study area

The three study sites were situated in a lowland rain forest at the base of the Caribbean slopes of the Cordillera Central in La Selva Biological Station, Heredia province, Costa Rica (10.4° N, 84.0° W, Fig. 1, Table 1). The annual precipitation is ca. 4000 mm per year with March being the driest month (average 152 mm), and July being the wettest (average 480 mm; Sanford, Paaby, Luvall, & Phillips, 1994). The average monthly air temperature is 25.8 °C and differs little between the months (Sanford et al., 1994). The vegetation in the vicinity of the sampling sites consists of primary rain forests including forested swamps, open

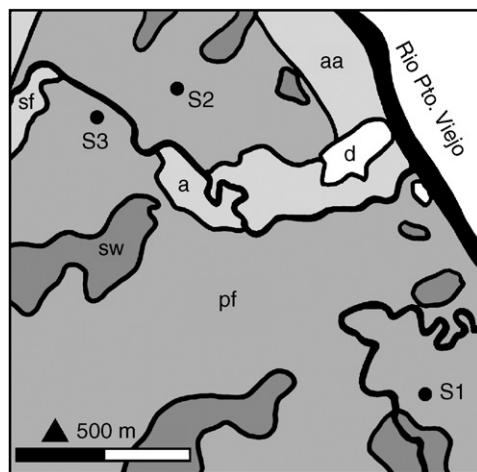


Figure 1. Study area in La Selva Biological Station, province Heredia, Costa Rica (10.4° N, 84.0° W). S1–S3: Sites 1–3; a: Arboretum (light grey) aa: Abandoned agroforestry (light grey), d: Developed area (white) pf: Primary old growth forest (medium grey), sf: Secondary forest (light grey), sw: Forested swamp or open swamp (dark grey). Narrow black lines: habitat and land use borders, bold black lines: rivers. Information simplified from a GIS map by the Organization for Tropical Studies.

swamps, secondary forests, abandoned plantations and managed habitats (Hartshorn & Hammel, 1994). All the study sites were located within primary forest (Fig. 1). This habitat is characterised by the dominance of the tree species *Pentaclethra macroloba* (Willdenow) O. Kuntze (Fabaceae) which comprises about 40% of the timber volume of the forest (Hartshorn & Hammel, 1994). Another typical feature of this vegetation is the occurrence of subcanopy palms. In the understorey, a large number of tree species attain sexual maturity at a small size (<5 m), but relatively few perennial herbs occur on the forest floor (Hartshorn & Hammel, 1994). Tree heights range between 28 and 38 m (Lieberman, Lieberman, Peralta, & Hartshorn, 1996). Topography was level at sites 1 and 2, and inclined (ca. 20°) at site 3.

Sampling design

The moths were collected using automatic UV funnel-traps (ENTO-TECH, B. Skule, Denmark, Fig. 2). The 8 WUVA fluorescent tubes (Sylvania, F8W/T5/BL350) were run with lead batteries. At each of the three sites, traps were operated in the understorey (U1–U3, symbol ●), and in the canopy (C1–C3, symbol □), respectively, from dusk to dawn (ca. 18.30–5.30 h) using photoswitches. Understorey traps were installed on the ground at a height of 0.5–2 m. Canopy traps were either lifted upwards with a rope on strong tree branches or were lifted or installed on climate towers (height: 22–30 m). Understorey and canopy traps were situated in close proximity, but were not visible from each other. Each site was sampled between five and eight times. Nightly samples of each trap site were pooled since the sample sizes of single catches were too small for a meaningful analysis. Table 1 and Appendix A (Table 1) provide detailed information about collecting sites, dates and numbers of individuals sampled at each date. At site 1, a temporary climate tower was used in June and July 2003. Since this tower was not available later, traps were installed in 2004 in close proximity (ca. 50 m) in the crown of a tree. All other sites were sampled only in February and March 2004. The pooling of samples from 2 years maximised the number of available specimens for the statistical analysis. This was justified by the comparative approach of the study and was supported by its consistent results.

Identification

The moths were identified in various museums (see Acknowledgements) by comparison with original

Table 1. Locality data of three sites, sample numbers and numbers of individuals of Arctiidae and Geometridae sampled in a lowland rain forest in Costa Rica

	Site 1	Site 2	Site 3
Traps	U1, C1	U2, C2	U3, C3
La Selva trail	CCL 350	CES 550	SUR 900
Canopy site	Temporary tower (2003), <i>Lecithys ampla</i> Miers (2004)	Old climate tower	<i>Dipteryx panamensis</i> (Pittier) Record
Elevation (a.s.l.)	50 m	40 m	45 m
Height of canopy trap	30 m	30 m	22 m
Sample n	8	7	5
Sampling season	June–July 2003, March 2004	February–March 2004	March 2004

U = understorey, C = canopy.

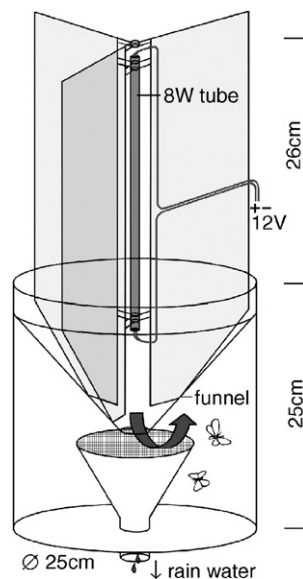


Figure 2. Light trap used in this study. The insects were attracted by a weak 8W ultraviolet fluorescent tube. Moths glided down the transparent vanes through the funnel inside a bucket where a killing agent was applied. Vanes were held with elastic grips (not shown). Rain water was allowed to flow through a second funnel. The inside was filled with egg carton in order to avoid damage to the insects. At each site, one trap was operated at ground level, and another in the canopy.

type specimens or other reliably identified material. Of the 288 separated morphospecies collected, 197 (68%) were identified provisionally at species level by comparing external characters and, in doubtful cases, male genitalia structures. In the Geometridae, the nomenclature follows Pitkin (2002) for the largest subfamily Ennominae and otherwise Scoble's (1999) catalogue. The higher classification of the Arctiidae is according to Jacobson and Weller (2002). In the Arctiinae

(Arctiini, Pericopini, Phaegopterini) the nomenclature follows Watson and Goodger (1986). Where species names could not be checked using a species catalogue (Arctiinae: Ctenuchini, Euchromiini; Lithosiinae), information was extracted from an online database (<http://internt.nhm.ac.uk/jdsml/perth/lepindex/index.dsml>). A complete species – site matrix is provided as Supplementary material (see Appendix A, Table 2).

Statistical analyses

In accordance with previous diversity studies, and in order to ensure the reliability of the results, three different measures were applied to determine alpha diversity of the moth ensembles: Rarefied species number, Fisher's alpha, and the Jackknife 2 estimator. Fisher's alpha and rarefied species numbers measures have proven to be sample size independent (Brehm, Süßenbach, & Fiedler, 2003). Rarefied species were calculated using a program developed by Kenney and Krebs (2000). Fisher's alpha was calculated using EstimateS 7.50 software (Colwell, 2005) with 50 randomisations. The fit of the log-series distribution was tested using a program by Henderson and Seaby (1998), and only two samples failed to fit (Arctiidae: site U2 and pooled understorey samples). The Solow test implemented in Henderson and Seaby's (1998) programme was used to test for significant differences in diversity. In addition, a range of estimators was calculated using EstimateS. The Jackknife 2 estimator was the most appropriate following Brose and Martinez' (2004) recommendation. Dominance was measured as the proportion of individuals of the commonest species in a sample (Berger–Parker index). The pooled samples were ordinated using non-metric multidimensional

Table 2. Parameters of species richness and diversity of arctiid and geometrid moths in the understorey (U) and canopy (C) of a lowland rain forest in Costa Rica

	Arctiidae		Geometridae			
	U	C	U	C		
Individuals	326	520	373	573		
Observed species	65	120	98	84		
Fisher's alpha \pm SD	24.4 \pm 2.2	48.9 \pm 3.4	44.0 \pm 3.6	27.1 \pm 1.9		
Jackknife 2 estimator	113.3	200.4	173.5	137.2		
Dominance (Berger-Parker-index)	0.32	0.12	0.14	0.41		
	Exclusively U	Shared	Exclusively C	Exclusively U	Shared	Exclusively C
All species (including rare species)	28 (19%)	37 (25%)	83 (56%)	56 (40%)	42 (30%)	42 (30%)
Abundant species (≥ 5 individuals in total)	1 (2%)	26 (63%)	14 (34%)	6 (16%)	28 (74%)	4 (11%)

Samples of three study sites were pooled.

scaling (NMDS) based on the NESS index with the sample size parameter m set to its maximum (Brehm & Fiedler, 2004; Grassle & Smith, 1976) yielding very low stress values in the ordinations (< 0.001). NESS values were calculated using a program provided by Meßner (1996). Ordinations based on m set to other values, and on Sørensen's index yielded very similar results and are not shown. Faunal composition was measured in the same way as in previous studies (Brehm & Fiedler, 2003). Arctiidae were analysed at the level of the subfamilies Lithosiinae and Arctiinae (including tribes), and Geometridae were analysed at the level of subfamilies. Adults were classified by sight as 'cryptic' or 'conspicuous'. Geometrids were generally classified as cryptic because none of the examined species exhibited conspicuous aposematic colouration. On the contrary, most arctiids (16 exceptions, Appendix A; Table 2) were classified as conspicuously coloured. Using only two classes of colouration is a relatively simple approach that cannot account for intermediate colour types, but it was regarded as sufficient for the purpose of this study. Host plant information was mainly extracted from Janzen and Hallwachs' (2005) database, with additional information from Brehm (2002, 2003). Most available records were from NW Costa Rican habitats, and a high floristic overlap with the La Selva area, at least at genus level, was expected. Host plants were categorised with respect to their growth forms using online databases (e.g. <http://www.mobot.org>). Standard statistical analyses such as χ^2 tests and Kolmogorov–Smirnov tests were performed using the Statistica 5.5 software (StatSoft, Tulsa, USA).

Results

A total of 846 arctiid moths (148 species) and 946 geometrid moths (140 species) were collected at the three sites (understorey+canopy) in 20 nights. The number of specimens collected varied strongly (Appendix A; Table 1). Although in both families more individuals were sampled in the canopy compared with the understorey (Table 2), differences between the average catch sizes were not statistically significant (Kolmogorov–Smirnov test: $P > 0.10$). The overall higher abundance of moths in the canopy was mainly caused by two sampling nights in June 2003 (Appendix A; Table 1).

Figure 3 shows rarefaction curves for the pooled understorey and canopy samples of both moth families. While arctiid moths were more species-rich in the canopy, the pattern is reversed for geometrid moths. Fisher's alpha and the Jackknife 2 estimator show similar patterns (Table 2), and differences between the strata were significant (Solow's test: $P < 0.001$). The dominance of single species shows an opposite trend compared with species richness and diversity in both families (Table 2). In the Arctiidae, the dominating species included the genera *Isanthrene*, *Calodesma* (canopy), and *Virbia* (understorey). In the Geometridae, the pattern was inverse: the less diverse canopy samples were more dominated by a single species than were the understorey samples (Table 2). Both strata, especially the canopy, were dominated by the same *Leuciris* species. Other common species included the genera *Physocleora* and *Pleuroprucha* in the canopy, and *Glena* and *Physocleora* in the understorey.

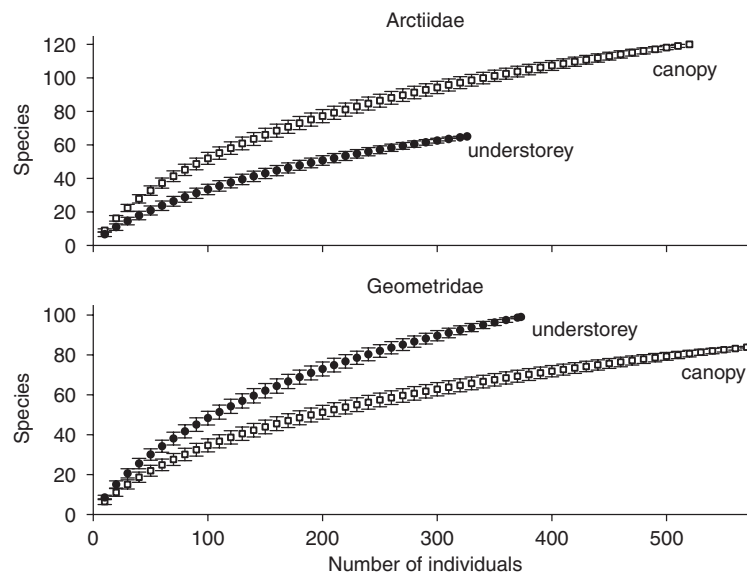


Figure 3. Rarefied species numbers of Arctiidae and Geometridae in the canopy and understorey of a rain forest in Costa Rica based on cumulative samples. Error bars show SD.

Species overlap between the strata was relatively low in both families. However, this appeared to be an artefact because of the occurrence of many singletons. Table 2 shows species exclusive to one or the other stratum, and the species that were shared between both strata. If only the commoner species are considered (≥ 5 individuals in total), the proportion of shared species strongly increases from 25% to 63% in the Arctiidae, and from 30% to 74% in the Geometridae. The ordinations show a distinction between the understorey and the canopy samples along the first dimension (Fig. 4). Ensembles were clearly separated in both families. The second axis tends to separate the three sites. In both ordinations, samples from site 1 were ordinated at one extreme of the axis. However, distances were small, and Sites 2 and 3 were not clearly separated in the second dimension. Table 3 gives the similarity values used to obtain the ordinations.

Figure 5 shows that the proportions of taxa within both families differed between the strata. In both families, no significant differences were detectable between the strata based on species composition (Geometridae: $\chi^2 = 0.52$, d.f. = 3, Arctiidae: $\chi^2 = 6.51$, d.f. = 4), but ensembles weighted for individuals were significantly different (Geometridae: $\chi^2 = 29.32$, $P < 0.001$, d.f. = 3, Arctiidae: $\chi^2 = 331.65$, d.f. = 4). Fifty-seven species (35.0%) among 163 species in the understorey were conspicuously coloured, whereas 106 species (52.0%) among 204 species in the canopy had colourful patterns. The difference between the strata was significant ($\chi^2 = 10.6$, $P < 0.005$, d.f. = 1).

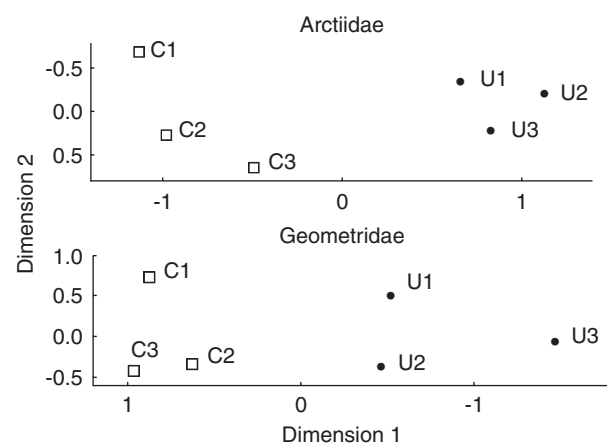


Figure 4. Non-metric two-dimensional scaling of ensembles of Arctiidae and Geometridae from three canopy (C) and three understorey (U) sites in a rain forest in Costa Rica. The NESS index of similarity (m_{\max}) was used (Arctiidae: $m_{\max} = 31$, Geometridae: $m_{\max} = 38$). Note that the y-axis was inverted in the upper graph for clarity.

Host plant data allowing for an assignment of plant growth forms were available for 67 species, representing a total of 343 individuals (113 understorey, 230 canopy). Species were grouped into 11 categories, including feeders on mixed growth forms. A χ^2 test indicated a significant difference between the distribution of growth form types between the two strata ($\chi^2 = 103.90$, $P < 0.001$, d.f. = 10). Analysis of single categories revealed that a higher proportion of individuals collected in the understorey belonged to species feeding on

trees, herbs, and shrubs+trees. On the other hand, individuals of species recorded on lianas, lianas+trees, and trees+vines had a significantly higher proportion in the canopy (Table 4). See Supplementary material (Appendix A, Table 2) for detailed information on all species, their recorded host

plants and the plant growth form assigned to each species.

Discussion

Stratification and resource availability

The null hypothesis of equal diversity of arctiid and geometrid moths was clearly rejected. Diversity showed contrasting patterns in the two taxa: arctiids were more diverse in the canopy whereas geometrids were more diverse in the understorey. Ensembles of the two strata differed significantly in their composition and dominance structure. Although more individuals were collected in the canopy, the results were not statistically significant. Differences in abundance were mainly caused by samples taken on two nights at site 1 in June/July 2003 when exceptionally large numbers of specimens were collected (particularly *Leuciris* sp. near *fimbriata* in the canopy). Heavy rain combined with a new moon phase might have been responsible for the high abundance of moths on these two nights as compared with the other samples. An extended study over longer periods of time could give a better

Table 3. NESS m_{\max} similarity matrices of Arctiidae (Arc) and Geometridae (Geo) from three understorey (U) and three canopy (C) sites in a rain forest in Costa Rica

	U2	U3	C1	C2	C3
Arc $m = 31$					
U1	0.95	0.87	0.52	0.57	0.58
U2	1	1.04	0.26	0.42	0.48
U3		1	0.36	0.55	0.67
C1			1	0.80	0.66
C2				1	0.81
Geo $m = 38$					
U1	0.91	0.79	0.69	0.69	0.62
U2	1	0.85	0.58	0.81	0.72
U3		1	0.45	0.48	0.44
C1			1	0.81	0.78
C2				1	1.08

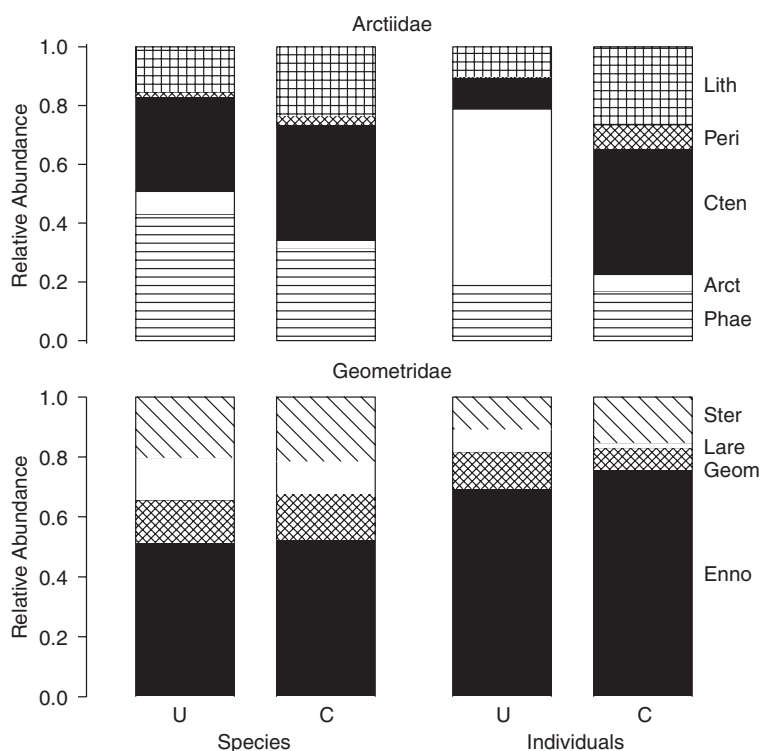


Figure 5. Faunal composition of Arctiidae and Geometridae from pooled understorey (U) and canopy (C) samples from a rain forest in Costa Rica. Analyses were either based on species numbers (left) or on the numbers of individuals (right). Subfamilies and tribes of the Arctiidae: Lith = Lithosiinae, Peri = Pericopini, Cten = Ctenuchini/Euchromiini, Arct = Arctiini, Phae = Phaegopterini; Subfamilies of the Geometridae: Ster = Sterrhinae, Lare = Larentiinae, Geom = Geometrinae, Enno = Ennominae.

Table 4. Host plant growth form assigned to 67 arctiid and geometrid moth species (343 individuals) from a rain forest in Costa Rica

Host plant growth form	Species	Individuals			χ^2	P
		Total	U	C		
Tree	18	140	66	74	21.59	<0.001
Tree, vine	1	60	0	60	35.73	<0.001
Liana, tree	5	45	3	42	16.19	<0.001
Liana	8	33	5	28	5.23*	0.022
Herb	11	27	22	5	12.85	<0.001
Shrub, tree	5	11	8	3	8.14	0.004
Liana, shrub, tree, vine	5	8	1	7	—	
Herb, liana, shrub, tree	5	7	2	5	—	
Herb, shrub, tree, vine	5	6	2	4	—	
Vine, liana	3	4	2	2	—	
Vine	1	2	2	0	—	
Sum	67	343	113	230		

U = understorey, C = canopy. See Appendix A; Table 2, for a full species and host plant list. χ^2 tests were only performed for samples > 10. *Result is not significant when the table is corrected for the false discovery rate (FDR, Benjamini & Hochberg, 1995).

insight into such fluctuations in abundance, the role of seasonality, and the influence of weather and moon (DeVries et al., 1999; Muirhead-Thomson, 1989; Yela & Holyoak, 1997).

Among the four potential determinants for vertical stratification (see Introduction), resource availability can best explain the observed patterns whereas the other factors appear to be of less importance and/or are difficult to observe. Abiotic factors seem to be of little significance overall for the abundance and diversity of nocturnal adult moths. For example, humidity is usually lower and wind speed is higher in the higher strata of a lowland rain forest. Both factors would have been expected to lead to a decreasing abundance of moths in the canopy (McGeachie, 1989), but no such effect was visible. The roles of forest physiognomy and arthropod behaviour are difficult to judge because much more autecological knowledge is required to test for these factors. A link to behavioural ecology is provided by the fact that most arctiids are conspicuously coloured whereas geometrids are not. A higher overall proportion of colourful species occurred in the canopy than in the understorey, because both families showed inverse diversity patterns. However, such patterns are difficult to explain without a better knowledge of the individual behaviour and chemical defences of the moth species.

The available host plant data suggest that larval resource availability is an important factor determining the flight height of adult moths. Although the host plant list is far from complete and mainly covers specialized moth species, it shows a link

between plant growth form and moth flight height as illustrated by the following examples. Larvae of the geometrid genus *Eois* are specialised feeders of the plant genus *Piper* (Brehm, 2002; Dyer et al., 2003; Marquis & Braker, 1994). *Piper* are usually herbaceous shrubs (counted as herbs in this study) and typical components of the understorey in the forest at La Selva whereas they are absent from the canopy. As a consequence, among the 23 individuals of *Eois* (belonging to 9 species), 19 were sampled in the understorey. As opposed to that, the genera *Aclytia*, *Macrocneme* and *Poliopastea* (Arctiidae) were mostly sampled in the canopy. Data from Janzen and Hallwachs' (2005) database suggest that caterpillars of these genera are specialized feeders of Apocynaceae and Asclepiadaceae, such as *Forsteronia* and *Prestonia*. All these plants are lianas, whose leaves and inflorescences are available to chewing herbivores mostly in the canopy. An example of an unstratified flyer is the geometrid *Cyclomia disparilis* which was sampled in equal numbers in both the canopy and the understorey (13 vs. 12). Larvae of *Cyclomia* have been found exclusively on the medium-sized tree *Colubrina spinosa* (Rhamnaceae) (L. Dyer, pers. comm.; G. Brehm, pers. observ.), the leaves of which are available in both the understorey and in the lower canopy of the forest.

These results confirm previous studies on butterflies in discovering a link between adult flight height and larval resource availability. For example, Beccaloni (1997) showed that the distribution of ithomiine butterflies in an Ecuadorian lowland rain forest correlated with the height of their host plants. He

also reported a relationship between the flight height of British woodland butterflies and their host plants. Schulze et al. (2001) correlated the main occurrence of satyrine and morphine butterflies in the understorey of a Bornean rain forest with the availability of their potential monocotyledonous larval hosts. Resource availability for the adults rather than the larvae appeared to determine the stratification of sphingid moths in the same forest (Schulze et al., 2001). Most sphingids depend on the uptake of nectar for their energy-consuming flight. Since nectar resources occurred more frequently in the canopy, sphingids were significantly more abundant and diverse in this stratum. This probably also applies to neotropical forests, but the numbers of individuals collected with light traps in this study were not sufficient for a quantitative analysis. Schulze et al. (2001) also showed that the proportion of arctiid moths (subfamily Arctiinae) with reduced mouthparts was significantly higher in the understorey (ca. 90%) compared with the canopy (ca. 60%) in a Bornean rain forest. In the neotropical region, genera with a reduced proboscis are much less frequent: all species (Arctiidae and Geometridae) examined in the present study have a (probably functioning) proboscis (G. Brehm, unpubl. data). However, the proboscis is particularly short in all *Virbia* species (see also Jacobson & Weller, 2002). *Virbia* strongly dominate the understorey arctiid ensembles with 58% of all individuals collected. It is probable that the mouthparts of these moths only allow the uptake of fluids from the surface and this might be an adaptation to life in the potentially nectar-poor understorey.

Methodology and conclusions

Measuring species richness and diversity of tropical arthropod communities is a methodological challenge because such communities are usually very species rich and contain many rare species (Novotny & Basset, 2000). Species names are not available for a significant proportion of the material, and the separation of taxa is sometimes difficult or doubtful. Sampling methods are biased to a certain extent, and spatial and temporal replication of the sampling is often not fully satisfactory. All these problems potentially apply to this study, but none of them is likely to undermine the main conclusions presented here, and the patterns were confirmed by various statistical methods. The use of light traps has been specifically criticised because of potential problems such as its selectiveness, the attraction of insects from a distance, and the dependence of the method on habitat

structures (see Schulze & Fiedler, 2003, for a detailed discussion). However, light sampling can easily be standardised, and it is known to attract most species of the target groups of this study (Brehm, 2002).

This study provided an initial insight into the vertical stratification of two speciose moth taxa in a neotropical rain forest, and showed that resource availability is likely to be an important determinant. However, available life-history data is still scarce, and the conclusions about the underlying causes of moth vertical stratification still have a preliminary character. Carrying on from this, future studies could extend the spatial and temporal scale in order to achieve a more complete picture of the moth ensembles. More specific questions could be addressed, e.g. which role particular (flowering) tree species play, and whether differences occur in different habitat types. DeVries et al. (1997, 1999) and DeVries & Walla (2001) pointed out that canopy or understorey samples alone might be poor estimators of butterfly species richness. The present study also showed that purely ground-based inventories of moths could potentially be insufficient in neotropical lowland rain forests, notably in the Arctiidae, but future studies in other types of forested habitats are needed to confirm the results. It is likely that stratification in inclined areas, and at higher elevations (with smaller trees, fewer liana species; Lieberman et al., 1996) is less pronounced. In addition to sampling with light traps, larvae need to be collected at different heights in the forest and reared to adults. Sound studies of the natural histories of the species involved are essential not only for a better understanding of the spatial distribution in animal communities, but also for an understanding of insect host plant specialisation and aposematism in tropical forests.

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Appendix A. Supplementary material

The online version of this article contains additional supplementary data. Please visit [doi:10.1016/j.baee.2006.02.002](https://doi.org/10.1016/j.baee.2006.02.002)

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