

Vertical stratification of moths across elevation and latitude

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ABSTRACT

Aim There is little consensus as to whether stratification of arthropods between canopy and understorey in tropical and subtropical forests is commonplace and if the magnitude of stratification changes across different elevations and latitudes. We investigated broad-scale patterns of vertical stratification of moths collected from extensive cross-continental fieldwork in a variety of forest types, climates, elevations, latitudes and areas with differing biogeographical history.

Location Tropical and subtropical rain forest in eastern Australia; tropical, subtropical and subalpine forest in Yunnan Province, China; and tropical rain forest in Panama, Vietnam, Brunei and Papua New Guinea.

Methods Night-flying moths were trapped from the upper canopy and understorey. We generated a total of 64 data sets to quantify vertical stratification of moths in terms of their species richness, using coverage-based rarefaction, and assemblage composition, using standardized hierarchical beta diversity. Based on the average temperature lapse rate, we incorporated latitudinal differences into elevation and generated 'corrected' elevation for each location, and analysed its relationships with the magnitude of stratification.

Results We found consistent differences between canopy and understorey assemblages at almost all rain forest locations across corrected elevational gradients. The magnitude of vertical stratification in species richness did not change with increasing corrected elevation. In contrast, the difference in assemblage composition increased with increasing corrected elevation in the Northern Hemisphere, while the opposite, albeit weak, trend was found in the Southern Hemisphere.

Main conclusions Clear vertical stratification was evident in moth assemblages regardless of elevation and latitude. However, the degree to which assemblages are stratified between canopy and understorey is not uniformly related to elevation and latitude. Inconsistencies in the magnitude of vertical stratification between the Northern and Southern Hemisphere, may reflect, on one hand, deep-time biogeographical differences between the land masses studied and, on the other, place-to-place differences in resource availability underpinning the observed moth assemblages.

Keywords

beta diversity, biodiversity, canopy, elevation, IBISCA, Lepidoptera, macroecology, macrolepidoptera, tropical rain forest, vertical compartmentalization

INTRODUCTION

Tropical rain forests contain a significant proportion of the world's animal diversity (Wilson, 1992) with most of this diversity made up of arthropods, particularly insects (May, 2010). It has long been hypothesized that the majority of tropical insect species are associated with the crowns of forest trees and their associated epiphytes (Novotny *et al.*, 2003). Tropical canopy assemblages can be highly diverse, with some species restricted to the canopy, including many arthropods (Sutton *et al.*, 1983; Basset, 2001) and canopy plants (Madison, 1977). However, whether canopy assemblages are more diverse than understorey assemblages has yet to be resolved.

Forest canopies are the interface between the atmosphere and the biosphere (Ozanne *et al.*, 2003), presenting a different suite of environmental conditions when compared with the understorey. These include a harsher ultraviolet regime and greater temperature fluctuations, as well as higher evaporation rates and wind speeds (Lowman & Rinker, 2004). In moving from the understorey to the upper canopy, a suite of environmental factors shift, creating a matrix of microclimates and the potential for partitioning of ecological niche spaces (Richards, 1984). Nutrients and water availability change across strata, as do floristic composition, leaf area, biomass and resource availability associated with these environmental factors (Basset *et al.*, 2003).

Arthropod diversity in undisturbed rain forests is strongly vertically 'stratified' with more or less distinct assemblages of species occupying closely adjacent habitat components within a forest (Basset *et al.*, 1992). The degree to which arthropod communities are vertically stratified has a substantial impact on the description of, and hypotheses to account for, the extraordinary diversity of arthropods in tropical forests (Erwin, 1982; Hamilton *et al.*, 2010). Previous authors have tested this stratification with particular reference to Diptera (Kitching *et al.*, 2004), Collembola (Rodgers & Kitching, 1998), Isoptera (Roisin *et al.*, 2005), Araneae (Sorensen, 2003), and Coleoptera (Stork & Grimbacher, 2006).

Night-flying moths are particularly useful in the study of vertical stratification. Lepidoptera are the largest group of phytophagous insects and are sensitive to floristic change, being closely linked to their host plants. Lepidoptera are also hyperdiverse yet taxonomically well-known, with globally an estimated 50,000 species (Gaston, 1991). As ectotherms, they are strongly influenced by environmental factors and many groups within the Lepidoptera have very low dispersal ability, a characteristic that increases with increasing elevation (Roff, 1990). Finally, they are abundant and easy to sample in large numbers using automated light traps, which have an attraction radius of between 10 and 27 m, depending on the family (Merckx & Slade, 2014).

Stratification studies involving Lepidoptera have been undertaken in several bioregions, focusing on particular taxa and using a variety of sampling methods. For example, Brehm (2007) found distinctive assemblages of Arctiinae

(Erebidae) and Geometridae in the canopy and understorey in a Costa Rican rain forest using UV funnel traps. The Arctiinae, a more conspicuously coloured group, were dominant in the canopy, while Geometridae were dominant in the understorey. Fermon *et al.* (2003) baited butterflies in managed West African rain forests and found stronger vertical stratification in undisturbed rather than disturbed forests. They suggested this may be due to the relative availability of canopy resources such as fruit. Schulze *et al.* (2001) studied two taxa of night-flying moths (Sphingidae and Arctiinae) and butterflies in Borneo using bait traps, standardized counts and black light traps. Frugivorous butterflies declined in the canopy, whereas nectar-feeding groups increased. The authors attributed these patterns principally to nectar availability and predator avoidance, with larval host plant preferences playing only a minor role for some ground-zone species. In contrast, vertical stratification of Neotropical ithomiine butterflies was correlated with the height of their host plants (Beccaloni, 1997). Several additional papers have focussed exclusively on butterflies, using fruit-baited traps, netting and visual observations, with a generally consistent pattern of vertical stratification (e.g. DeVries *et al.*, 2012).

Latitudinal and elevational gradients allow us to investigate the forces driving patterns of diversity (Hillebrand, 2004; Hodkinson, 2005). In lowland tropical forests, we expect to find large differences between canopy and understorey assemblages as tropical canopies present a suite of different environmental conditions, are structurally complex and can be upwards of 35 m distant from the understorey (Stork *et al.*, 1997; Basset, 2001). As we move further from the equator or upslope in elevation, structural complexity, vertical distance between canopy and understorey, and plant species richness generally declines (Richards, 1996; Hillenbrand, 2004; DeFrenne *et al.*, 2013), due to the complex interplay of environmental factors including changes in temperature, potential evapotranspiration, precipitation regime and historical human disturbance (Kreft & Jetz, 2007). As herbivores are closely tied with plants, we hypothesize that vertical stratification of moths decreases with increasing latitude and elevation. We focused upon the tropics and subtropics and avoided high-latitude temperate areas as other confounding factors such as historical human disturbance and the extent of past glacial maxima may influence diversity patterns of plants and in turn moth community structure (Hannah *et al.*, 1995; Qian & Ricklefs, 2000).

In this paper we present the first global comparative analysis of canopy/understorey moth assemblages based on a series of forest studies using standardized sampling methods. We use data sets from tropical Panama, Papua New Guinea, Borneo and Vietnam, tropical and sub-tropical eastern Australia, and tropical, subtropical and temperate China. Using all or subsets of these canopy and understorey data sets from across continents, forest types and climates, we investigate the generality of vertical stratification of night-flying forest Lepidoptera.

METHODS

Study areas

Moths were collected from a total of 13 locations and included tropical and subtropical locations in the Northern and Southern Hemisphere (see Table 1 and Appendix S1 in Supporting Information for details). We also collected at one sub-alpine location in the Northern Hemisphere. Seven locations (four in Australia and three in China) were elevationally stratified into four to six zones separated by *c.* 200 m of elevation. In Australia, two locations were established in subtropical rain forests of eastern Australia (Border Ranges and Lamington National Parks), and two in tropical rain forests of north-eastern Australia (Eungella and Mt Lewis National Parks). In China, all three locations were in Yunnan Province, southern China, one each in tropical monsoonal rain forest (Mengla), subtropical broad-leaved evergreen forest (Ailao Shan) and subalpine conifer forest (Lijiang). Australian locations were surveyed two or three times (once at the onset of the wet season and once or twice at its close), whereas only one summer survey was conducted in Chinese locations. In Atherton (tropical rain forest of far-north Queensland, Australia), a 25 ha permanent area established as part of the Terrestrial Ecosystem Research Network (TERN) Project was surveyed three times over 3 years. Four

locations, Paluma (Australia), Oomsis (PNG), Cat Tien (Vietnam) and Batu Apoi (Brunei), were surveyed as part of extensive general arthropod and plant surveys of one-hectare areas between 1995 and 2000 (Kitching *et al.*, 2001, 2005). In San Lorenzo (Panama), the survey was made within a half-hectare section of the San Lorenzo Protected Area (see Basset *et al.*, 2007, 2012). The data collected from these 13 locations were subdivided into a total of 64 data sets representing temporally, spatially and elevationally different components (see Appendix S2a).

Moth trapping

Each data set consisted of samples of moth assemblages in both the canopy and the understorey from three to eight replicate plots for each stratum (Table 1). In almost all cases we circumvented the difficulties of canopy access by using a modified compound bow to shoot canopy lines. Canopy traps were hung from emergent branches, with the aim of sampling moths at the top of the canopy. For the Panama studies a variety of access methods were used including a canopy crane (see Basset *et al.*, 2007). At all locations, canopy traps were placed as high as possible in the canopy. Understorey traps were set 1.5 m from the ground.

All samples were made using Pennsylvania-style light traps. The number of trap nights per plot varied according to the

Table 1 Summary of the 13 locations (AU, Australia; CN, China; PG, Papua New Guinea; PA, Panama; VN, Vietnam; BN, Brunei) which comprised a total of 64 temporally and elevationally stratified data sets. Latitude and longitude, forest type, number of data sets, number of plots within each data set are shown.

Location	Lat and long	Forest type	Survey occasion	Elevation (m a.s.l.)	No of data sets	No of plots per data set	
						Canopy	Understorey
Border Ranges (AU)	28.2°S 153°1'E	Subtropical rain forest	Apr 2010	300,500,700,900,1100	5	4	4
			Nov 2010	300,500,700,900,1100	5	4	4
Lamington (AU)	28.1°S 153°1'E	Subtropical rain forest	Oct 2006	500,700,900,1100†	4	4	4
			Mar 2007	300,700,900,1100†	4	4	4
Eungella (AU)	21.1°S 148°3'E	Subtropical rain forest	Mar 2013	400,600,800,1000	4	5	5
			Nov 2013	200,400,600,800,1000,1200	6	4	4
			Mar 2014	200,400,600,800,1000,1200	6	4	4
Mt Lewis (AU)	16.3°S 145°2'E	Tropical rain forest	Nov 2009	400,600,800,1000,1200	5	4	4
			Apr 2011	400,600,800,1000,1200	5	4	4
Mengla (CN)	21.4°N 101°3'E	Tropical Rain forest	Jul 2012	800,1000,1200,1400	4	5	5
Ailao Shan (CN)	24.2°N 101°2'E	Subtropical rain forest	Jul 2011	2000,2200,2400,2600	4	5	5
Lijiang (CN)	27.1°N 100°1'E	Sub-alpine forest	Aug 2012	3200,3400,3600,3800	4	5	5
Atherton (AU)	17.1°S 145°4'E	Tropical rain forest	Nov 2009	720	1	5	5
			May, 2010	720	1	5	5
			Apr 2011	720	1	5	5
Paluma (AU)	18.6°S 146°1'E	Tropical rain forest	Jun 1999	1000	1	3	3
Oomsis (PG)	6.4°S 146°4'E	Tropical rain forest	Jul 2000	70	1	3	3
San Lorenzo (PA)*	9.2°N 80°0'W	Tropical rain forest	Oct 2008	110	1	8	8
Cat Tien (VN)	11.3°N 107°2'E	Tropical rain forest	Jul 2002	200	1	3	3
Batu Apoi (BN)	4.3°N 115°1'E	Tropical rain forest	Aug 1995	30	1	3	3

*Target taxa were the Pyraloidea, Arctiidae and Geometridae only.

†300 m (Oct 2006) and 500 m (Mar 2007) samples were not included as unequal number of plots were surveyed between canopy and understorey strata.

design of each study, but the same or comparable numbers of trap nights were employed at canopy and understorey (see Appendix S2a). Within each stratum at each plot, moths from all trap nights were pooled to produce a single canopy or understorey sample. Light traps comprised a vertical 8-watt actinic tube surrounded by three transparent vanes which knock insects down into a collecting funnel and bucket mounted below. Traps were powered by 12 volt gel-cell batteries. With a well maintained, fully charged battery, traps remained illuminated for up to 12 h. Both the trap and battery were mounted within a frame with a rain-cover above them. Insects were killed *in situ* by including a strip of resin impregnated with dichlorvos within the collecting bucket.

Sample sorting

At all locations, except Panama, moths with a forewing length greater than 1 cm (loosely referred to as macrolepidoptera) were recorded. In addition, moths belonging to the superfamily Pyraloidea (i.e. families Crambidae and Pyralidae), regardless of size, were processed. In Panama, only Geometridae, Arctiinae and Pyraloidea were targeted. Moths from each sample were sorted to morphospecies in field laboratories, and assigned to family or subfamily where possible.

Data analysis

We first used nonmetric multi-dimensional scaling (NMDS) ordinations (with 25 random restarts to find the lowest stress levels) to illustrate beta diversity among plots and between canopy and understorey assemblages within each data set. NMDS ordinations were generated using the Sørensen dissimilarity measure based on presence/absence data. We used permutational analysis of variance (PERMANOVA) to test for significant differences among canopy and understorey strata, based on matrices of Sørensen index values. For elevationally stratified locations, elevation and its interaction with stratum were included as factors. Both NMDS and PERMANOVA were executed using PRIMER6 and PERMANOVA+ add-on software (Clarke & Gorley, 2006).

We quantified differences between canopy and understorey in terms of species richness and assemblage composition using a number of different techniques (see Table 2). For species richness, we first calculated the difference in observed number of species between canopy and understorey within each data set. We converted the difference to a proportion by dividing it by the number of species in the richest stratum, either canopy or understorey. We assigned a positive value to the proportional difference if the canopy was richer, and a negative value if the understorey was richer. Observed species richness was, however, greatly biased by differences in sample coverage (see below). Sample coverage greatly varied due to differences in sampling intensity and other factors (e.g. moon phase). Therefore, we also estimated species richness using coverage-based rarefaction curves (Chao & Jost, 2012). Coverage-based rarefaction curves plot species richness against sample coverage which represents the proportion of the total number of individuals in a given community represented by a given sample size (Chao & Jost, 2012). For each data set, we generated two coverage-based rarefaction curves based on canopy and understorey moths, using the `rNEXT R` package 1.0 (Hsieh, 2013). We then extrapolated the curves by doubling the number of moth individuals. For each data set we then estimated the number of species in the canopy and understorey based on the sample coverage achieved in the undersampled stratum. As for observed species richness, differences in estimated species richness were transformed to proportions and assigned positive and negative values.

We also calculated the mean and standard deviation of the difference in observed species richness between the canopy and understorey plots within each data set. We then calculated standardized mean differences by dividing the mean by the standard deviation. This is analogous to meta-analytical approaches which quantify the strength of evidence (effect size) by calculating the strictly standardized mean difference. Unlike estimated species richness, however, this meta-analytical approach cannot control for differences in sample coverage.

To quantify differences in assemblage composition, we employed additive, hierarchical, diversity partitioning to calculate beta diversity between canopy and understorey (Crist

Table 2 Metrics generated to quantify vertical stratification in terms of moth species richness and assemblage composition for each data set ($n = 64$). Observed metrics used the actual data obtained, whereas controlled metrics used estimated species richness and standardized beta deviation in order to control for the influence of differences in sample coverage (species richness) and gamma diversity (assemblage composition). A meta-analytical approach was used to calculate effect sizes (standardized mean difference) of the differences between canopy and understorey in each data set.

	Observed	Controlled	Effect size (meta-analysis)
Species richness	Proportional difference in observed number of species*	Proportional difference in estimated number of species	Standardized mean difference in species richness
Assemblage composition	Observed beta diversity*	Standardized beta deviation	Standardized mean Sørensen dissimilarity values

*Statistical analysis was not conducted on these metrics due to their inherent bias (see Results for more details).

et al., 2003). Beta diversity was separated into between-plot and between-stratum components within each data set. Gamma and alpha diversities are the total number of species within each data set and the average number of species per plot respectively. Hence, the species richness of each data set (gamma) is given by: $\gamma = \alpha_1 + \beta_1 + \beta_2$, where α_1 is the average species richness of the plots of both strata included, β_1 is the species turnover between plots given by $\beta_1 = \alpha_2 - \alpha_1$ where α_2 is the average species richness of the two strata (i.e. samples within each stratum are combined), and β_2 is the species turnover between strata given by $\beta_2 = \gamma - \alpha_2$ (Crist *et al.*, 2003). As observed beta diversity changes with the size of the species pool (gamma diversity) due to sampling effects (see Results), we corrected this by null model analysis as proposed by Kraft *et al.* (2011). For each data set, a null expectation was generated by randomly shuffling moth individuals among plots, while retaining relative abundances of species within each data set and the total number of individuals in each plot, in order to correct for the influence of gamma diversity (Kraft *et al.*, 2011). We then calculated β_2 based on the null, shuffled data. We repeated this 999 times and measured the difference between observed and average expected beta diversity (β_2) generated from the null model. Differences (deviations) were then divided by their standard deviations of the 999 expected beta diversity values to calculate standardized beta deviation.

We also employed a meta-analytical approach to quantify differences in moth assemblage composition. We measured Sørensen distances between canopy and understorey plots within each data set. To avoid overestimation of beta diversity, singletons (moth species with only one individual per sample) were removed from each data set before calculating Sørensen values. We then calculated effect sizes for each data set by dividing mean Sørensen values by their standard deviations. Unlike standardized beta deviation, however, this meta-analytical approach cannot control for differences in gamma diversity.

These metrics quantifying vertical stratification (Table 2) were used to investigate the influence of elevation and latitude separately, or in combination. The average temperature lapse rate predicts that the decrease in average air temperature with 1° latitude is equivalent to a 110 m increase in elevation (Jacobson, 2005). Based on this, we incorporated latitudinal differences into elevation and generated 'corrected' elevation for each location. We used linear models or mixed-effect linear models to analyse whether the magnitude of differences between canopy and understorey assemblages was related to latitude, elevation or 'corrected' elevation. We used four subsets of data to test the effect of 'corrected' elevation: all data sets ($n = 64$); low elevation data (i.e. excluding Ailao Shan and Lijiang locations which were over 2000 m a.s.l., $n = 56$, see Appendix S2b for more details); and, data sets from the Southern ($n = 49$) and Northern Hemispheres ($n = 15$). For analysis of latitudinal influence, we minimized the influence of elevation and seasonality by

excluding high elevation locations (Lijiang and Ailao Shan) and selecting only one data set from other locations ($n = 11$). We selected either a data set from the lowest elevation (200–800 m asl) and/or March–April (end of wet season) for Australian locations with multiple data sets. For analysis of elevational influence, we used only data sets from elevationally stratified locations and linear mixed-effect models with among-data set variation (season and latitude) specified as a random factor. Analyses were conducted using the LME4 package in R 3.1.0. For mixed-effect models we calculated Type III *P* values based on Kenward–Roger approximations (Judd *et al.*, 2012) for known degrees of freedom, available in the AFEX R package.

RESULTS

A total of 175,768 individual moths were sampled across the 13 locations. Vertical stratification (Sørensen dissimilarity) was significant (see Appendix S2c), with distinctive assemblages in the canopy and understorey (see Appendix S2d), except for three locations with small numbers of survey plots (see Table 1). However, for some locations incorporating elevationally stratified plots, there were interaction effects between elevation and stratum, with post hoc tests showing no significant differences between canopy and understorey assemblages at some elevations (results not shown).

Although proportional differences in observed species richness appeared to increase (i.e. more species in understorey) with increasing 'corrected' elevation (see Appendix S2e), this is an artefact due to its strong correlation with proportional differences in sample coverage (see Appendix S2f). Higher sample coverage in the understorey resulted in more species. When we controlled for the influence of sample coverage using proportional differences in estimated species richness, the negative relationship with 'corrected' elevation disappeared (Fig. 1). This was confirmed by a lack of a significant relationship using linear regression (Table 3). In the Northern Hemisphere, generally more species were estimated in the understorey than the canopy regardless of 'corrected' elevation (Fig. 1). 'Corrected' elevation was not significantly related to differences in estimated richness between understorey and canopy in any subsets of data (low elevations, Southern or Northern Hemisphere). Analysis of actual latitude and elevation also showed nonsignificant results for all analysed data sets (Table 3). The meta-analytical approach using standardized mean differences in species richness showed an apparent but nonsignificant increase in effect size with increasing 'corrected' elevation (see Appendices S2g and S2h).

Observed beta diversity between canopy and understorey assemblages was very variable across 'corrected' elevation (see Appendix S2i). Most variation came from elevationally stratified locations in China (circled in Appendix S2i) where beta diversity decreased with increasing 'corrected' elevation. Observed beta diversity between canopy and understorey was strongly and positively correlated with gamma diversity (see

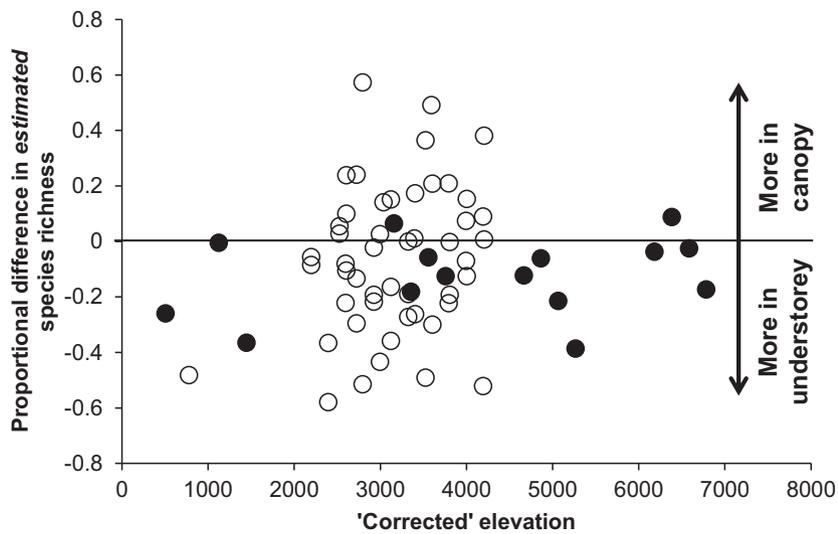


Figure 1 Proportional difference in estimated species richness between canopy and understorey strata of 64 moth data sets collected from 13 locations from Northern and Southern Hemispheres, plotted against 'corrected' elevation (see Methods for more details). Closed points are Northern Hemisphere and open points Southern Hemisphere locations. Positive values indicate that more estimated species in the canopy and negative values more in the understorey.

Table 3 Summary statistics of linear regression and mixed-effect linear regression investigating the effects of 'corrected' elevation, latitude and actual elevation on proportional differences in estimated species richness and standardized beta deviations of moth assemblages between canopy and understorey strata. Different subsets of data were analysed: all available data sets; data sets from low elevations (i.e. excluding Ailao Shan and Lijiang locations which were over 2000 m a.s.l.); and those from Southern and Northern Hemispheres (see Supporting Materials S3 for data sets included in each analysis). For mixed-effect linear regression, differences among data sets (which represent different locations and survey occasions) were treated as a random factor. Significant *P*-values ($\alpha = 0.05$) are shown in bold.

Response variables	Proportional difference in <i>estimated</i> species richness			Standardized beta deviation		
	Est. coef.	<i>t</i> value	<i>P</i>	Est. coef.	<i>t</i> value	<i>P</i>
Linear regression						
<i>'Corrected' elevation</i>						
All data sets (<i>n</i> = 64)	-0.00003	-1.561	0.124	0.0005	2.042	0.045
Low elevations (<i>n</i> = 56)	-0.00002	-0.788	0.434	-0.0002	-0.746	0.459
Southern Hemisphere (<i>n</i> = 49)	-0.00003	-0.870	0.389	-0.0011	-2.386	0.021 †
Northern Hemisphere (<i>n</i> = 15)	-0.00001	-0.864	0.403	0.0007	3.087	0.009
<i>Latitudes</i>						
All data sets (<i>n</i> = 11)	-0.01058	-2.016	0.075	0.0223	0.255	0.805
Mixed-effect linear regression						
<i>Elevation</i>						
All data sets (<i>n</i> = 56)	0.012	0.02	0.63	0.793	2.28	0.04
Low elevations (<i>n</i> = 48)	0.030	1.30	0.21	-0.480	-1.45	0.16
Southern Hemisphere (<i>n</i> = 44)	0.043	1.72	0.10	-0.721	-2.12	0.04
Northern Hemisphere (<i>n</i> = 12)	0.055	0.86	0.59	0.223	0.40	0.77

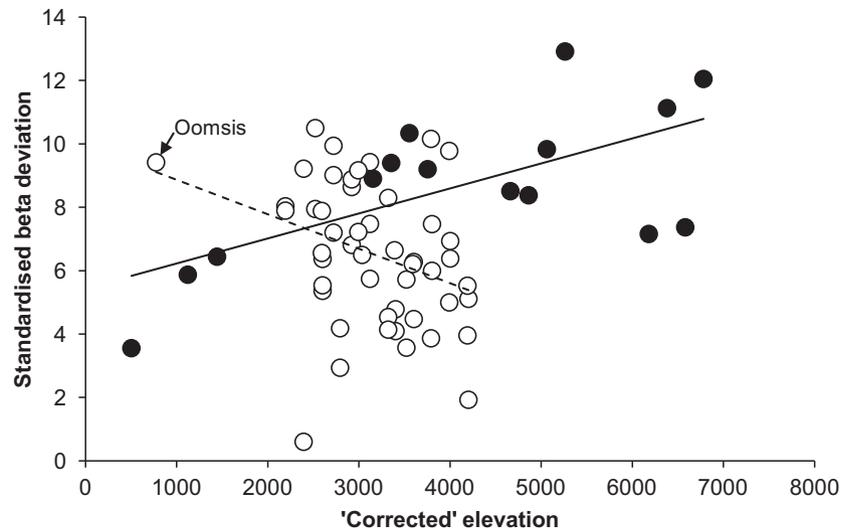
†The results became nonsignificant when one location (Oomsis) was removed from the analysis ($P = 0.058$).

Est. coef. = estimated coefficient

Appendix S2j). We therefore controlled for this in further analyses by using standardized beta deviation. When all data sets were used together, standardized beta deviation was significantly (but only marginally, Table 3) and positively correlated with 'corrected' elevation (Fig. 2). When using data sets from the Southern Hemisphere, standardized beta deviation was significantly and negatively correlated with 'corrected' elevation, whereas the opposite was found for Northern Hemisphere data sets (Table 3, Fig. 2). However, the negative relationship in the Southern Hemisphere became nonsignificant when one location (Oomsis) was excluded ($P = 0.058$). Standardized beta deviation was not

affected by latitude, but was marginally but significantly driven by elevation when all data sets (positive relationship) and the Southern Hemisphere data sets (negative relationship) were used (Table 3). The meta-analytical approach using standardized mean Sørensen dissimilarity between canopy and understorey showed no significant relationship with 'corrected' elevation (see Appendices S2h, S2k). However, when data sets were subdivided between hemispheres, those from the Southern Hemisphere showed a significant and negative relationship between vertical beta diversity and 'corrected' elevation (see Appendix S2k). Thus, the magnitude of the difference in assemblage composition between

Figure 2 Standardized beta deviation between canopy and understorey strata of 64 moth data sets collected from 13 locations from Northern and Southern Hemispheres (see Methods for more details), plotted against 'corrected' elevation. Closed points are Northern Hemisphere and open points Southern Hemisphere locations. Trendlines were drawn for Northern (solid line) and Southern (dashed line) Hemisphere locations which showed significant correlation with 'corrected' elevation (however, results became nonsignificant for the Southern Hemisphere when one location, Oomsis, was removed from the analysis).



canopy and understorey decreased with increasing 'corrected' elevation. However, as for standardized beta deviations, this relationship became nonsignificant when Oomsis was excluded ($P = 0.490$, see Appendix S2 h).

DISCUSSION

This is the first multi-country study of vertical stratification in a key herbivore group. We found an over-arching pattern of vertical stratification within forest moth assemblages across elevation, latitude and forest types. We also found differences in the direction and strength of vertical turnover across 'corrected' elevation between Northern and Southern Hemispheres. The concept of vertical stratification is a fundamental tenet in ecology (Ozanne *et al.*, 2003), but there remains little consensus on the degree to which vertical stratification occurs across different taxa. There have been many single location canopy studies on a range of taxa (Wardhaugh *et al.*, 2012). However, in order to understand the ecological and evolutionary processes involved, we first need descriptive data on vertical ecological patterns, across forest types, climates, continents with contrasting biogeographical histories (Stork *et al.*, 1997) and between Northern and Southern Hemispheres (Qian *et al.*, 2013). Differences in sampling methods used in previous canopy studies make wider comparisons and interpretations difficult, confounding variation between studies. We employed a standardized trapping approach in sampling canopy and understorey arthropods across all our study sites.

Explanatory hypotheses for strong vertical stratification of moths

The clear distinction between understorey and canopy assemblages across almost all our sites, regardless of elevation, latitude and forest type, supports the fundamental idea of vertical stratification in arthropods (Sutton *et al.*, 1983;

Basset *et al.*, 2001; Brehm, 2007). Differences between assemblages of adult moths encountered in the understorey level and the canopy may be explained by either, or both, of the following hypotheses. The first explanation is that the species encountered within understorey and canopy assemblages occur where they do because that particular stratum of the forest defines their lifetime *habitat*. In other words, the adult insects we encounter in our traps reflect the larval assemblages occurring in that stratum. This in turn indicates that the food resources of the species encountered at each level are themselves stratum-limited. Testing the veracity of this hypothesis requires knowledge of the food plants of the species that occur in each level. The contrasting, but not mutually exclusive, hypothesis is that encountering particular species in particular strata reflects the *behavioural* preferences of the adults of those species, the food plants of which may occur elsewhere. Availability of nectar, mates or mating locations are the obvious alternative resources which could produce vertical stratification (Basset *et al.*, 2003).

The above hypotheses require information on host plant associations if they are to be tested. Some information for Panamanian moths is available, cataloguing many years and many tens of thousands of rearings from adjacent Costa Rica (<http://janzen.sas.upenn.edu/caterpillars/database.lasso>). Accordingly we have made a preliminary analysis based on that database plus plant information available (Croat, 1978). Examination of food-plant records for the Panamanian species suggests there is support for both hypotheses. The occurrence of moth species, which have larval habitats at understorey level (such as the larvally *aquatic* Crambidae: Acentropinae), in the canopy, as also noted by Schulze & Fiedler (2003), is evidence for behavioural stratification. Alternatively, differences in food-plant specialization among canopy and understorey sampled adults suggests that a substantial percentage of species are reflecting available larval resources within the stratum in which they are encountered.

Only natural historical studies of individual species will allow species to be placed unequivocally in one or other category. Support for food resource stratification of adults exists for butterflies in Borneo (Schulze *et al.*, 2001) and Panama (Beccaloni, 1997). In Costa Rica, Brehm (2007) found that stratification of geometrid and arctiine moths was associated with host plant height. Generally, however, there is little information on food resource stratification for moths, which has made interpretation of observed differences in moth distributions difficult. In principle, testing this idea would involve knowing not only where particular species breed but also what their diel shifts in flight level might be.

Vertical turnover across elevation and latitude

Moths are almost universally herbivorous and often closely associated with their host plants (Common, 1990). We therefore expected to find lower vertical stratification of moth communities at higher elevations and latitudes, driven by declines in forest structural complexity, plant species richness, tree density, canopy height and the abundance of lianas (Richards, 1996; Lieberman *et al.*, 1996 and see supporting materials S21). Assuming that these patterns of plant diversity drive those of their herbivores (Novotny *et al.*, 2006; Kitching & Ashton, 2013) this could potentially account for any patterns detected in herbivorous taxa. Examining patterns of diversity across different continents at different latitudes requires separating data into Northern and Southern Hemispheres, as there are key differences in environmental and biotic characteristics (Jobbagy & Jackson, 2000; Qian *et al.*, 2013). In fact we found an *increase* in vertical beta diversity with increasing 'corrected' elevation in our Northern Hemisphere locations, contrary to our expectations. We found the opposite pattern in the Southern Hemisphere, although it was very weak, and became non-significant when an outlier was removed. This parallels the results of Qian *et al.* (2013), who examined shifts in spatial (not vertical) beta diversity of woody stems > 2.5 cm d.b.h. across latitude and found beta diversity decreased with increasing latitude in the Northern Hemisphere (New World north and China) and increased with increasing latitude in the Southern Hemisphere (New World south).

The strong Northern Hemisphere result in the current study – increasing vertical beta diversity with 'corrected' elevation – was not driven by differences in forest type, and was apparent even when we look at only the tropical data. This is in spite of the observed reductions in the distance between the canopy and understorey and a simpler forest structure with increasing latitude. Although there were also significant, albeit weak changes in beta diversity between strata in the Southern Hemisphere, we did not find the northern pattern of increasing turnover with increasing 'corrected' elevation. There are several possible explanations for the increase in vertical turnover across 'corrected' elevation in the Northern Hemisphere, which was not found in the Southern Hemisphere.

First, these differences may reflect the size of the regional species pool which may drive differences even after statistical

correction. The Chinese locations were far more species-rich than any of our southern sites (see Appendix S2a). The differences in the regional species pool may be in part due to the contrasting biogeographical histories of each region. Our Chinese locations are at the centre of mainland East Asia; a large and historically more stable area of heterogeneous mountain landscapes (Tang *et al.*, 2006). In contrast, Australia was, until the mid-Miocene, primarily covered in rain forest. During the late Pliocene the rain forest retracted to the east coast and this was followed by a series of climatic oscillations and associated contractions and re-expansions (Kooyman *et al.*, 2011). This periodic contraction and drying of Australian rain forest may have generated a greater proportion of generalist moth species that could utilize both the canopy and understorey in rain forest refugia (higher latitudes and elevation). Our results, therefore, may reflect this greater and more stable long-term diversity in the Northern Hemisphere producing stronger patterns in vertical stratification with latitude and elevation.

The increase in the magnitude of the contrasts in moth assemblages with increasing 'corrected' elevation in the Northern Hemisphere could also have a structural explanation. If the herbivore assemblage observed in a particular stratum represents the availability of plant hosts within that stratum, then differences between host resources will produce differences in their associated herbivores. In the more tropical, lower elevation environments many plant resources are, arguably, available at all levels from the understorey to the canopy – lianas, encrusting and free epiphytes, even tree canopies at different heights reflecting disturbance histories. The understorey plants may simply be shorter versions of their canopy counterparts. This distribution of resources may lessen the distinctions between understorey and canopy faunas. In more temperate or higher elevation environments the available host plants are more likely to be *either* canopy *or* understorey based leading potentially to clearer separation between understorey and canopy moth assemblages. This remains a hypothesis and finer scale analysis of forest structures will be required to test it.

We note that the elevational transects we studied in China differed substantially in their median elevations. This was in contrast with the Australian transects which had more or less identical median elevations. This was inevitable given the relative topographies of the two regions.

Conclusion

We have conducted 20 years of extensive sampling, collecting and identifying over 100,000 individual moths across elevational and latitudinal gradients. The major conclusion, based on sampling in many habitats, forest types and areas of differing biogeographical history, is that for night-flying moths, canopy assemblages are *different* from understorey assemblages, but not necessarily more *diverse*. In addition, the degree to which assemblages are stratified between canopy and understorey is not uniformly related to elevation and

latitude as we found inconsistent patterns between the Northern and Southern Hemispheres. Obviously, the results of our study have important implications for research, which, hereto, has usually been carried out either in the canopy or at understorey level. Our results suggest that sampling in the canopy *and* at understorey level is essential to capture the full diversity of the forest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed descriptions of study locations.

Appendix S2 Supplementary tables and figures.

BIOSKETCH

Louise Ashton is a postdoctoral fellow at the Natural History Museum, London. Her research focuses on climate change impacts on biodiversity, tropical community ecology and understanding the factors shaping community assembly across environmental gradients, primarily using insect herbivores.

Author contributions: L.A.A., A.N., Y.B., E.G.O., J.S. and R.L.K. conceived the research ideas; L.A.A., A.N., C.J.B., M.C., R.E., E.O., E.G.O., K.H., S.M., J.S., Z.H.S., Y.T., T.W. and R.L.K. collected moths; M.J.L. and W.J.F.M. surveyed plants; L.A.A., A.N., M.K. and J.M. analysed the data (A.N. and M.K. wrote the code and ran the R program); L.A.A., A.N., C.J.B., and R.L.K. led the writing.

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