

Chapter 11.3

Variation of Diversity Patterns Across Moth Families Along a Tropical Altitudinal Gradient

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11.3.1 Introduction: Altitudinal Gradients and Insect Diversity

Comparative and experimental investigations along the steep altitudinal gradient that is characteristic for Andean ecosystems have formed one of the central paradigms of research at the RBSF in southern Ecuador summarized in the present volume (Lomolino 2001; Rahbek 2005; see Chapter 6 in this volume). For ectothermic insects the increasingly harsher climatic conditions at higher elevations alone impose severe constraints (McCoy 1990; see Chapter 8). Herbivorous insects find fewer plant species and less plant biomass available as nutrient resources at high elevations (see Chapter 10.1). Herbivorous insects are one of the most diverse guilds in terrestrial ecosystems, and within this guild phytophagous beetles and the Lepidoptera (moths and butterflies) are especially species-rich. Available studies on Lepidoptera (the taxonomically best known large insect group) often revealed a mid-elevation bulge of species richness (Holloway and Nielsen 1999; Rahbek 2005). However, many variations occur to this general pattern. For example, on Mt. Kilimanjaro, diversity in the moth family Geometridae is surprisingly low and decreases but slightly throughout the montane forest belt at 2000–3000 m (Axmacher et al. 2004). In the Ecuadorian Andes, in contrast, diversity in the same moth family is exceptionally high and remains almost constant at 1000–2700 m (Brehm et al. 2003b). Yet, these Andean geometrid ensembles (for terminology, see Fauth et al. 1996) change fundamentally with regard to species composition, representation of higher taxa, and body sizes (Brehm and Fiedler 2003, 2004a; Brehm et al. 2003a, b). In this chapter we extend and summarize our investigations of moth diversity in this Andean altitudinal gradient by integrating data on two further, very species-rich moth taxa, viz. Pyraloidea and Arctiidae.

The three taxa were selected because:

1. They represent large proportions of moth diversity globally (numbers of described species: Geometridae: 21 000; Pyraloidea: 16 000; Arctiidae: 11 000; Scoble 1992) as well as in the Neotropical region (numbers of described species: Geometridae: 6450; Pyraloidea: 4562; Arctiidae: 5931; Heppner 1991; Munroe et al. 1995; Scoble 1999).

2. They differ markedly from one another in many bionomic traits, body size, and host plant affiliations.

Pyraloidea are usually small (forewing length mostly <30 mm), slender and delicate (Munroe and Solis 1999). Pyraloid larvae are concealed feeders which bore inside stems or fruits, or live in webs or leaf rolls (Munroe and Solis 1999). Concealed feeders are typically more specialized with regard to host plants (Gaston et al. 1992). Few pyraloids are chemically defended by sequestered plant metabolites or toxic gland secretions. Most Geometridae species are also rather delicate moths, but are generally larger in size than pyraloids. The naked caterpillars are mostly ectophagous on foliage, with exceptions in the Geometrinae and the speciose Eupitheciini many of which are hemi-endophagous in inflorescences. As in the Pyraloidea, aposematic coloration and sequestration of plant toxins are rare in the Geometridae. In contrast, Arctiidae moths are larger (fore wing length often >20 mm, especially in the subfamily Arctiinae) and more robust (for Ecuadorian samples, see Hilt 2005). Many arctiids are aposematically colored and chemically well defended (Häuser and Boppré 1997; Kitching and Rawlins 1999; Weller et al. 1999). Arctiid larvae possess a dense cover of setae, feed externally on a wide range of plants, and a substantial fraction of them appears to be less specialized with regard to host plants (Kitching and Rawlins 1999; Holloway et al. 2001).

We here address three questions:

1. How does species diversity change in all moths, in the three moth clades, and in their larger subordinated taxa, along an altitudinal gradient?
2. Does the gross taxonomic composition of moth ensembles (i.e. representation of subfamilies and tribes) change with altitude, or do certain taxa contribute a rather invariant share at all elevations?
3. How does species composition of the moth ensembles change with altitude?

11.3.2 Methods: Sites, Sampling and Data Processing

We sampled moths at 22 sites situated at 1040–2677 m a.s.l. (two replicate sites at each level of altitude; for locality data and a map, see Brehm and Fiedler 2003; Brehm et al. 2005) at the northern border of the Podocarpus National Park and in the adjacent Reserva Biológica San Francisco. Chapters 1, 8, 10.1, and 10.3 provide details on the topography, climate, and vegetation of the study area along the altitudinal gradient.

Moths were attracted to weak artificial light sources (2×15 W) at ground level and manually sampled (Axmacher and Fiedler 2004; Brehm and Axmacher 2006). Assuming an attraction radius of 50–100 m of the light sources, the total sampling area amounted to just 0.17–0.69 km². Light-trap samples do not perfectly represent actual populations but rather reflect the activity of species attracted to light (Muirhead-Thomson 1991; Butler et al. 1999). However, for nocturnal Lepidoptera this sampling method is unrivalled in terms of specimen and species numbers that can be gathered (for a critical evaluation of the methodology, see Schulze and Fiedler 2003; Wirooks 2005).

Sampling was restricted to the evening hours between 1830 hours and 2130 hours, local time. Hence 'late night species' were not covered. We collected moths during three field periods (April to May 1999, October 1999 to January 2000, October to December 2000; for catch dates, see Süßenbach 2003) and pooled replicate catches from each site into one sample. Two to four nightly catches were combined for the Geometridae (which occurred in larger numbers), whereas up to nine catches per site were collated for the less abundant Arctiidae and Pyraloidea (Table 11.3.1).

Specimens were taxonomically identified using published literature and reference collections (see Acknowledgments; Table 11.3.1). In view of the tremendous species richness of moths (see Chapter 2 in this volume), this process provided a great challenge on its own (see Chapter 5). Species lists are available by Süßenbach (2003), Brehm et al. (2005), and Hilt (2005). Voucher specimens are deposited in the State Museum of Natural History, Stuttgart, Germany.

As a robust measure of local diversity we used Fisher's α of the logseries (e.g. ; Hayek and Buzas 1997; Beck et al. 2002; Axmacher et al. 2004). Species numbers are less informative for rich communities of mobile organisms, unless near-complete inventories are achieved (Gotelli and Colwell 2001). Logseries-type rank-abundance distributions are common in nature (Engen and Lande 1996; Hubbell 2001). To extend comparisons to lower taxonomic scales with smaller sample sizes, we calculated taxon ratios based on the data shown in Table 11.3.2 (Brehm and Fiedler 2003).

We ordinated moth samples by non-metric two-dimensional scaling based on Bray-Curtis similarities (Legendre and Legendre 1998). Raw data were fourth-root transformed to alleviate dominance effects. Ordinations based on other similarity measures (Sørensen index, CNESS index for various values of the sample size parameter m) as well as application of other ordination techniques (correspondence analysis, detrended correspondence analysis) all yielded very similar results (e.g. Brehm and Fiedler 2004b). Two-dimensional ordinations were deemed sufficient due to their low stress (stress is a measure of poorness-of-fit between the configuration in reduced ordination space and the original similarity matrix; Clarke 1993).

Relationships between diversity measures or with environmental variables were assessed using standard correlation and regression techniques. The match between matrices of faunal similarity was assessed using permutation tests for matrix rank correlations. If multiple tests of significance were performed, we used Benjamini and Hochberg's (1995) approach to control for a table-wide false discovery rate.

11.3.3 Results and Discussion

11.3.3.1 Local Diversity of Moth Ensembles

We recorded 28 743 moths representing 2129 species (or 'parataxonomic units' in the case of moths that we could not formally identify; Krell 2004) of the three focal taxa. Geometridae were by far the most abundant and speciose family. Values of Fisher's α for all 22 sampling sites cumulated across the gradient were: 250.1 (Geometridae),

Table 11.3.1 Numbers of moth species (*S*) and individuals (*N*) at the 22 light trapping sites along the altitudinal gradient in the Ecuadorian Andes. 'identified' refers to the fraction where taxonomic determinations were achieved at species level

Site	Altitude (m a.s.l.)	Arctiidae		Geometridae		Pyraloidea		All combined	
		<i>S</i>	<i>N</i>	<i>S</i>	<i>N</i>	<i>S</i>	<i>N</i>	<i>S</i>	<i>N</i>
1a	1040	52	108	134	410	220	696	406	1214
1b	1040	149	712	247	976	315	1352	710	3039
2a	1380	59	155	200	623	166	892	425	1670
2b	1380	54	159	158	393	135	528	347	1080
3a	1800	59	175	203	496	92	368	354	1039
3b	1800	59	153	171	384	94	331	324	868
4a	1850	60	192	178	473	78	250	316	915
4b	1875	90	354	225	649	155	442	470	1445.0
5a	2005	75	434	202	618	114	323	391	1375
5b	2005	49	186	190	429	80	232	319	847
6a	2112	49	140	217	782	87	269	353	1191
6b	2113	61	187	177	440	85	257	323	884
7a	2180	50	135	292	1200	89	315	431	1650
7b	2212	52	290	273	1116	72	415	398	1822
8a	2290	49	138	200	683	75	506	324	1327
8b	2308	48	202	144	384	77	455	269	1041
9a	2375	50	173	201	725	77	586	328	1484
9b	2387	46	128	259	981	68	617	374	1726
10a	2524	55	123	191	596	70	296	316	1015
10b	2558	65	135	192	447	62	268	319	850
11a	2671	34	82	167	473	65	306	266	861
11b	2677	40	100	209	660	86	640	335	1400
Total		371	4461	1013	13 939	748	10 344	2132	28 744
Identified (%)		64.7	63.8	64.7	72.2	10.3	19.5	45.6	51.9

185.1 (Pyraloidea), 96.1 (Arctiidae), and 531.6 (all three moth taxa combined). This high diversity was not uniformly distributed along the altitudinal gradient. The expected decline in the diversity of ectothermic herbivores occurred in the Pyraloidea and among all moths combined (Fig. 11.3.1; statistics: Table 11.3.3).

We observed no such decrease in the Geometridae. Brehm et al. (2003b) showed that, within the Geometridae, diversity of species belonging to the subfamily Larentiinae even increased at higher altitudes, whereas Ennominae diversity did not change along the gradient. In the Arctiidae the altitudinal decrease was just marginally significant. Analyzing the two subfamilies of Arctiidae separately revealed that only diversity of Lithosiinae decreased with increasing altitude, whereas in the far more species-rich Arctiinae diversity did not change consistently with elevation. There was also no significant pattern in the two largest Arctiinae clades (viz. Phaegopterini, Ctenuchini–Euchromiini; the latter termed 'Ctenuchini' in the following for the sake of brevity), but sample sizes were low, limiting the power of tests. Within Pyraloidea, the altitudinal decline of diversity was stronger in the family Crambidae rather than in Pyralidae. The subfamily Pyraustinae was by far the largest

Table 11.3.2 Higher classification of Geometridae, Arctiidae, and Pyraloidea with numerical representation of the groups in the cumulative sample along the altitudinal gradient (1040–2677 m a.s.l.). Systematics: Scoble (1999) and Pitkin (2002) for Geometridae; Munroe et al. (1995) for Pyraloidea; Jacobson and Weller (2002) for Arctiidae

Taxon	Species	Individuals	Taxon	Species	Individuals
Geometridae	1013	13939	Pyraloidea	748	10344
Desmobathrinae	1	2	Crambidae	638	9829
Ennominae	502	6636	Crambinae	35	596
Geometrinae	57	715	Schoenobiinae	5	128
Larentiinae	381	5721	Cybalomiinae	3	16
Oenochrominae	3	23	Glaphyriinae	8	162
Sterrhinae	69	842	Scopariinae	18	644
			Musotiminae	29	322
Arctiidae	371	4461	Midilinae	1	3
Lithosiinae	68	1941	Acentropinae	28	258
Arctiinae	303	2520	Odontiinae	6	293
Arctiini	7	13	Evergestiinae	2	18
Phaegopterini	169	1139	Pyraustinae	503	7389
Ctenuchini	116	1313			
Pericopini	11	55	Pyralidae	105	475
			Pyralinae	4	4
			Chrysauginae	12	56
			Galleriinae	10	180
			Epipaschiinae	18	50
			Phycitinae	61	185

and strongly dominated this pattern. Other pyraloid taxa were too small to allow for meaningful calculation of diversity statistics. The altitudinal decrease in diversity was 5–10 times steeper (t -test, $P < 0.05$) within Pyraloidea, Crambidae, and all moths combined, than in Arctiidae or Lithosiinae.

Local diversity of Geometridae and Arctiinae was largely unrelated to diversity patterns in any other of the moth groups examined (Table 11.3.4). Diversity patterns were more similar between Pyraloidea, all Arctiidae, Lithosiinae, and all moths combined.

11.3.3.2 Changes in Taxonomic Composition with Altitude

Representation of moth subfamilies and tribes along the altitudinal gradient varied considerably within the Arctiidae, Pyraloidea (Table 11.3.5), and Geometridae (Brehm and Fiedler 2003). Among Arctiidae, species proportions of Phaegopterini increased and Ctenuchini decreased with altitude. Lithosiinae had an increasingly higher share of individuals and species at high elevations, whereas Ctenuchini and Pericopini contributed less to Arctiidae ensembles at higher altitudes. Ctenuchini comprised a sizeable proportion of the arctiid ensembles at 1040–1875 m (>35% of species and individuals), but accounted for usually ca. 20% and less at higher elevations.

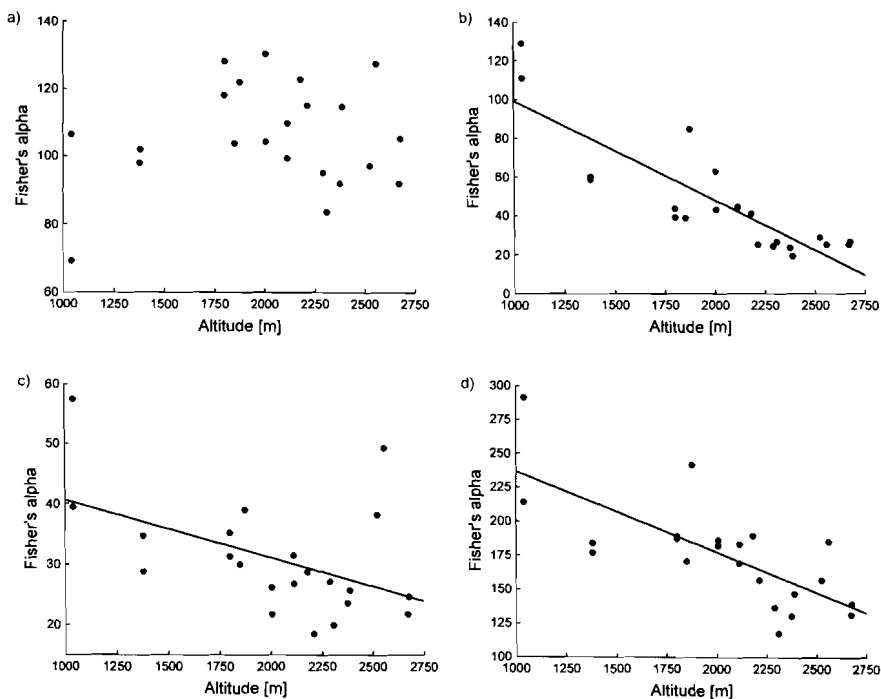


Fig. 11.3.1 Relationship between altitude and local diversity (measured as Fisher's α) of various moth groups. **a** Geometridae, **b** Pyraloidea, **c** Arctiidae, **d** all these moths combined. The linear least squares regression line is included where significant. For statistics, see Table 11.3.3

Table 11.3.3 Results of linear regressions of alpha diversity (measured as Fisher's α) against altitude. Given are regression coefficients b , their standard errors $SE(b)$, the coefficient of determination R^2 , and the error probability P (significant results printed in *italics*; * significant after correction for a table-wide false discovery rate at $P=0.05$). $N=22$ sites.

Taxon	b	$SE(b)$	R^2	P
Geometridae	0.0050	0.0071	0.0243	0.488
Pyraloidea	-0.0512	0.0071	0.7212	<i><0.0001*</i>
Crambidae	-0.0495	0.0058	0.7835	<i><0.0001*</i>
Arctiidae	-0.0095	0.0039	0.2285	<i>0.024</i>
Arctiinae	0.0035	0.0038	0.0415	0.363
Phaegopterini	0.0051	0.0028	0.1427	0.083
Ctenuchini	-0.0026	0.0023	0.0567	0.286
Lithosiinae	-0.0033	0.0010	0.3364	<i>0.005*</i>
All moths combined	-0.0592	0.0126	0.5250	<i>0.0001*</i>

Within the Pyraloidea, at higher altitudes the family Pyralidae increased and the Crambidae decreased in their proportions of species, but this was not significant for fractions of individuals. At the subfamily level, Scopariinae, Odontiinae, Galleriinae, and Phycitinae tended to be more prevalent at higher altitudes,

whereas Pyraustinae, Acentropinae, Musotiminae, and Glaphyriinae were more important at lower elevations. Schoenobiinae exclusively occurred in low numbers at medium elevations (1800–2300 m). Only three of the more abundant pyraloid subfamilies did not show any clear altitudinal pattern (Crambinae, Chrysauginae, Epipaschiinae).

Table 11.3.4 Correlation of local diversity between moth groups ($N=22$ sites), based on Fisher's alpha. Within each cell, the upper entry is Pearson's r_P , the lower entry gives the corresponding P value. *n.s.* not significant ($P>0.05$). All significant results (printed in italics) remained so after correction for a table-wide false discovery rate of $P=0.05$.

	Pyraloidea	Arctiidae	Arctiinae	Lithosiinae	All moths combined
Geometridae	-0.177 <i>n.s.</i>	0.123 <i>n.s.</i>	-0.169 <i>n.s.</i>	-0.130 <i>n.s.</i>	0.287 <i>n.s.</i>
Pyraloidea	-	0.641 <i>0.001</i>	0.002 <i>n.s.</i>	0.767 <i><0.001</i>	0.874 <i><0.001</i>
Arctiidae	-	-	0.567 <i>0.006</i>	0.800 <i><0.001</i>	0.777 <i><0.001</i>
Arctiinae	-	-	-	0.325 <i>n.s.</i>	0.016 <i>n.s.</i>
Lithosiinae	-	-	-	-	0.751 <i><0.001</i>

Table 11.3.5 Relationship between subfamily or tribe proportions with altitude (Spearman's rank correlation r_S , $N=22$ sites). The arctiid tribe Arctiini and four pyraloid subfamilies were disregarded because of low representation (Cybalomiinae, Midilinae, Evergestiinae, Pyralinae; cf. Table 11.3.2). Significant results ($P<0.05$) printed in italics.; * significant after correction for a table-wide false discovery rate of $P=0.05$.

Taxon	Individuals		Species	
	r_S	P	r_S	P
Arctiidae				
Lithosiinae	0.630	<i>0.002*</i>	0.472	<i>0.026</i>
Arctiinae	-0.630	<i>0.002*</i>	-0.472	<i>0.026</i>
Phaegopterini	0.345	0.115	0.696	<i><0.001*</i>
Ctenuchini	-0.838	<i><0.001*</i>	-0.867	<i><0.001*</i>
Pericopini	-0.455	0.033	-0.405	0.0618
Pyraloidea				
Crambidae	-0.327	0.138	-0.558	<i>0.007*</i>
Pyraustinae	-0.335	0.128	-0.437	<i>0.042</i>
Acentropinae	-0.917	<i><0.001*</i>	-0.765	<i><0.001*</i>
Crambinae	-0.390	0.073	0.320	0.147
Schoenobiinae	-0.252	0.258	-0.178	0.429
Glaphyriinae	-0.532	<i>0.011*</i>	-0.191	0.395
Scopariinae	0.784	<i><0.001*</i>	0.823	<i><0.001*</i>
Musotiminae	-0.858	<i><0.001*</i>	-0.400	0.065
Odontiinae	0.720	<i><0.001*</i>	0.710	<i>0.001*</i>
Pyralidae	0.390	0.073	0.529	<i>0.011*</i>
Chrysauginae	0.268	0.228	0.380	0.081
Galleriinae	0.528	<i>0.012*</i>	0.508	<i>0.016*</i>
Epipaschiinae	-0.331	0.132	-0.159	0.479
Phycitinae	0.426	<i>0.048</i>	0.652	<i>0.001*</i>

11.3.3.3 Species Turnover Along the Altitudinal Gradient

Ordinations of all moth taxa revealed very similar altitudinal gradients of species turnover (Fig. 11.3.2). No clustering of ensembles was detectable, as would be expected if moth ensembles of particular altitudinal zones were to form distinct associations. The gap between sites at altitudinal levels 1 and 2 versus levels 3 and higher in the ordination diagrams reflects the larger altitudinal distance between sampling sites (Table 11.3.1). For the seven moth taxa with sufficient sample sizes (Arctiidae, Arctiinae, Phaegopterini, Ctenuchini, Lithosiinae, Pyraloidea, Geometridae), as well as for all moths combined, there was a highly significant (and linear) correlation between the first ordination axis and altitude ($rP = 0.877\text{--}0.975$, $P < 0.001$). Correlations of species turnover with mean air temperature during nightly catches at the sampling sites were also all very close ($rP = 0.885\text{--}0.980$, $P < 0.001$). Finally, similarity matrices for all these moth groups were highly correlated to each other ($rS = 0.838\text{--}0.986$, $P < 0.001$).

11.3.3.4 Moth Diversity, Elevation, and Thermal Ecology

The diversity of the three moth (super-)families was exceptionally high at the scale of individual sampling sites and impressively so if viewed for the entire study landscape. With far more than 2100 moth species representing the three studied families

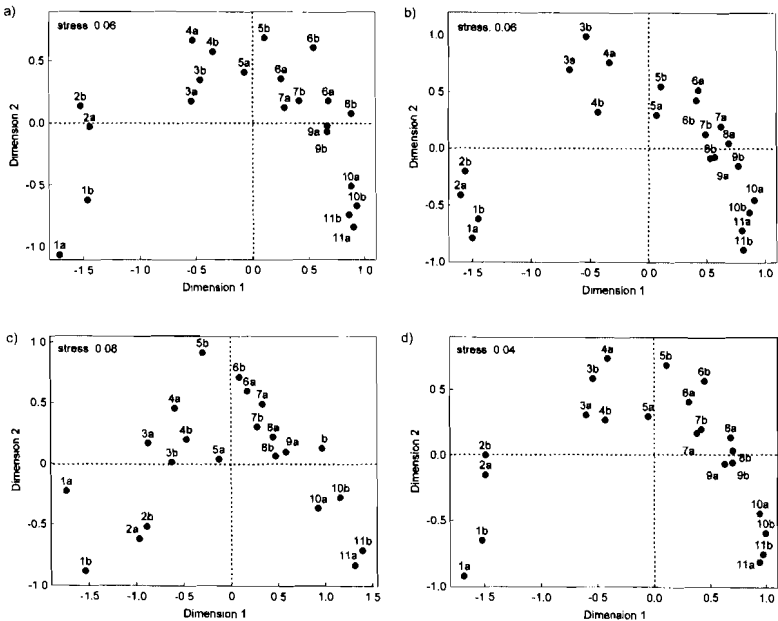


Fig. 11.3.2 Ordination of moth samples by non-metric two-dimensional scaling based on Bray-Curtis similarity matrices (raw abundances fourth-root transformed). **a** Geometridae, **b** Pyraloidea, **c** Arctiidae, **d** all these moths combined. In all cases moth samples are ordinated according to altitude

sampled from a small area, the montane forest belt of the Eastern Cordillera in the southern Ecuadorian Andes qualifies as a global hotspot of moth diversity (Myers et al. 2000; Brummitt and Lughadha 2003; Brehm et al. 2005; see Chapter 2 in this volume). In the two 'macro-moth' families Arctiidae and Geometridae, ca. 64% of the species and ca. 70% of the individuals could be formally identified thus far (see Chapter 5). The remainder includes mostly undescribed species whose taxonomic evaluation is now under way (Brehm 2004, 2005; Pitkin 2005). The identification rate was much lower for the taxonomically less known Pyraloidea. Still, our para-taxonomic sorting in this clade followed by evaluation aided through taxonomists should allow for meaningful analyses of gross patterns (Krell 2004).

As was expected for ectothermic herbivorous insects, the total moth diversity significantly declined in the montane forest zone of southern Ecuador at 1040–2677 m elevation, even though at the highest sites the moth diversity was still remarkably high (Fisher's α : 120–185). Such a decrease in diversity is concordant with the cooler, more humid environmental conditions, and lower resource diversity at higher altitudes.

However, this overall decline in moth diversity did not uniformly recur at smaller systematic scales. Importantly, exceptions from that rule were not confined to small lineages with 'aberrant' ecological requirements, but occurred in large species-rich taxa. Brehm et al. (2003b) showed that diversity of Geometridae was constantly high along the investigated altitudinal gradient, with one large subfamily not responding to altitude (Ennominae), while in the other large subfamily (Larentiinae) diversity even increased towards higher elevations. With the subfamily Arctiinae we found one more speciose moth group whose diversity did not decline with altitude in the studied elevational range. Rather, in this subfamily diversity was lowest at intermediate altitudes (2000–2200 m; α : 15–25), whereas ensembles at higher and lower elevations were almost equally diverse (2290–2677 m, α : 30–50; 1040–1875 m, α : 25–45).

The reasons why Geometridae and Arctiinae do not follow the common trend of declining diversity at higher elevations might possibly differ. Geometridae moths are known to fly at unusually low thoracic temperatures, often just marginally above ambient temperature (Heinrich and Mommsen 1985; Utrio 1995, Rydell and Lancaster 2000). This physiological specialization should make them less sensitive to the linear decline in ambient temperatures from 22 °C mean annual temperature at the lowest to 12 °C at the highest sampling sites (see Chapter 8 in this volume). Thus, due to their flight physiology even delicate, slender, small geometrids may be able to remain active at low temperatures, and this might also allow the smaller and less robust Larentiinae to dominate at higher altitudes (Brehm and Fiedler 2004a). Arctiinae, in contrast, usually require higher thoracic temperatures (above 30 °C) to commence flight activity (Rydell and Lancaster 2000). However, many Arctiinae are robust moths with a dense thoracic hair cover. This is particularly true for the Phaegopterini and Arctiini, whereas Ctenuchini or Pericopini are often more slender, less hairy, and are thus less robust flyers. We therefore hypothesize that their better isolation against thermal losses, rather than an adaptation of flight metabolism to lower temperatures, allows Phaegopterini moths to thrive in large numbers along the entire altitudinal gradient.

Moth taxa where we observed a clear decline in diversity with elevation are rather delicately built, and less well isolated by hair-like thoracic scales. This applies to the majority of Pyraloidea, but also to the arctiid subfamily Lithosiinae. The proportional decrease of Ctenuchini and Pericopini relative to all arctiid moths also fits here. The Pyraloidea showed the overall largest reduction of diversity from the warm lower montane forest to the cool cloud forest zone. While at the lowest sites at Bombuscaro (1040m) pyraloid ensembles were exceptionally diverse ($\alpha > 100$), ensembles at elevations above 2200 m were much less rich ($\alpha < 35$).

11.3.3.5 *Moth Diversity and Host Plants*

Most moths have herbivorous larvae, which tend to be specialized with regard to host plant use (Scoble 1992; Holloway et al. 2001). One would therefore predict that moth diversity mirrors plant (i.e. resource) diversity. Plant diversity in Ecuador is extremely high (Madsen and Øllgaard 1994, Jørgensen and León-Yáñez 1999), yet floristic data for our study area are still incomplete (see Chapter 10.1 in this volume). Knowledge of the host plant relationships of most recorded moth species is very fragmentary (Brehm 2002; Süßenbach 2003; see also Dyer et al. 2007; Janzen and Hallwachs 2007). This limits the search for relationships between plant and insect diversity. In the study area the forest at elevations between 2100–2700 m largely consists of mono-dominant stands of the tree *Purdiaea nutans* (see Chapter 19), but this was hardly mirrored by moth diversity patterns. Only among Pyraloidea (especially Crambidae, Pyraustinae) was the diversity almost constant and low (α : 15–25) throughout the *Purdiaea* forest zone. Whether this finding reflects reduced resource availability in this unusual cloud forest remains to be tested.

Pertinent host plant data are yet unavailable for most moth species that we have recorded. Certain changes in community patterns can nevertheless be linked to resource affiliations at a higher taxonomic scale. Most clades among the Lepidoptera have characteristic feeding specializations which are often conserved even across continents (Powell et al. 1999; Holloway et al. 2001). Pyraloid larvae are frequently endophagous or shelter-building and tend to be more specialized than ectophagous caterpillars (Gaston et al. 1992). Moreover, smaller-sized moth species generally tend to be more specialized with regard to host plants (Loder et al. 1998). Thus, higher host plant specialism might contribute to the steeper decline of pyraloid diversity as opposed to the more polyphagous arctiids, whose diversity changed much less in response to altitude.

Within the Arctiidae, Ctenuchini and Pericopini (many aposematic species with complex chemical defence) decreased considerably at higher elevations, whereas Phaegopterini (robust, often cryptically colored, putatively more polyphagous species) proportionally increased. The larvae of Lithosiinae often feed on algae, lichens, and liverworts, although certain Neotropical genera

have angiosperm host plants (Dyer et al. 2007; Janzen and Hallwachs 2007; F. Bodner, M. Zimmermann, and K. Fiedler, unpublished observations). Despite the abundance of lichens in the cloud forest zone, Lithosiinae diversity significantly decreased with elevation. However, at high altitudes Lithosiinae usually comprised more than 50% of all arctiid individuals in our samples, suggesting that the few species adapted to the upper cloud forest zone have ample resources there.

Four pyraloid subfamilies (Scopariinae, Odontiinae, Galleriinae, Phycitinae) proportionally increased at higher elevations. Scopariinae larvae often feed on mosses or ferns; in the tropics the subfamily is most prevalent in montane habitats (Munroe and Solis 1999). Thus their commonness in the upper cloud forest zone was expected. The host plant relationships and habitat requirements of Neotropical Odontiinae, Galleriinae, and Phycitinae are too incompletely known (Munroe and Solis 1999) to relate their unexpected proportional increase at high elevations to life history traits.

The pyraloid subfamilies Acentropinae, Glaphyriinae, and Musotiminae proportionally decreased with altitude. Acentropinae larvae often feed on aquatic plants (Munroe and Solis 1999). Our light-trapping sites at elevations of 1040–2000 m were close to streams, so the distributional pattern of Acentropinae in our samples could indeed reflect an association with freshwater habitats. Musotiminae are fern feeders (Munroe and Solis 1999). It was thus surprising that moths of this subfamily became scarce at elevations above 2100 m, while ferns were still abundant and diverse (Kessler 2001). The feeding habits of Glaphyriinae larvae are so diverse that no inferences can be made at subfamily level.

11.3.3.6 Taxonomic Composition, Scale, and the Problem of Biodiversity Indication

Brehm et al. (2003a, b) and Brehm and Fiedler (2003) observed that taxonomic composition significantly changed along the altitudinal gradient within the moth family Geometridae, depending on taxonomic scale (family, subfamily, tribe). Our analyses revealed that similar variation recurs also in two other large moth clades. Patterns partially contrasted from the tribe (e.g. Ctenuchini: altitudinal decrease) nested in a subfamily (Arctiinae: no clear altitudinal change) which is again nested in a family (Arctiidae: weak altitudinal decline). The gross taxonomic composition of moth ensembles also profoundly changed with altitude. It was thus surprising that species turnover was highly concordant across all moth groups. Patterns of beta diversity were also invariant to taxonomic scale. All our ordinations revealed the same, recurrent pattern: a steady altitudinal change of species composition, with no evidence for the existence of faunal zones. In all cases ordinations nearly perfectly mirrored the altitude of sampling sites. This suggests that, apart from all idiosyncrasies in host-plant use, physiology or habitat requirements, one major variable must govern species turnover in all investigated moth groups in much the same

way. Given the large differences in feeding habits and behaviour between the study groups, the most likely candidate for a master variable regulating species turnover among ectothermic invertebrates in the montane forest zone is temperature. Indeed, correlations between scores of samples in ordination space and temperature were all highly significant.

Over the past ten years, many efforts have been devoted to the establishment of 'biodiversity indicators' (e.g. Schulze et al. 2004). The main idea behind this search is that wherever complete inventories can almost never be achieved (as with rich tropical arthropod faunas), or where results are required within short periods of time (e.g. urgent conservation decisions), it would be ideal to restrict monitoring and assessment effort to a few taxa that can easily be investigated. Such indicators should be easy to sample, they should represent the same proportion of the fauna at all study sites (Pearson 1994; Beccaloni and Gaston 1995), identification should be easy, and conclusions drawn from such indicators should be transferable to other groups of organisms.

Among the moths investigated here, Arctiidae (especially Phaeopterini) appear to be good candidates at first sight. They can easily be sampled by attracting them to light, and species identification is possible to an unusually high degree (as compared to other tropical invertebrates). Yet, at a closer look the suitability of arctiids as biodiversity indicators becomes questionable. Their diversity patterns are poorly correlated with those seen in other moths. Also, within the Arctiidae the discordant diversity patterns at lower taxonomic scales and variable taxon ratios further undermine their versatility. These same arguments apply to every other moth group we have studied here or previously (Geometridae: Brehm and Fiedler 2003). More generally, correlations among diversities of various organisms were sometimes found (Schulze et al. 2004), but were also absent or erratic in many other studies (Lawton et al. 1998; see also Simberloff 1998). Our study along an altitudinal gradient is particularly intriguing for the problem of biodiversity indication, since a common environmental 'master variable' (viz. temperature) was supposed to concomitantly reduce diversity in ectothermic herbivorous moths in much the same way. But, while this influence does exist with regard to species turnover, it does not uniformly exist with regard to local species diversity.

11.3.4 Conclusions and Perspectives

Our study of moths along an altitudinal gradient in the Ecuadorian Andes revealed remarkable idiosyncrasies in patterns of alpha diversity across various moth groups and taxonomic scales. These render extrapolations from one exemplar group to others, or upscaling to the entire guild of herbivorous insects, impossible. In contrast, species turnover was extremely concordant across groups with very different life-history characters, suggesting that temperature – and not the availability of plant resources – plays the leading role in governing community change. It would have been desirable to extend sampling to lower as well as higher elevations to capture

altitudinal patterns more completely (Rahbek 2005). At present, therefore, we cannot ascertain whether moth richness would become even higher at lower elevations, or whether some groups at least have true mid-elevation peaks (Brehm et al. 2007).

We still know little about the functional role the exceptionally high diversity of moths plays in Andean mountain forests. The elevational decline of Arctiidae and Pyraloidea diversity is mirrored by a concomitant decrease in abundances in these same taxa (Pearson correlations of mean log-transformed catches per night, after controlling for effects of canopy closure as a proxy for vegetation density; Arctiidae: $rP = -0.591$, $P = 0.006$; Pyraloidea: $rP = -0.742$, $P = 0.0002$). Thus these two moth groups become, as a whole, increasingly less important as herbivores or as prey organisms for insectivores or parasitoids at higher elevations. Yet individual species or subordinated taxa may still be significant in the food webs at high altitudes, such as the lichen moths or Scopariinae pyraloids that occur in substantial numbers above 2400 m a.s.l. Moreover, in the especially diverse family Geometridae, the decline in moth abundance was far less pronounced and not significant ($rP = -0.332$, $P = 0.15$). Overall, moths form an abundant and diverse component of food-webs throughout the mountain forest belt, even though their precise functional role awaits to be quantified.

Hence, what is most urgently desired is a better understanding of the functional interrelationships between moths, their host plants and natural enemies to allow for more precise interpretation of diversity patterns. Large-scale rearing programs similar to those initiated by Dyer et al. (2007) or Janzen and Hallwachs (2007) are a necessary next step. Since Andean moth communities are among the richest that have been documented globally thus far, but are under severe threat through continuous deforestation (Doumenge et al. 1995; see Chapter 4), the time-window for improving our understanding of these organisms may close soon.

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