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Seasonality in the altitude–diversity pattern of Alpine moths

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Abstract

Altitudinal gradients are frequently used to study environmental effects on species diversity. Recent quantitative studies on Lepidoptera focussed on tropical mountain systems and often reported unimodal diversity peaks at "mid-elevations";, a pattern also often found in other taxa. Here we used methodologically comparable, nocturnal Macrolepidoptera samples from the Swiss Alps to analyze environmental correlates of diversity. Using seasonal data (monthly samples from April to November at altitudes between 600 and 2400 m a.s.l.) allowed to decouple altitude and some climate variables for analyses. We found that the altitude–diversity pattern changes with season. In spring and autumn, diversity decreased with increasing altitude, while we found a unimodal peak of diversity at mid-elevations during summer. This excluded all hypothetical causes of diversity variation that do not allow for seasonality. Temperature was an important correlate of diversity, whereas precipitation was not. These results were separately corroborated for the two most common families (Noctuidae and Geometridae). However, diversity patterns of the two families were not particularly close, and unexplained variance of climatic explanations was substantial in all cases. The patterns of faunal overlap did not explain the unimodal diversity pattern, and we claim that we lack a generally valid explanation for this common phenomenon.

Zusammenfassung

Höhengradienten werden gerne verwendet, um Zusammenhänge zwischen Umwelt und Biodiversität zu untersuchen. Jüngere, quantitative Arbeiten an Lepidopteren konzentrierten sich auf tropische Bergregionen, wo oft Diversitätsmaxima in mittleren Höhen gefunden wurden. Wir verwendeten methodisch vergleichbare Aufsammlungen nachtaktiver Makrolepidopteren aus den Berner Alpen (Schweiz), um Umweltkorrelate mit der Diversität zu untersuchen. Die Verwendung von saisonalen Daten (monatliche Aufsammlungen von April bis November, von ca. 600–2400 m ü. NN) erlaubte uns, Höhe und einige Klimavariablen in unseren Analysen voneinander zu entkoppeln. Wir beobachteten, dass sich das Diversitätsmuster entlang des Höhengradienten mit der Jahreszeit verändert–von abnehmender Diversität im Frühjahr zu einem unimodalen Muster im Sommer, und zurück zu abnehmender Diversität im Herbst. Dies alleine schliesst diejenigen Hypothesen zur Kausalität dieser Verteilung aus, die keinen Raum für Saisonalität lassen. Wir fanden, dass Temperatur, nicht jedoch Niederschlag, mit Diversität korrelierten. Diese Ergebnisse bestätigten wir auch in separaten Untersuchungen für die beiden arten- und individuenreichsten Familien, Geometridae (Spanner) und Noctuidae (Eulenfalter). Die Diversitätsmuster der beiden Gruppen sind jedoch nicht eng

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aneinander gekoppelt, und die von Klimakorrelaten unerklärte Varianz blieb in allen Fällen relativ gross. Wir fanden keine Hinweise auf Faunenüberlappung als Erklärung für das unimodale Diversitätsmuster, und wir stellen fest, dass eine hinreichende, allgemeingültige Erklärung für dieses häufig gefundene Phänomen weiterhin fehlt.

Introduction

Altitudinal gradients have frequently been used to study links between diversity and the environment (e.g. Grytnes & Vetaas 2002; Rahbek 2005; Grytnes & Beaman 2006; Kluge, Kessler, & Dunn 2006; McCain 2007a, 2007b; Grytnes, Heegaard, & Romdal 2008). They are viewed by many as convenient model systems to investigate the validity of general ideas on how environmental factors, such as climate (e.g. water–energy dynamics, Hawkins et al. 2003; Field et al. 2008; temperature, e.g. Stegen, Enquist, & Ferriere 2009), affect biodiversity. McCain (2007a), for example, explained mid-altitudinal peaks in bat species richness with water and energy limitation. Other mechanisms have been put forward to explain altitudinal diversity patterns, such as an altitudinal species-area effect (Rahbek 2005; Beck & Kitching 2009), the controversial mid-domain effect (Dunn, McCain, & Sanders 2007; McClain, Ethan, & Hurlbert 2007), an overlap of lowland and highland faunas (e.g. Herzog, Kessler, & Bach 2005), or effects of evolutionary history and speciation (Smith, de Oca, Reeder, & Wiens 2007, but see Algar, Kerr, & Currie 2009). Frequently observed patterns of diversity on altitude gradients are a decline with altitude or a unimodal relationship with a peak at 'mid-altitudes' (Rahbek 2005; Nogués-Bravo, Araújo, Romdal, & Rahbek 2008).

However, many environmental conditions are inevitably correlated with altitude – e.g. temperature (due to the adiabatic link of temperature and air pressure) or area size. This weakens many previous studies because correlations with such environmental variables may offer little more than a description of the altitudinal pattern (note the parallelism with investigations of latitudinal patterns, e.g. with regard to temperature).

Vascular plants, birds and small mammals are the best-studied groups in the context of altitude–diversity relationships, while among insects, Lepidoptera have often been used to address this topic. Many recent studies on altitude–diversity patterns have been carried out in tropical systems, including studies on moths (e.g. Axmacher et al. 2004; Brehm, Colwell, & Kluge 2007; Fiedler, Brehm, Hilt, Süßenbach, & Häuser 2008; Beck & Chey 2008; Beck & Kitching 2009). Comparable data regarding methods and study aim are conspicuously lacking for temperate moths despite the fact that much better data on faunistics, taxonomy and general biology are available. Consequently, we have only a vague knowledge on altitudinal diversity patterns formed by temperate taxa, and no information on seasonal variation of these patterns (Summerville & Crist 2003).

Here we addressed several of these issues. We documented the altitudinal diversity pattern for nocturnal Macrolepidoptera in the European Alps, including its seasonality, while using methods comparable to recent studies from the tropics. Furthermore, we used our data to address some hypothetical explanations regarding climatic determinants of diversity. We could decouple correlated effects, in particular between altitude and temperature, by utilizing both the spatial and the temporal variability of temperature in our data. We also carried out separate analyses for the two largest families (Geometridae and Noctuidae), which differ considerably in ecological traits.

Methods

Study site and field methods

The study was carried out in the "Bernese Alps", a part of the northern Swiss Alps (approximate latitude/longitude: N46°35′, E7°44′), where an altitudinal range from ca. 500 to >4300 m can be found. For the purpose of this study, Lake Thun at ca. 560 m a.s.l. was considered "lowland". Mountains directly surrounding the sampling region reach up >3600 m. Table 1 gives details on the 14 sampling sites along the altitudinal gradient. Wherever possible, sampling sites were positioned in near-natural habitat (e.g. forested sites at lower elevations), but the long-time impact of humans on the northern Alps (Stöcklin et al. 2007) makes it impossible to find entirely pristine habitats. However, the upper part of the sampling region, which is in parts utilized for sheep grazing, has a protected status as a game reserve. None of the sampling sites have been directly impacted by forestry or grazing during 2007 or 2008. The (horizontal) extent of the sampled gradient was about 19 km; the altitudinal range was from 600 m to 2400 m a.s.l. (see Table 1 for details). In late June we also sampled at two sites higher than that (2850 m and 3000 m; one night each, dusk to midnight) without finding any moths.

Moths were attracted to blacklight (output equivalent to 15 W) and lead through a funnel into a bucket outlined by cotton fabric and equipped with an egg carton (battery-driven Heath trap; http://www.bioform.de, article no. 1001-02). Cloth and egg cartons were treated with a contact poison (a pyrethroid), which killed most specimens and immobilized the rest. Traps were operated from dusk till dawn. They were checked every day of operation, moths being collected and batteries renewed. Automated traps are known to be

Table 1. Details on the 14 regular sampling sites. An extended table, containing locality data including coordinates, is available in). Altitudes [in m] stem from repeated GPS measurements. Numbers of specimens (N) and taxa (S), pooled over all sampling periods, are given.

Site	Altitude	Habitat	N	S
1	621	Mixed deciduous forest, dominated by beech (*Fagus*)	375	95
2	768	Mixed forest of deciduous trees and fir (*Abies*)	793	102
3	799	Mixed forest of deciduous trees and fir (*Abies*)	317	79
4	872	Steep slope with bushes (*Alnus*, *Salix*) and ferns	1000	156
5	950	Mixed forest with fir (*Abies*) and spruce (*Picea*)	759	157
6	1173	Alder thicket (*Alnus*) on former landslide	428	71
7	1213	Mixed forest with spruce (*Picea*), pasture nearby	296	79
8	1282	Spruce-dominated forest, pasture nearby	163	60
9	1448	Spruce forest with thick undergrowth (*Vaccinium*)	233	75
10	1657	Steep slope with conifers (*Picea*, *Larix*) and grasses	674	105
11	1811	Alpine pasture with *Vaccinium*, *Rhododendron*	296	57
12	1995	Alpine meadow	340	31
13	2218	Alpine meadow	126	25
14	2397	Alpine meadow between gravel and rockface	82	19

less efficient than hand-collecting at light sources (Brehm & Axmacher 2004) and specimens are left in poorer condition, but carried the advantage that we could collect at many sites simultaneously during the same nights, thereby reducing variability due to temporal factors.

In 2008 we carried out eight sessions of moth sampling (four nights each) at or close to new moon. Exact dates of sampling were April 3–6 (henceforth called APRIL), May 2–5 (MAY), June 1–4 (JUNE), June 30–July 1 (JULY), July 31–August 3 (AUGUST), August 29–September 1 (SEPTEMBER), September 26–29 (OCTOBER), and October 31–November 3 (NOVEMBER).

Snow and nightly temperatures below zero were encountered in APRIL and NOVEMBER in most sites; hence our samples cover the entire vegetation period in the region. Some of the high-altitude sites could not be accessed due to deep snow in APRIL, MAY and NOVEMBER, accounting for reduced sample sizes. Data at each site were pooled for each sampling period (4 nights) for analyses. Details on the data can be found in Appendix A (Table S1).

At each sampling site we positioned a temperature logger to take hourly temperature data throughout the whole study period. In forested habitats temperature loggers were placed in undergrowth trees at 1.5 m height, whereas, above the tree line, we positioned them under stones to avoid measuring effects of direct solar radiation.

Species identification and data analyses

Specimens were pinned and mounted according to standard procedures and pre-sorted (Fajčik & Slamka 1998, 2003). They were then identified to the species level, mostly based on external wing-patterns. Several hundred specimens were dissected and the genitalia were examined to confirm identification (especially for worn-off specimens). Eleven difficult taxon complexes were treated as tentative morpho-

types (usually sibling species; this applies to ca. 3% of taxa, 16% of individuals). Throughout this article, we treat them as individual species. About 7% of all collected specimens were in unidentifiable condition and were excluded from all analyses. The collection is currently stored at the University of Basel for further research, whereas it will eventually be deposited at a Swiss museum.

As a metric of species diversity we applied the concept of "effective number of species" (see Jost 2006 for rationale), the exponent of Shannon's entropy H (i.e., e^H). However, H is affected by incomplete sampling of local species communities. Chao and Shen (2003) have published a bias-correction to correct for undersampling artefacts (H_{bc}), and Beck and Schwanghart (2010) have recommended the effective number of species based on H_{bc} to measure diversity. We used BiodivToolbox (software by Beck & Schwanghart 2010) to compute $e^{H_{bc}}$. This metric is undefined where no specimens have been found (despite equal effort at sites) or where the number of specimens is equal to the number of species. We set diversity to zero in the former case, while we used e^H in the latter case, but we repeated all analyses omitting these data without finding qualitative variation in results. In our data, $e^{H_{bc}}$ is correlated to Fisher's α ($r^2 = 0.81$) as well as other metrics of diversity, such as rarefied species richness (see Table S2, Appendix A), but it is only moderately related to observed species richness ($r^2 = 0.39$), which is certainly biased by undersampling.

We present analyses of "ecologically relevant climate" defined as temperature and precipitation means for the 4 weeks between a current and the previous sampling session (i.e., we presume that conditions during these periods may strongly affect growth and development of the specimens caught). Temperature data were means of hourly measures at sites. For APRIL, we could only use mean temperatures during the 5 days field work period, but we recalculated relevant analyses (see Table S3, Appendix A) to assure that conclusions were not dependent on these slightly differently

defined data. We did not have direct measurements of precipitation, so we used 30-year monthly averages (again, the month prior to sampling) from www.worldclim.org. We also had precipitation data from a weather forecast model for our study period (3 km resolution; M. Müller, pers. comm.; see www.meteoblue.ch). However, r^2-values were equal or worse for analyses using the latter data (Table S3, Appendix A). We repeated main analyses for mean temperature and precipitation of the 8, respectively 12, weeks prior to sampling (Table S3, Appendix A) as complete development times of many species are actually longer than 4 weeks. We could not, however, control for the fact that some early spring species had gone through larval development in summer or autumn of the year before sampling (overwintering as pupa or adult) as we did not collect temperature data in 2007.

Following advice in Beale, Lennon, Yearsley, Brewer, and Elston (2010; see also Bini et al. 2009), we addressed the problem of spatial non-independence of data by applying a multivariate model that assumes spatial structure in its error term (generalized least squares, GLS; software SAM 3.1, http://www.ecoevol.ufg.br/sam/; details in Table S3, Appendix A). We had to slightly manipulate locality data to avoid temporal replicates being exactly on the same spot (leading to locality changes in the range of some meters). Using the same software, we also used spatial correlation (Dutilleul's adjustment of degrees of freedom) to test some univariate correlations. In some instances we investigated patterns without explicitly considering spatial structure. Here we compared models based on the small-sample Akaike information criterion (AICc), which is less affected by spatial non-independence than significance tests (Diniz-Filho, Rangel, & Bini 2008).

Potential non-independence of temporal replicates is a related point of concern for some of our analyses (see "Discussion"). As a tentative estimate of species turnover in time, we compared differences in community composition between months and sites using rank-based permutation tests of a similarity matrix (nested ANOSIM; sites within months; Bray-Curtis similarity, square root transformation of abundances; software Primer-E 5).

We carried out analyses for pooled data of all 10 recorded families of Macrolepidoptera, and separately for the subsets of Geometridae and Noctuidae (excluding Arctiidae).

Results

The altitude–diversity pattern

A total of 5882 individuals were caught in 396 trap-nights, representing 318 species from 10 families. Geometridae (1992 specimens, 103 species) and Noctuidae (2863 specimens, 163 species) were the most important families (Table S1, Appendix A). Trap yield per site varied, for four night periods, from 0 to 358 specimens representing 50 species (median: 29 specimens, 12 species). Total indi-
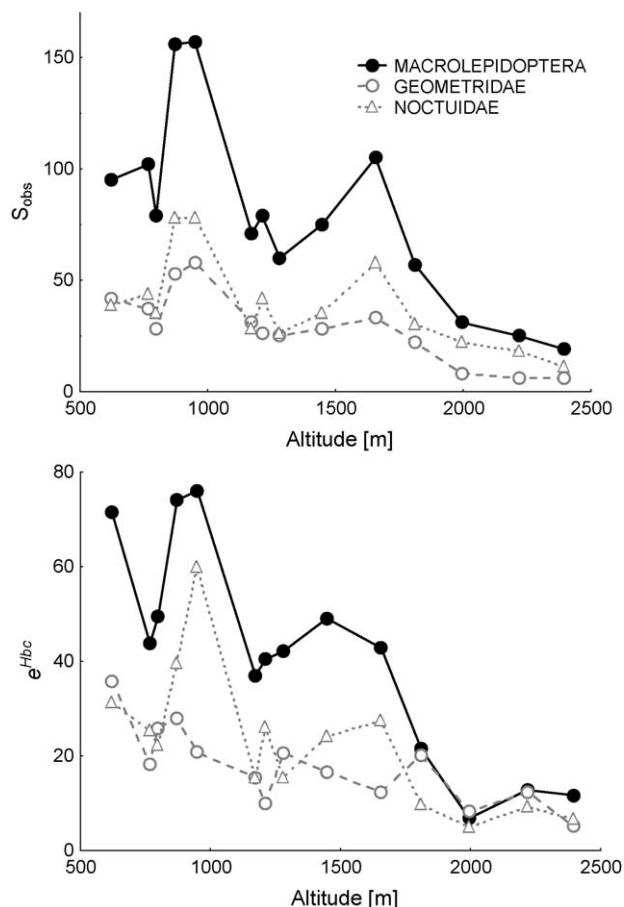

Fig. 1. Altitudinal pattern of diversity from pooled data (across 8 monthly samples). Upper graph: observed species richness (S_{obs}). Lower graph: bias-corrected diversity (effective number of species, $e^{H_{bc}}$). Note that the bimodal patterns never actually occurred at any one sampling period (see Fig. 2).

vidual numbers (not shown), and (less clearly) observed species richness and diversity (Fig. 1), had a bimodal shape if pooled over the entire study, with peaks at 700–900 m and 1400–1700 m. However, these pooled diversity patterns never actually occurred at any one time.

Fig. 2 shows patterns of species diversity in different months. Despite some scatter in data, there was a decreasing trend of diversity with altitude in spring, while during summer months (June–August) a unimodal peak of diversity shifted increasingly higher (up to ca. 1800 m in August). A decreasing pattern is found again in autumn samples. We substantiated this description by comparing polynomial models of the altitude–diversity relationship by their AICc weights. This analysis indicated higher importance of a quadratic term (i.e., curved relationship), compared to a linear term, in JUNE, JULY and AUGUST, but not in other months (data not shown). Rank correlations of altitude and diversity were strong in spring and autumn (Spearman's $R < -0.6$, $p < 0.05$ except APRIL), but much weaker during summer ($R > -0.5$, n.s.). Diversity was highest in June and July.
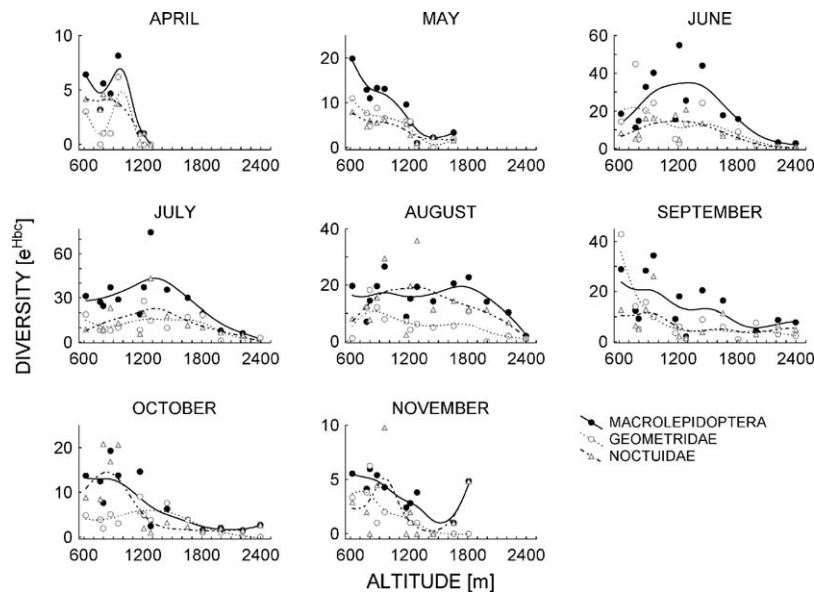
Fig. 2. Altitude–diversity relationship for eight sampling periods, for all Macrolepidoptera and the two most abundant and speciose families, Geometridae and Noctuidae. Diversity of moths was measured as (bias-corrected) effective number of species (see "Methods"). Distance-weighted least square regressions are drawn to illustrate main patterns more clearly. Note the differently scaled y-axes, reflecting huge differences in overall diversity across seasons.

Patterns for Noctuidae often reflected diversity for all moths, whereas Geometridae appeared to be more diverse at lower elevations in most months. Geometridae and Noctuidae diversity were only weakly correlated ($r^2 = 0.108$).

Climatic predictors of diversity: temperature, precipitation, or both?

Multivariate models were of moderate predictive quality, explaining only ca. one quarter to one third of diversity variability (Table 2). Only temperature was significant as an environmental predictor throughout all models (see also extended model comparisons in Table S3, Appendix A), whereas we could not observe any relevant effects of precipitation. These conclusions also apply to the separate models for Geometridae and Noctuidae. We analyzed patters separately (1) for summer months only, for which unimodal peaks of diversity were observed (Fig. 2), and (2) for the combined data from the spring and autumn samples, for which declining altitude–diversity patterns were found. Results for spring and autumn samples were qualitatively similar as for data reported above (Table S3, Appendix A), but model fit was better ($r^2 > 0.5$). Models for summer data (including those for Geometridae and Noctuidae, not shown) were non-significant and of poor quality ($r^2 < 0.05$).

We examined the spatial distribution of residuals from models containing temperature and precipitation, but we could not identify any obvious patterns that would generate further hypotheses (e.g. sites consistently deviating, forested vs. open sites, etc.). We conclude that temperature is related to diversity, while we failed to find effects of precipitation. However, Fig. 3 shows that this relationships leaves a lot

of variability unexplained. We investigated likely sources of deviation by highlighting summer month lowland vs. mid-altitude samples in the figure. Many lowland samples had lower diversity than expected by their temperature while some mid-altitude samples had very high residual diversity, but this pattern did not apply to all summer sites. Residuals from temperature–diversity regressions still indicated a uni-
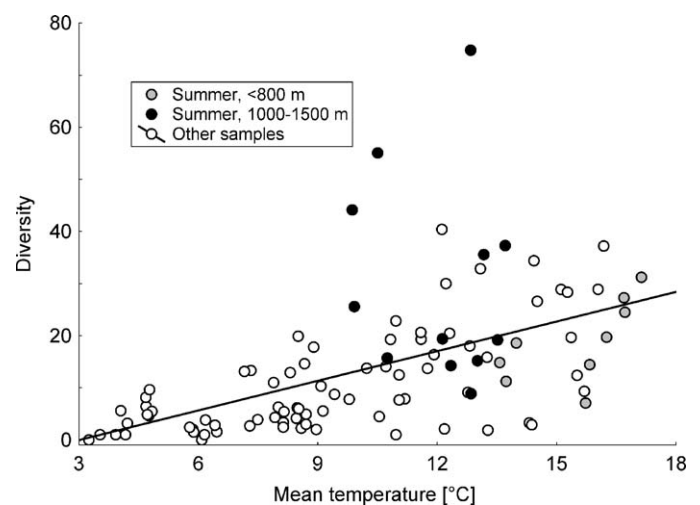

Fig. 3. Temperature 4 weeks prior to sampling and moth diversity (effective number of species, as $e^{H_{bc}}$) for 99 site-month combinations. Ordinary least squares (OLS) were used to fit the regression (explaining ca. 28% of diversity variability), whereas an alternative model assuming a Poisson-distributed error (not shown) did not lead to a substantially different fit. Potentially interesting site-month combinations were highlighted with different symbols ("summer" = June, July, August).

Table 2. Results from multivariate generalized least squares (GLS) models, testing for relationships of diversity with temperature [in °C] and precipitation [in mm/month]. For all models $n = 99$ site-sampling period combinations (4 nights of sampling each) were used. See) for expanded results of other data and models, as well as further detail.

		Predictors:	GLS coeff.	t	p
All Macrolepidoptera					
Only predictors	$r^2 = 0.295$, AIC $= 764.4$	Temperature	1.872	6.290	<0.001
Predictors + space	$r^2 = 0.331$, AIC $= 759.2$	Precipitation	0.036	1.019	0.311
Model significance	$p < 0.001$				
Geometridae					
Only predictors	$r^2 = 0.240$, AIC $= 677.6$	Temperature	1.007	5.491	<0.001
Predictors + space	$r^2 = 0.363$, AIC $= 660.2$	Precipitation	0.003	0.141	0.888
Model significance	$p < 0.001$				
Noctuidae					
Only predictors	$r^2 = 0.224$, AIC $= 677.3$	Temperature	1.016	5.274	<0.001
Predictors + space	$r^2 = 0.224$, AIC $= 677.2$	Precipitation	−0.040	−0.447	0.656
Model significance	$p < 0.001$				

modal relationship with altitude in July, and more weakly in June and August (data not shown). For Geometridae and Noctuidae, when analyzed separately (Fig. S1, Appendix A), we found similar patterns, and again not all highlighted summer samples showed consistent patterns of deviation.

The total number of individuals correlated weakly but significantly with diversity ($r^2 = 0.068$; spatial correlation: $F_{adj} = 7.4$, $df_{adj} = 102.3$, $p < 0.01$) and with temperature ($r^2 = 0.12$, $F_{adj} = 12.7$, $df_{adj} = 90.1$, $p < 0.001$). However, there was no clear altitudinal pattern in the number of individuals (data not shown). We found no evidence for an overlap of faunas creating the unimodel pattern of diversity during summer months (investigated by visual inspection of data, Fig. 4).

Differences in species composition between all pairs of sampling months, controlled for site identity, were significantly different from randomized similarities (nested ANOSIM, all $p < 0.001$; different months have different communities) except for APRIL–MAY ($p = 0.083$). However, measures of determination for the ANOSIM (Spearman R of pairwise comparisons) are weaker for neighbouring months ($R = 0.13–0.61$) than for other pairs (all $R > 0.5$).

Discussion

Our data provided three main results that shall be discussed in turn.

(1) The shape – rather than just the magnitude – of the altitude–diversity relationship changed seasonally. Thus, all suggested mechanisms that cannot accommodate a seasonal component – e.g. the altitudinal distribution of area size, or the mid-domain effect – can be excluded as primary drivers of diversity, without any further quantitative investigation. This conclusion was corroborated from analyses of observed species richness (data not shown). Also, our data suggested a high relevance of the seasonal timing of the sampling, at least in temperate mountains. Very different conclusions would

have been drawn if we had not collected through all seasons. It remains unclear whether such qualitative changes in pattern also occur on tropical mountains, since hardly any study regularly re-sampled altitudinal gradients there (see Sanches-Cordero 2001 for seasonal mammal data from Mexico).

(2) There is evidence that temperature is correlated to diversity even when decoupled from altitude – i.e., the previously reported effect of temperature is not an artefact of variable collinearity. There was, on the other hand, no strong indication that precipitation (i.e., water availability) played an additional role in the relatively cool, wet ecosystem studied here. Our results are consistent with Hawkins, Field, Cornell, Currie, and Guégan (2003), who claimed sole dependency of species richness on energy north of some taxon-specific threshold.

Our data represent a single altitudinal gradient, sampled during 1 year and with regard to one taxonomic group only. Only a larger number of future studies of similar design could confirm the general applicability of the patterns reported. Our data allowed only very limited further inference on the mechanism causal to the temperature–diversity relationship. A causal link through productivity, which should lead to more individuals, is a common interpretation of water–energy relationships with diversity. However, productivity–diversity relationships are controversial and the empirical evidence is weak (Currie et al. 2004), whereas direct tests of individuals–diversity relationships have only rarely been attempted. Under the simplifying assumption that the numbers of individuals at light (i.e., density) is a proxy for abundance in a region, we found only very weak (yet statistically significant) relationships of individuals with diversity or temperature. Beck, Brehm, and Fiedler (in press) found stronger individuals–diversity relationships in Neotropical moth samples.

Neither temperature, nor temperature and precipitation, however, allow to explain the diversity pattern as good as a simple, descriptive model of altitude and "summer" (ranked
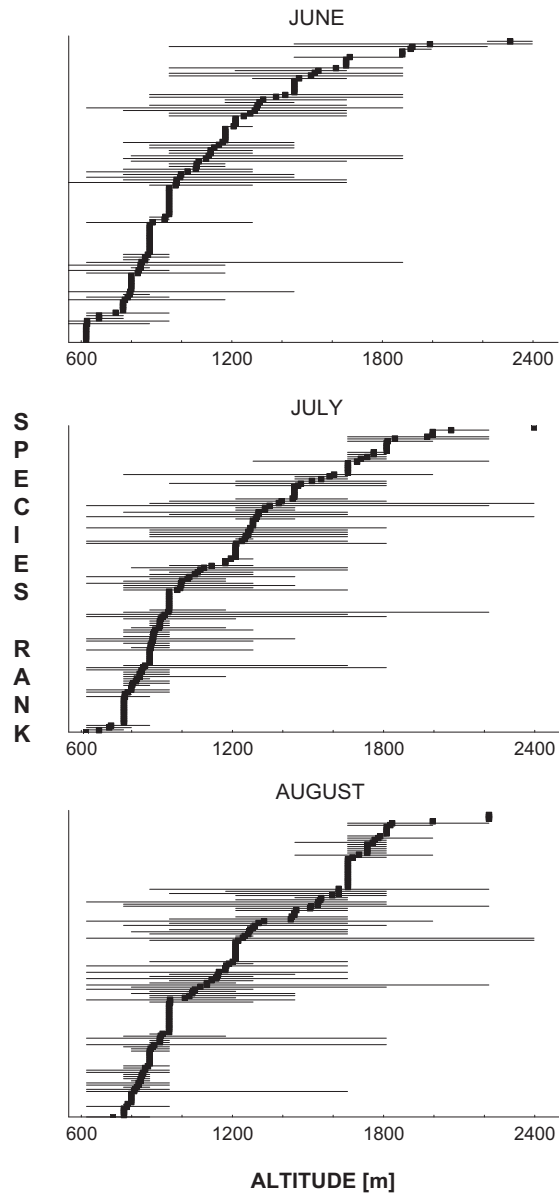
Fig. 4. Altitudinal centres (mean, weighted by abundance), minima and maxima for moth species (y-axes, sorted by altitudinal centre) collected during summer months. If diversity peaks (Fig. 2) would be due to an overlap of distinct highland and lowland faunas, there should be only few species with their altitudinal centre at mid-elevations.

as number of months from JULY), accounting for ca. 40% of data variability. This is reminiscent of analyses of global analyses of species richness, which is often best explained by latitude and altitude, two "non-functional" variables.

Plant diversity patterns have sometimes been portrayed as a determinant of herbivore insect diversity (e.g. Summerville & Crist 2003; Novotny et al. 2006). We found broad congruence between plant and moth diversity (4 m^2 samples per site), but plant data are not directly comparable to moth data (only

pooled data across the seasons were available; not shown). Furthermore, this type of explanation would only shift the initial questions one trophic level down.

Some of our conclusions depend on the presumption that monthly replicate samples constitute independent data. Population dynamics of some species may theoretically lead to violations of this assumption (i.e., a species may be common in a month as a consequence of being common in the previous month), although ANOSIM permutation tests (see "Results") corroborated that local communities were changing significantly from month to month. We assume that flight and diapause periods evolved to maximise fitness, given the available resources and conditions. In a highly seasonal landscape, we would therefore expect that observed diversity is reflecting current conditions, rather than lags from previous months. Furthermore, temporal non-independence of diversity data would show up as spatial autocorrelation over very short lag distances (i.e., among identical sites), whereas the opposite was observed (large "nugget effects", not shown). Applying a spatially explicit GLS model for hypothesis testing controlled for such spatial effects (Beale et al. 2010).

(3) The temperature–diversity effect is relatively weak (Fig. 3). It does not sufficiently explain the most interesting part of the altitudinal pattern, namely the low diversity of the lowlands compared to mid-altitudes during the warmer parts of the year (cf. Beck & Chey 2008). Lack of water, the mid-domain effect, overlap of faunas, and effects of phylogenetic history (cf. Smith et al. 2007) are, to our knowledge, the main hypotheses that would predict such a pattern. We have rejected the former three as single drivers of diversity (see above), therefore we must tentatively conclude that either phylogenetic history (which we have not tested), or an unknown mechanism, or complex interactions of several mechanisms (e.g. Grytnes & Vetaas 2002), must be causal to this commonly observed phenomenon.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae. 2010.08.009.

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