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Is the ecological belt zonation of the Swiss Alps relevant for moth diversity and turnover?

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ABSTRACT

Mountain ecosystems are traditionally envisioned as elevational belts of homogenous vegetation, separated by intervening ecotones. Recent research has cast doubt on such predictable layering at least in animal communities. We test the link of two *a priori* defined ecological belt zonations to noctuid moth distributions in the Swiss Alps. Predictions, in particular, were a coincidence of proposed ecotones with increased range endpoint frequencies and with increased species turnover or species richness between equidistant elevational bands. Using >320,000 distributional records for >500 noctuid species, we found no support for these three predictions despite several contrasting analytical approaches. Concurrent with recently published vertebrate data, we conclude that simple ecological belt zonations are unrelated to the moth communities found along mountain slopes. Rather, species are distributed idiosyncratically following their specific niche requirements. Additional rigorous evidence, particularly comparing insect clades spanning a spectrum of host-plant relationships, may be required to support the relevance of the ecological belt concept in structuring mountain ecosystems beyond tree and plant communities.

1. Introduction

Mountains are often depicted as a vertically ordered array of different ecological zones (vegetation belts; e.g., hill, submontane and montane forests, subalpine and alpine meadows, snow & rock zone). These differ in environmental characteristics and are often defined by structurally dominant plants, such as common tree species. This view of mountains as stacked elevational zones was shaped by classical biogeographers (von Humboldt, 1849; Merriam and Stejneger, 1890; see also Ebach, 2015; Fattorini, 2016) and still dominates textbooks today (Cox and Moore, 2010; Lomolino et al., 2010). While it may still be a valuable concept didactically, its scientific merit rests on the assumption that such a zonation conveys more information than the presence of the species used to define and recognize a particular zone. It implicitly assumes that many other species are equally bound to these zones, either because they have the same environmental preferences or because species are associated by biotic interaction. The view of (plant) species communities as "packets" of co-occurring species was first shaped by Clements (1916), and it is still popular in applied European vegetation science in particular (e.g., Braun-Blanquet, 1932; Ellenberg, 2009; see also Whittaker, 1960, 1967). Assuming that animal communities are bound to these zones in the same manner is also prevalent in current literature (e.g., Moritz et al., 2008; Tingley and Beissinger, 2013).

A converse view to this concept of zonal organisation is to focus on ecotones located between borders of adjacent zonal communities. Ecotones are predicted to be characterized by high species turnover and high species richness due to the co-occurrence of species from both abutting communities (Lomolino, 2001). Ecotones may feature unusually steep gradients of abiotic environmental change – either as a cause to biotic species turnover (e.g., humidity gradients due to cloud levels may restrict plant growth in arid regions), or as a consequence of biotic change (e.g., microclimatic conditions due to the presence of trees; Körner, 2007).

A series of zonal communities with clearly defined ecotones between them leads to a prediction of several interrelated phenomena (Fig. 1): (1) There should be a higher concentration of species' range endpoints in ecotones because species would typically occur throughout a zone but not in the next. (2) As a

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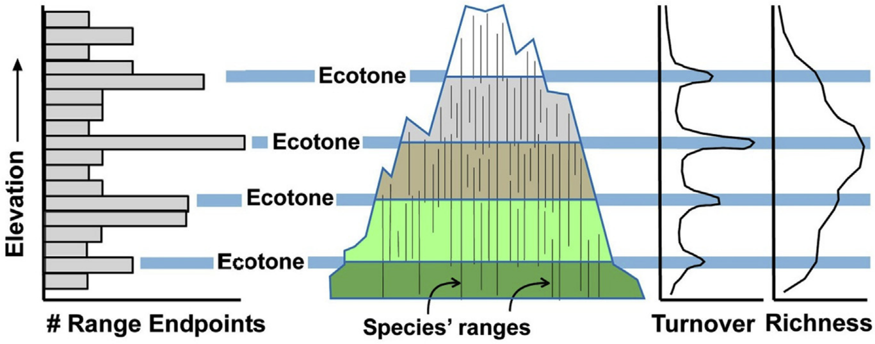

Fig. 1. An idealized sketch of the hypothesized assemblage structure along a mountain gradient *[centre]* with five *a priori* defined zones and four ecotones between them. Species' elevational ranges are shown as vertical grey lines. We derive and test prediction on three features from such an assemblage structure: *[left]* The frequency of range endpoints should be highest at ecotones, because few (if any) species will occur in different zones (hence overlap ecotones). *[right]* Species turnover of adjacent 100 m-bands should follow the range endpoint pattern, hence be highest at ecotones (because many endpoints mean high turnover). Similarly, the full assemblage dissimilarity matrix (all 100 m-bands with each other, not show in the graph) should contain a signal of ecotone locations. Species richness peaks should occur at ecotone locations, and the richness pattern should be related to band-wise assemblage turnover (because ranges of species from different zonal communities should overlap at ecotones; Lomolino, 2001). Other assemblage structures would be inconsistent with the elevational zonation concept as presented in textbooks.

consequence, there should be heightened species turnover at ecotone elevations compared to regions within zonal communities. (3) The overall structure of community dissimilarities (beta diversity) should reflect the zonality of the gradient (i.e., low dissimilarity of sites within the same zones, higher dissimilarity of sites from different zones), even after accounting for gradual changes in environmental conditions. (4) Furthermore, high range overlap (i.e., high turnover) should be correlated to species richness (Lomolino, 2001; see also Brown, 2001; Heaney, 2001; Herzog et al., 2005). (5) In consequence, richness peaks should be associated with ecotone elevations. Unlike the extensively studied species richness patterns along elevation gradients (e.g., McCain and Grytnes, 2010), there is relatively little general, consolidated empirical knowledge about the patterns of range overlap, beta diversity, or turnover, along such gradients (McCain and Beck, 2016).

McCain and Beck (2016) have recently tested some key predictions of the “zonal communities” concept (Lomolino, 2001): the existence of regular, predictable peaks of species turnover, implicitly located at the ecotones between ecological zones; and the correlation of turnover and species richness patterns. Using a large dataset of vertebrates along many elevation gradients across the globe, they neither found repetitive patterns of assemblage turnover, nor was there a link between turnover and species richness patterns. These results question the relevance of traditional ecological zonations of mountains for understanding the structure of animal communities along elevation gradients, favouring a view where each species follows its own environmental requirements, and co-occurrence patterns are rather individualistic (Gleason, 1926; MacArthur and Wilson, 1963). However, McCain & Beck (2016) could not explicitly test the hypothesis of a link between *a priori* defined ecotones between mountain zones and peaks in assemblage turnover, because for many geographical regions there are no clear, operational delineations available.

We test the ecotone hypothesis using a diverse and well-sampled insect clade in the Swiss Alps, considering two alternative delineations of mountain zonation (Schröter, 1926; Dufour, 1986). Noctuid moths (Lepidoptera) are strong test organisms of the ecotone hypothesis for multiple reasons. First, noctuids are a very species-rich group with more than 500 species in the study region (Steiner et al., 2014; Wymann et al., 2015; Zahiri et al., 2011), allowing a fine resolution of assemblage patterns. Second, they are abundantly sampled using light traps (a standard method of field collection for nocturnal lepidopterans), hereby reducing effects of undersampling (Beck et al., 2013; Coddington et al., 2009). Third, they are herbivores with intermediate to high degrees of host plant specialization (typically, plant genus-level), and therefore directly linked ecologically to plant community composition. And finally, noctuid ranges are well-known in the Swiss Alps based on a large and well-attended distributional database (*Centre Suisse de Cartographie de la Faune*, http://www.cscf.ch/).

To test the validity of the zonal concept for noctuids, we evaluate the predictions that pre-defined ecotones between mountain zones coincide with a high frequency of range endpoints, with peaks of assemblage turnover and dissimilarity patterns, and/or with patterns or peaks of species richness along the elevational gradient (Fig. 1). Such quantitative tests are needed to rigorously assess whether zonal communities exist as a general, cross-taxon pattern with larger ecological implications (e.g., biotic interaction), or whether they are only valid descriptors of dominant tree or vegetation patterns in particular regions.

2. Methods

2.1. Research region and mountain zonation

Our study region was the Swiss part of the Western Alps. The Swiss Alps are heterogeneous biogeographically as they form the climatic boundary between Central Europe and the Mediterranean, and because of their glaciation and refugial history (Ozenda, 1988). Patterns of species distributions may therefore not be comparable across the entire region. Considering biogeographical regionalizations by Gonseth et al. (2001) and Ozenda (1988), we divided the region into three parts (Marginal Northern Alps, Inner Alps, Marginal Southern Alps; see Appendix A for map) and carried out analyses separately for each region.

Elevational zonations are a contentious topic in the European Alps. Several different proposals exist, but some among them are quantitatively too vague to be operational (Landolt, 1983; Ozenda, 1988; Reisigl and Keller, 1989). Here we employ two different proposals. First, the zonation proposed by Schröter (1926), which is based on vegetation differences, demarcated for the three main regions (Fig. 2). Analyses presented in the main text are based on this proposal. A very similar zonation by Jenny-Lips (1948) was not included separately. Second, the zonation proposal by Dufour (1986) is based on mean annual temperatures, where four zones are defined by the intervening isotherms of 1°, 4° and 8 °C. To

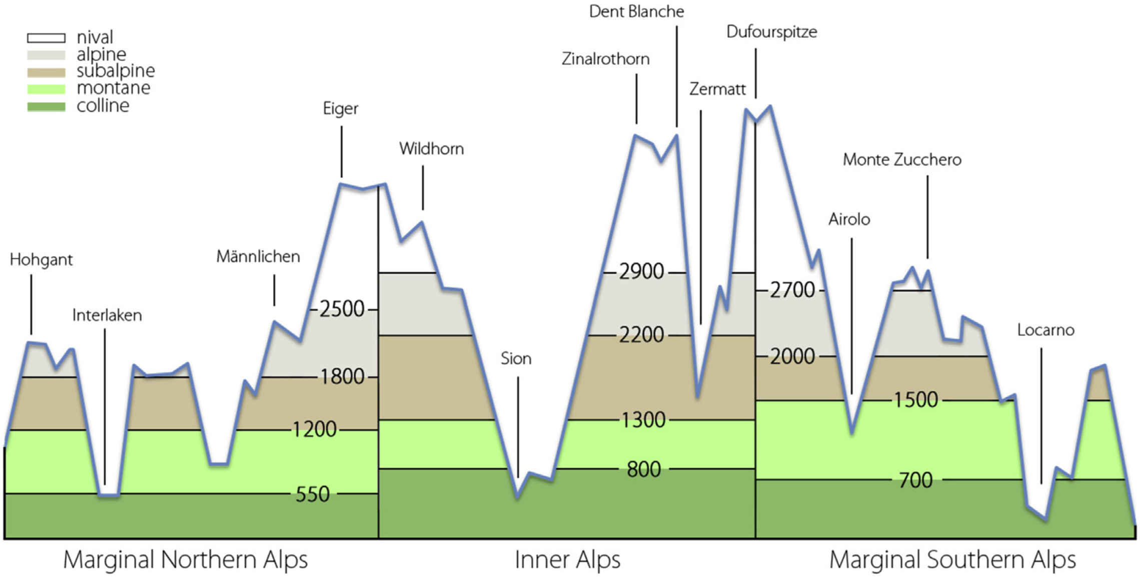

Fig. 2. Idealized North-South cross-section of the Swiss Alps, with sub-regions shifted in relation to each other following the mountain zonation by Schröter (1926; elevations are in meters a.s.l.). Well-known peaks and towns are indicated for orientation. For an alternative delineation see Appendix B.

place these boundaries elevationally, we accessed mean annual temperature data from 102 meteorological stations and calculated averages for the period from 1981 to 2010 (IDAweb, http://www.meteoswiss.admin.ch). We used the lapse rate from linear regressions of elevation and average temperature to model the elevation of three zonal boundaries for each of the three regions. A graphical illustration of, and test results for, this proposal are presented in Appendix B.

2.2. Species distribution data

Noctuid raw distribution data are from *Centre Suisse de Cartographie de la Faune* (CSCF; http://www.cscf.ch/), a national data collection centre for specimen records. The noctuid part of this dataset included 320,935 entries, containing locality coordinates, elevation, and year of collection (1886–2014). The large number of records, long time span, and country-wide extent make it unlikely that these data are strongly biased by single collectors' preferences for particular sites, biotopes or species (see also Fattorini, 2014). The noctuid part of the database has recently been taxonomically and geographically vetted, and edited for the purpose of a monograph (Wymann et al., 2015), which heightens our confidence in their reliability.

For analyses we divided the landscape into 100 m elevational bands. We assessed noctuid sampling completeness and potential biases by plotting individual numbers as well as unique sampling locations per band (Appendix A). We concluded that sampling intensity was very high up to ca. 2600 m but dropped sharply above. As we could not assess whether this drop is due to a lack of effort or due to a genuine reduction of noctuid occurrence, we analyse data only up to the elevational band ending at 2593 m (100 m bands start at Switzerland's lowest elevation, 193 m). This excluded a total of 88 individual records from the data, and it led to the exclusion of one species from one of the three regional datasets. As an additional measure against undersampling artefacts, we interpolated species' elevational ranges, assuming that each species must occur at all elevations between its lowest and highest record within each region (a standard practice in elevational studies; McCain, 2004). Number of records per species varied from 1 to 12,207 (median = 198; data for three regions combined). While some very rare species occurred in this dataset, there were at least 10 records for >90% of species and at least 20 records for >85% of species. Hence, undersampling of species ranges is unlikely to cause bias in the investigated assemblage-wide patterns. Species known only from a single locality were assigned an elevational range of 10 m (i.e., recorded elevation ± 5 m) to facilitate their inclusion in analyses.

2.3. Range endpoints and turnover measurement

We plotted the frequency of range endpoints within 200 m-elevational bands (i.e., combining two adjacent 100 m-bands; McCain and Beck, 2016), expecting frequency peaks in bands including ecotones (we ignored peaks at gradient limits). However, range endpoint frequencies are also affected by richness variation between nested assemblages in bands, so they do not indicate species turnover in a strict sense. Following methods of McCain and Beck (2016; cf. Baselga, 2010), we measured richness-independent turnover within 200 m elevational bands as Simpson's dissimilarity of their component neighbouring 100 m bands (Simpson, 1943; Baselga, 2010; for consistency with McCain and Beck, 2016 we call this 'elevational turnover'). This allows plotting turnover patterns over elevation and comparing them with suggested ecotone locations. We used VBA software written by CMC (available at http://spot.colorado.edu/~mccainc/simulation_programs.htm) for computing elevational turnover. We also computed Simpson dissimilarity matrices of all possible pairwise combinations of bands (using the R package *betapart*).

We evaluated the prediction of a link between ecotones and noctuid moth assemblage structure with a variety of methods.

(1) We judged visually whether the main peaks of range endpoint frequencies or of elevational turnover were occurring at ecotone elevations. We defined a main peak as maximum value within a region, and co-occurrence as occurrence within the same 200 m elevational band.
(2) As a more relaxed qualitative analysis, we assessed whether any turnover peak co-occurred with an ecotone (i.e., including 'minor peaks', i.e. any value that is higher than the value below and above). Because such a co-occurrence

might arise due to chance alone, we estimated the significance of such co-occurrences using simple stochastic reasoning. If there are n turnover values available on a gradient, and k ecotones defined within their range, and turnover peaks are randomly assigned to bands, then the probability p of hitting an ecotone once by chance are k/n, for hitting twice $p = k(k-1)/n(n-1)$, and for hitting a triple $p = k(k-1)(k-2)/n(n-1)(n-2)$ (the number turnover peaks was always $> k$). Because gradients were truncated at ca. 2600 m, k is in the range of 2–3, while n varies between regional datasets (range = 17–21). Calculating p showed that ca. 1 random co-occurrence can be expected per 6–12 turnover peaks (depending on dataset and zonation; $p = 0.08–0.17$). Only for two or more co-occurrences is $p < 0.05$, which would support the hypothesis of a non-random association.

(3) To investigate the link of elevational turnover and ecotones quantitatively, we used a logistic regression model to assess relationships. This tests whether an increase in turnover allows predicting the existence of an ecotone. Note that because our 200 m-bands of turnover measurement are overlapping each other and hence based in parts on the same input data, there is some pseudo-replication of data that potentially biases p-values downward. Given our results, controlling for this would not have changed conclusions.

(4) We used the entire matrix of pairwise Simpson dissimilarities of elevational bands and searched for significant ecotone effects by partial Mantel correlations. As a predictor matrix, we used a binary matrix of whether two samples were located in the same hypothetical mountain zone or not. We controlled these by a covariant matrix of elevational distance between bands (i.e., spatial autocorrelation and/or gradual environmental change with elevation). This tests, therefore, whether ecotone definitions have explanatory potential beyond the expected (continuous) similarity decay with increasing elevational distance (software: R package *vegan*).

(5) We plotted species richness over elevation and assessed whether it showed any patterns that could be related to ecotone positions (e.g., coincident richness peaks). We used rank correlations to test for a link between elevational turnover and richness of combined neighbouring bands (i.e., 200 m-bands, following methods of McCain and Beck, 2016). Given that there was no indication of a relationship between turnover and richness we did not include further statistical analysis.

We also tried cluster analysis of assemblage dissimilarity metrics (Fattorini, 2014), but results were inconclusive and therefore not presented. In addition to replicating analyses for the three biogeographic regions within the Swiss Alps, we also analysed the combined data for the Swiss Alps. We also replicated analyses using only smaller-ranged species (smaller half to the range size distribution) to ensure that the larger-ranged, widely-overlapping species were not obfuscating a more fine-scaled pattern. Additionally, this reduced the patterning of turnover as a consequence of the mid-domain effect (MDE; Colwell and Hurtt, 1994; see McCain and Beck, 2016 for turnover simulations). Furthermore, we used noctuid data from a local transect study from the Northern Swiss Alps (14 sites, ca. 600–2500 m; details in Beck et al., 2010, 2016a) to assure robustness of analyses to different spatial designs. Data on combined data, on small-ranged species, and from the local transect are not shown in detail as they confirmed all conclusions presented from the three regional analyses.

3. Results

In total we used interpolated elevational ranges for 524 species across gradients from 193 to 2593 m. The three regional datasets contained 400 species from 293 to 2093 m in the Northern Alps, 479 species from 393 to 2593 m in the Inner Alps, and 442 species from 193 to 2193 m in the Southern Alps. Turnover patterns from the three biogeographical regions are not correlated to each other when analysed quantitatively (Spearman rank correlations, $\rho < 0.2$, $p > 0.45$), although some show similarity when broadly eyeballing patterns (Fig. 3).

Major turnover peaks were never located at proposed ecotones (Table 1), and even for minor turnover peaks we only rarely found correspondence with ecotones more often than expected by chance (i.e., >1 per analysis). Cases of two correspondences were restricted to the ecotone classification of Dufour (1986; Appendix B). Logistic regression models also showed no evidence for a link of turnover and ecotones (Table 1).

Considering all pairwise dissimilarities, rather than elevational turnover only, also did not indicate links between zonation proposals and turnover after controlling for elevational differences between bands (partial Mantel regression: partial $\rho = 0.033$ (Northern Alps), −0.153 (Inner Alps) and 0.012 (Southern Alps); all $p > 0.1$). Data for the alternative ecotone proposal by Dufour (1986) were very similar (not shown).

Species richness (Fig. 4) revealed similar patterns among the three regions and with the pooled data. These low plateau-patterns in diversity are consistent with many other published elevational richness data (McCain and Grytnes, 2010; Beck et al., 2016b). There was no discernible link between richness and ecotone locations (visual judgement, Figs. 2 and 3). Furthermore, there were no correlations between observed elevational turnover and species richness (all Spearman's $\rho < 0.3$, $p > 0.3$).

Results from pooling data for the entire Swiss Alps (all three regions), from the small-ranged species subset, and from a local gradient in the Northern Alps confirmed our main result of a lack of contingencies of noctuid assemblage turnover and proposed mountain belts or the ecotones between them (for all analysis types).

4. Discussion

Noctuid moth distributions in the Swiss Alps, a large (in independent observations and species) and well-documented dataset, did not support the hypothesis that elevational zonations shape animal assemblage structure. We observed no links between *a priori* ecotone locations and range endpoint frequencies, elevational turnover, patterns of assemblage dissimilarity, or richness patterns, and richness patterns were unrelated to elevational turnover. We therefore reject the ecotone hypothesis for this study system. This coincides with the conclusions of a global, multi-gradient analysis of vertebrate distributions (McCain and Beck, 2016).

Our data and analyses were biased to favour the hypothesis in various aspects, which adds to the relevance of our rejection. The studied taxa have intimate ecological links with plant community composition (via caterpillar host plant specialization), whereas for many other animal groups (e.g., predatory taxa) vegetation is merely shaping the microclimate and 3-D structure of the environment (hence, plant species identities would conceivably matter much less). If zones and ecotones are, explicitly or implicitly, defined by plant assemblages, it is plausible to expect links to noctuid assemblages. Furthermore, we carried out tests on several interlinked predictions (e.g., on range endpoint frequencies and turnover), we presented alternative analytical approaches, we

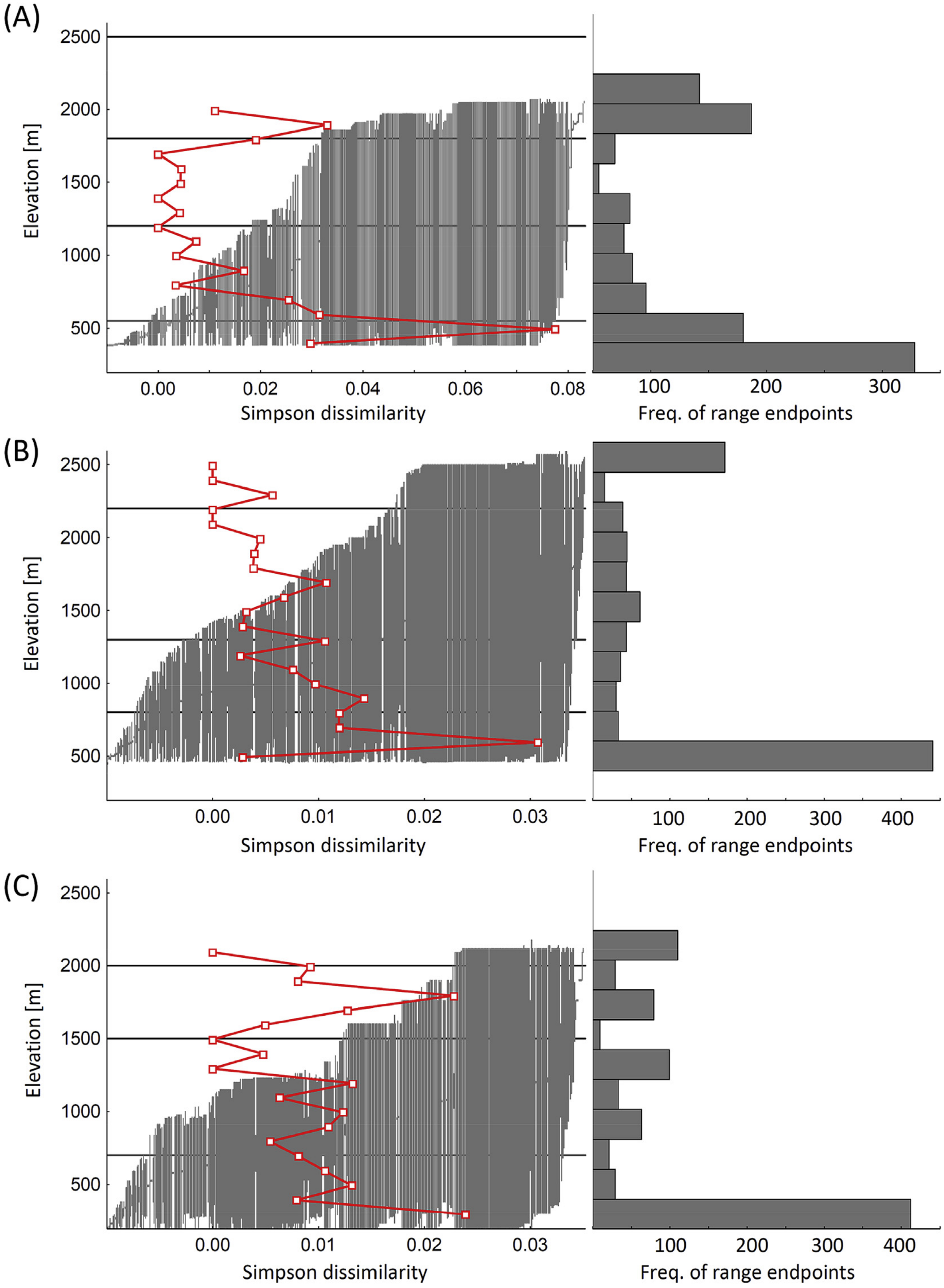

Fig. 3. Elevation (y-axis, note identical scaling for all graphs) and proposed ecotones according to Schröter (1926, solid horizontal lines; see Appendix B for an alternative classification). Elevational ranges are shown for all species (vertical light grey lines), sorted by range midpoint. Red squares represent turnover values (Simpson dissimilarity between neighbouring 100 m elevational bands). Dark grey bars on the right show the frequency distribution of range endpoints in 200 m bands (dark grey bars, right). (A) = Northern Alps, 400 species; (B) = Inner Alps, 479 species; (C) = Southern Alps, 442 species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

considered alternative zonation proposals (Dufour, 1986; Schröter, 1926) and we used various subsets of data (e.g., different regions, small-ranged species) without controlling for potential inflation of error probabilities in statistical analysis due to non-independent data (Forstmeier et al., 2016; applying such controls would not have changed our conclusions).

Observed elevational turnover of the three adjacent regions (Fig. 3) seemed unrelated, whereas one would have expected an elevational shift of otherwise identical (or very similar) patterns from the ecotone hypothesis. Earlier studies also observed a high variability of turnover patterns between different taxa within the same regions (Mena and Vazquez-Dominguez, 2005; McCain and

Table 1
Number of correspondences of ecotones with all (i.e., including ‘minor’) peaks of range endpoint frequencies and turnover, with ‘major peaks’ of turnover only, and logistic regression results predicting ecotones from turnover values. See Fig. 3 for a visualization of the data. One correspondence of “all” peaks is expected by chance alone (see Methods). Hypothetical ecotone locations are according to Schröter (1926); for an alternative classification (Dufour, 1986) see Appendix B. Data shown here are for all species; replicate analyses for small-ranged species led to the same conclusions (not shown).

Marginal Northern Alps ($n = 17$ turnover values)	
Correspondence:	
Peaks of range endpoint frequency	0
Major turnover peaks	0
All turnover peaks	1
Logistic regression ($df = 1$)	$\chi^2 = 0.01$, $p = 0.93$
Inner Alps ($n = 21$ turnover values)	
Correspondence:	
Peaks of range endpoint frequency	0
Major turnover peaks	0
All turnover peaks	1
Logistic regression ($df = 1$)	$\chi^2 = 0.03$, $p = 0.86$
Marginal Southern Alps ($n = 19$ turnover values)	
Correspondence:	
Peaks of range endpoint frequency	0
Major turnover peaks	0
All turnover peaks	1
Logistic regression ($df = 1$)	$\chi^2 = 1.16$, $p = 0.28$

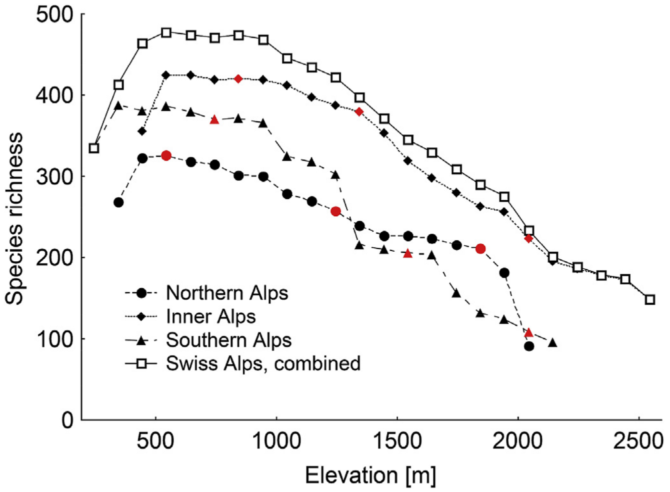

Fig. 4. Interpolated noctuid species richness per 100 m band, separately for each region and pooled for the entire Swiss Alps. Red symbols indicate proposed ecotone elevations (Schröter, 1926). Data do not show obvious linkage with ecotone positions (see Appendix B for alternative ecotone proposal). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Beck, 2016; Wilson and Shmida, 1984). Thus ordered, predictable species turnover that structures ecological systems on mountain seems unsupported and potentially over-simplistic, and warrants further critical analysis.

In contrast, there are also recent quantitative studies that reported supporting evidence for mountain zonations, particularly on plant communities (e.g., Hemp, 2006; Kessler, 2000). It remains to be investigated to what degree these conflicting results are due to differences in taxon and/or study design (e.g., use of *a priori* ecotones). The idea of mountain zonations was originally conceived based on vegetation patterns (Merriam and Stejneger, 1890; von Humboldt, 1849). Plant communities may show more structured community patterns than animals because they are sessile. Lowered mobility may reduce statistical noise in the association of where a specimen is found and what environmental conditions are requires for its sustenance (Kessler, 2000). Nevertheless, the ambiguity on actual ecotone positions even for a region like the Swiss Alps (i.e., various alternative proposal exist), intensely studied botanically for over a century, encourages our critical view of mountain zonations as a didactical concept with limited operational ecological reality in animal communities at least.

4.1. *Methodological considerations*

We suggest three interrelated methodological advices for studying elevational gradients in general and ecotones in particular.

(1) There is high value in reporting, storing and compiling point specimen records in all detail (i.e., locality, elevation; Meyer et al., 2015). This allows rigorous quantitative analyses, while vague distributional information such as “occurs in the montane forest zone” enforces the use of a concept that yet has to be confirmed in its validity for the taxon in question.
(2) Analyses of ecological patterns in mountains should always be carried out on measured data, such as elevational bands of equal breadth or quantitative environmental data. Aggregating data *a priori* into ecological zones may often be unwarranted and has potential for circular conclusions.
(3) Cluster analysis or ordination of dissimilarity matrices (Legendre and Legendre, 2012) are popular numerical methods of searching for and visualizing ecological community patterns. While we cannot draw conclusions on these directly from the above results, we feel a general warning is warranted due to their potential for falsely supporting expected patterns. These methods offer a lot of choice in application without established “best practice” standards (see Kreft and Jetz, 2010 for an attempt). Different dissimilarity metrics and cluster algorithms often lead to very different results; noisy and incomplete input data, which has to be expected in ecological field studies, will add to the variability of results (see simulations in Beck et al., 2013). A very thin line emerges between robustness evaluation by trying various methods on the one hand, and cherry-picking a particular result out of these on the other hand (cf. “researcher degrees of freedom”; Forstmeier et al., 2016). While these caveats may be no problem for exploratory analysis, they may hinder rigorous hypothesis testing.

4.2. *Conclusions*

We find no evidence for a link of ecological belt zonations and the noctuid moth communities found along Swiss mountain slopes. In light of this and concurrent published data on other animal groups (McCain and Beck, 2016; and references therein), we conclude that animal species are probably distributed idiosyncratically along gradients following their specific habitat requirements (MacArthur and Wilson, 1963). The elevational zonation concept should not be applied to animal communities except if its validity in a specific system was shown. Further, rigorous studies on a variety of taxa (particularly insect clades across a span of obligatory relationships with host plants) and regions, as well as meta-analyses, would be beneficial to evaluate whether mountain zonations are more applicable in plant communities, and why this may be so.

Author contributions

JB, CMR and CMC designed the study; CMR and JB analysed data; JB and CMC wrote the manuscript. All authors have approved the final article.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2017.02.001.

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