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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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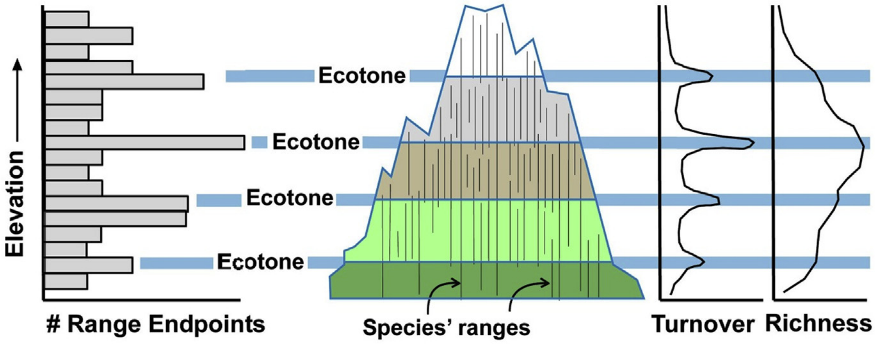

Fig. 1. An idealized sketch of the hypothesized assemblage structure along a mountain gradient *[centre]* with five *a priori* defined zones and four ecotones between them. Species' elevational ranges are shown as vertical grey lines. We derive and test prediction on three features from such an assemblage 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