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Mountain biodiversity and elevational gradients

This paper is part of an Elevational Gradients and Mountain Biodiversity Special Issue

Introduction to the special issue

Mountains are excellent systems for studying species responses to changing conditions because climatic conditions and related productivity measures change rapidly over short distances (Körner 2007). Mountains also often have high biodiversity and high levels of endemism (Hoorn et al. 2018, Rahbek et al. 2019), and are typically relatively less disturbed by people compared to flat lowlands. Although new insights about biodiversity patterns associated with mountains and elevation gradients have been achieved (Rahbek et al. 2019) the underpinning mechanistic causes of these biodiversity patterns are still open for debate (cf. Jablonski et al. 2006). This is the underpinning motivation for this special issue on *Elevational Gradients and Mountain Biodiversity*.

Why is the actual mechanism of these biodiversity patterns still elusive? I think this is in part because the debate is obscured by issues of scale, collinearity, and several expressions of energy and energy flow. The ecological setting prevents proper mechanistic experiments from being conducted, and the strong collinearity among the many climate variables causes similar predictions to be deduced from different theories and expressions of energy (Clarke and Gaston 2006, Vetaas et al. 2019).

An excellent solution to this challenge is to use extensive temperature-elevation gradients on large mountain ranges as *in situ* experimental sites. These temperature-elevation gradients are superior natural non-manipulative or observational experiments. Therefore, mountains may serve as good model systems facilitating stringent scientific studies searching for a better understanding of the fundamental processes shaping biological activity in general and species richness in particular.

To some extent, the variation in biomes along elevational gradients mimics the latitudinal gradient of biomes, but elevational gradients present fewer barriers than found horizontally with latitude across the continents and thermal energy typically declines more simply with elevation (although in certain circumstances temperature inversions can occur within such gradients). The generally simple decline of temperature with elevation is due to a decrease in air pressure that causes a decrease in temperature with elevation (consistent with Boyles' law). There are, however, several covariates along with the temperature-elevation gradient, so that they are often

classified as complex gradients. The growing season and water availability will decline with elevation as soon as one enters the elevation where frost occurs, and this will again influence the soil conditions physically and chemically. Despite these caveats, there is a consensus in macroecology and biogeography that these extensive elevation gradients are well suited to analyse various macro-scale theories and ecological models of biodiversity (McCain and Grytnes 2010, Quintero & Jetz 2018). This is confirmed historically. Several ecological theories and concepts have in part been developed at such sites, for instance, niche theory, the continuum concept, and the theory of numerical gradient analyses (McCain and Grytnes 2010). Elevation gradient studies have also made progress by refuting the old tenet that old families (for plants at least) are found on average in the sub-/tropical warm biomes, whereas the younger clades dominate in temperate to alpine biomes (Qian et al. 2019, and references therein). High mean phylogenetic ages have been found in the middle of the elevation gradients (Qian 2014, Qian et al. 2019, Tiede et al. 2016), which may support the 'out of tropics hypothesis' (Jablonski et al. 2006), however, if biodiversity does not increase unbounded through time, species richness may be unrelated to both the age of clades as well as diversification rate (Rabosky 2009).

The papers in the special issue

The special issue opens with a paper on the foundations and legacies that Alexander von Humboldt created for global high-elevation ecology and biogeography (Birks 2021). The paper is inspired by the fascination von Humboldt had for extreme alpine growing conditions. In it, Birks compiles and summarizes existing information about the world's highest vascular plants. In addition, various ecological limits such as treelines and elevational limits are compared between major mountain ranges in twenty-two different regions. He also reveals some recent high-alpine findings that would have doubtless been of great interest to von Humboldt, such as the special snow roots in some snow-bed plants.

The remaining papers in this special issue broadly speaking use temperature-elevation gradients to elucidate many of the topics I have listed above. These include the climate-based mechanistic explanation of biodiversity variation, evolutionary explanations

of phylogenetic diversity, seasonal variation in tropical mountains, as well as the classic dichotomy of facilitation and competition. The contributors have collated and analysed both data compiled from databases and new empirical data. The study systems include mountains featuring temperate, subtropical and tropical biomes, spread over three different continents. The papers follow a more recent tradition in biogeography that has been growing over recent decades, which is to utilize the extensive elevation gradients on large mountain ranges as *in situ* trial sites. Six papers take advantage of these experimental situations and four of them focus on the mechanistic and indirect factors that drive the changes in plant and insect diversity along the thermal-elevation gradient. The remaining two have a different focus, one being on plant assembly rules and the other on tropical seasonality and responses in nest making hymenopterans.

The flowering plant diversity papers report from studies in the Apuan Alps (Italy) (Musciano et al. 2021) and the Himalayas (Bhatta et al. 2021), the former from the warm temperate Mediterranean climate and the latter from subtropical monsoon climate. These two papers use an established approach of interpolated species richness from upper and lower range limits compiled from flora and/or enumerations. The approach assumes a continuous distribution between the warm (low) and cold (high) distribution limits for each individual species, which is the same assumption underpinning the continuum concept and the theory of gradient analysis (Ter Braak and Prentice 1988). The weak point is that infrequent (or rare) plants may sometimes be less continuously distributed along an elevational gradient.

These two papers demonstrate that the response in species richness along temperature-elevation gradient is scale-dependent. Across the very long Himalaya elevation gradient (5000 m a.s.l.) both trees and herbs have unimodal (hump-shaped) responses along the elevation gradients across the Himalayas (six sectors), whereas in the Apuan Alps (3000 m a.s.l.) the plant species richness (native and alien) decreased with elevation, while endemic species richness increased. See also the paper on butterflies in Sikkim (Dewan et al. 2021). However, different life forms may also have different responses, and in the Apuan Alps, the different Raunkiaer Life Forms show differentiated responses to the elevational gradient. Independent of life forms the endemic species increased with elevation, which is an important piece of information to better targeting conservation efforts because rare species at high elevation are likely to be threatened by light competition from woody species that may move upwards from lower elevations due to climate change (Theurillat and Guisan 2001).

The pan-Himalayan paper by Bhatta et al. (2021) focuses on the theoretical relationships between net primary production (NPP) and chemical energy as drivers of plant species richness versus kinetic energy as a regulator of water availability (water–energy dynamics, WED). The latter model provided the best explanatory

mechanism (much lower AIC, than NPP) for all the analyses on both trees and herbs from the humid eastern Himalayas (Bhutan) to drier western sectors (Kashmir). The explanatory values were found to be improved by including the interaction of precipitation and length of the growing season (i.e. Seasonal-WED= the photosynthetic active period for the plants). On a cruder scale, along the total Himalayan range, precipitation apparently drives plant richness in subtropical, temperate, and alpine bioclimatic zones. However, in mountainous landscapes where precipitation may encounter the ground as rain, snow, fog or clouds, the available liquid water may actually be absorbed by organisms somewhere downslope from where it was deposited. Nevertheless, the paper concludes that the seasonal-WED model, which is based on the thermodynamical transition between water phases, is reasonably good and can forecast peaks in species richness under different climate and primary production conditions. This strongly indicates that WED is a suitable theoretical framework for future diversity studies focusing on the ‘first principles’ factors underpinning diversity.

The other paper from the Himalayas (Sikkim) is an empirical analysis which also focuses on precipitation and other underlying mechanisms for butterfly species richness (Dewan et al. 2021). In similar fashion to the analysis of the life form groups in the Mediterranean study (Apuan Alps), Dewan et al. (2021) have divided total richness into smaller ecological defined subsets based on family, range size, biogeographic affinity, and host-plant specialization. All these groups respond differentially to environmental predictors, but species richness in the majority of the sub-groups declines monotonically with elevation. This is partly because the studied range spans only c. 3000 m a.s.l. – a feature shared also with the Apuan Alps study that similarly reported a linear decline (above). Dewan et al. (2021) report that butterfly richness is in general best explained by annual actual evapotranspiration (AET) based on the Turc-formula. This version of AET estimation is in general highly influenced by precipitation, and the results thus confirm the importance of water availability for butterfly richness and composition.

To some extent each of the studies that support the hypothesis based on energy-productivity or energy-water dynamics, emphasise how species are constrained by climate conditions and thus where species may coexist in the current climate. However, at a longer temporal scale, the fundamental causes of variation in species richness are in essence expressed in differences in rates of speciation, extinction, and migration. The paper from the American continent explores the role of evolution and diversification among ferns. This approach elucidates the historical processes and how these may influence current diversity patterns (Hernández-Rojas et al. 2021). It is well known that extensive elevational gradients may mimic the changes in biomes and diversity along the latitudinal gradient. With this in mind, the fern paper from the Americas is distinct within the special issue in its geographical approach. Whereas the other

diversity papers have used one main elevation gradient, or many along the same latitude (Himalayan range crudely 28° N), this paper uses 11 elevation gradients located from equatorial tropics to the subtropics 23.5° N (Tropic of Cancer). The authors show that the phylogenetic diversity (mean pairwise phylogenetic distance and mean nearest taxon distance) decreased with increasing latitude and elevation, but that these geographical factors per se were weak explanatory variables. The most striking result was that epiphytic fern assemblages were strongly influenced by climatic factors, but the terrestrial ferns were not. This may indicate that edaphic conditions and vegetation structure may have a stronger influence on the evolution and diversification of terrestrial ferns. The paper concludes that fern assemblages are strongly influenced by phylogenetic niche conservatism and environmental filtering, suggesting that the older age of many fern lineages includes historical signals that are not evident in the more recent angiosperm radiation.

That temperature-elevation gradients may work as superior non-manipulative experiments can be shown particularly well on discrete sample sites such as isolated oceanic islands with mountains (Whittaker and Fernández-Palacios 2007). One paper has utilized this special location on an oceanic island (La Palma) in the Canary Islands archipelago (Eibes et al. 2021). The experimental context was further refined/constrained by locating the gradient in a homogenous substrate of volcanic material, i.e. arid lapilli fields (tephra). Eibes et al. (2021) elucidate the classic dichotomy between facilitation and competition by co-occurrence analysis of vascular plant species in lapilli fields from 100 to 2000 m a.s.l. The study assumes that harshness decreases with elevation because more moist conditions are found at higher elevation due to fog and cloud precipitation (occult precipitation), hence the gradient is defined as a stress-gradient. The role of positive interactions between species (facilitation) was expected to increase with harshness (low land), but this hypothesis was rejected. The percentage of patches with positive species co-occurrences increased at higher elevations, which is in accordance with a refined stress-gradient hypothesis for arid sites, in which characteristics of the interacting species are incorporated.

The last paper in this special issue set deals with seasonality and its influence on hymenopteran behaviour, diversity and composition. The old tenet on tropical diversity was based on the idea of the equatorial tropics as stable ecosystems that had no seasonal variation. This narrative has been frequently used in textbooks to argue for stability as a driver of diversity, however, within science-based ecology and biogeography new knowledge has highlighted the importance of disturbance, succession, and climate variation as drivers of high diversity in the tropics (Willis et al. 2004). Indeed, on a finer temporal scale, it has been found that seasonal variation on tropical mountain can play a central role, particular within the lowlands, as is nicely elucidated in a study on Hymenoptera from Kilimanjaro (Mayr et al. 2021).

Nest-building activity showed strong seasonal trends in all three investigated trophic levels and peaked at the end of the short rainy season in the 'colline-zone' at low elevations. Seasonality was also found to influence degrees of parasitism and natural mortality, while life-history traits were mostly unaffected. Climatic conditions and flower availability were found to be capable of explaining some part of the seasonal patterns in activity of Hymenoptera, with different variables driving different rates, traits, and activity.

Concluding remarks

The papers in this special issue collectively demonstrate the importance of both thermal energy as a regulator and liquid water as the core vital resource. This is important given climate change, where an increase in temperature enforces dramatic changes in the distribution of liquid water which, in turn, influences biodiversity. It has now become urgent to find the actual mechanisms that determine species richness at various scales because changes in the global energy and water budgets are forcing biological species to change their geographical distributions. I hope this special issue will elucidate some of the scientific and biodiversity treasures found in these investigated global hotspots of extraordinary biodiversity, many of which represent deep-time evolutionary history well worth preserving in an era of rapid global changes.

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