



Plant evolutionary ecology in mountain regions in space and time

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Abstract

This special issue of the journal *Alpine Botany* brings together syntheses, macroecological and taxon-specific studies of patterns and processes of plant evolution in major mountain ranges across Europe, Africa, the Americas and Asia. Apart from reflecting current conceptual and methodological perspectives in the field, it contributes to our understanding of the interplay between factors determining the evolution and distribution of plant variation across topographically complex areas, and will help to identify the components necessary for building an integrative model of the origin and distribution of diversity in mountain areas.

Keywords Alpine biogeography · Biodiversity · Environmental heterogeneity · Plant diversification

Latitudinal and elevational gradients are increasingly investigated to understand ecological and evolutionary processes underlying patterns of biodiversity (e.g. Rangel et al. 2018). Although mountain regions contribute disproportionately to plant diversity (Körner 2021), the reasons for this are not yet fully understood and current hypotheses still fail to completely “explain this Humboldt’s enigma” (Rahbek et al. 2019). Indeed, despite Stebbins’ early reasoning about the role of specific mountain regions as museums, cradles or even graves of biodiversity (Stebbins 1974),

firm conclusions on this matter have not yet been reached (Antonelli et al. 2018; McFadden et al. 2019).

Topographically complex mountain regions differ from their lowland surroundings by encompassing remarkable ecological heterogeneity over short spatial distances. In particular, shortening of the yearly growing periods with increasing elevation strongly constraints the distribution and the adaptation of species and communities, and this translates into highly complex responses to climatic variation through time. Investigating evolutionary lineages from mountain regions accordingly enables to assess outcomes of stochastic and adaptive processes, and can help to disentangle signals left by biogeographical processes in space and time. The field of alpine botany can greatly contribute to our fundamental understanding of drivers of the distribution and evolution of taxa.

Case studies of alpine botany are traditionally published in a variety of journals with varied scopes, making it difficult to achieve a unified overview of patterns and processes acting in different mountain ranges. This special issue of the journal *Alpine Botany* brings together syntheses, macroecological and taxon-specific studies of patterns and processes of plant evolution in major mountain ranges across Europe, Africa, the Americas and Asia. Apart from reflecting current conceptual and methodological perspectives in the field, we hope that this special issue will contribute to deepening our understanding of the interplay between factors determining the evolution and distribution of plant variation across topographically complex areas, and will help to identify the

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components necessary for building an integrative model of the origin and distribution of diversity in mountain areas.

This issue starts with a methodological review paper by Larsson et al. (2021) on alpine Quaternary phylogeography. They not only provide a brief historical account of approaches in alpine phylogeography, but also describe the recent integration of distributional, demographic and coalescent (iDDC) modeling as a promising tool. According to them, this approach can be used to reliably infer the historical range shifts of alpine species and to efficiently test long-standing hypotheses such as the location of Quaternary glacial refugia. Despite challenges inherent to the accurate characterization of ecological factors across mountains, this paper shows one way to integrate distribution, demography and genetic relationships through time and how the comparison of hypothesis-driven scenarios yields increasingly credible inferences.

The European Alpine System, with its long-investigated and well-known flora, has been the starting point for many aspects of alpine biogeography. Parisod (2021) synthesizes our current knowledge of the main drivers of speciation in the continuous mountain range of the Alps. As the Alps have been very strongly affected by the climatic oscillations of the Quaternary, cycles of range contraction expansion appear to have resulted in homogenizing gene flow that counteracted speciation in many cases but also fostered the origin of hybrid species.

The analysis of the European clades of *Gentiana* by Favre et al. (2021) reveals an evolutionary radiation that has been driven by hybridization, polyploidy and chromosomal rearrangements. Noticeably, edaphic differentiation is a major factor structuring the diversity of European *Gentiana*. This makes it a promising study system to further examine the role of edaphic speciation in the evolution of plant lineages in the Alps.

Studying a subgroup of *Campanula* from the Pyrenees, Roquet et al. (2021) demonstrate the recent allopatric origin of two species distributed in the Central and Eastern Pyrenees plus Catalan Pre-Pyrenees, respectively, thus providing support for a recently advocated model of transverse speciation in mountain ranges. This is a timely reminder that spatio-temporal processes underlying biodiversity are far from being completely understood, that important discoveries for conservation management can be made even in well-explored mountain ranges.

East African high mountains have long fascinated botanists as “sky islands” for alpine plants. Revisiting classical hypotheses concerning the Afroalpine flora in the light of recent findings from densely sampled molecular and niche modelling studies, Brochmann et al. (2021) highlight the rather recent and only modest diversification of cold-adapted lineages that immigrated, often repeatedly, after the onset of harsh alpine conditions in that region.

Furthermore, the East African sky islands have largely remained isolated from each other and from other temperate regions throughout the climatic oscillations of the Quaternary. Despite rare inter-mountain dispersal, alpine species of the African flora appear genetically depauperate and vulnerable to extinction.

Evolution in the East African high mountains was investigated in great detail by Gizaw et al. (2021) for the iconic giant senecios (*Dendrosenecio*). Using Hyb-Seq sequence data from 1197 nuclear and 449 plastid loci from 42 samples representing all 11 currently recognized species, they found that lineage diversification started in the Late Miocene when high elevation habitats became first available. In this respect, *Dendrosenecio* clearly deviates from the mostly young diversification found in other lineages. Although diversification has been largely allopatric, hybridization appears to have played a role in the evolution of the group.

American mountain ranges have been the focus of multiple studies since Humboldt. Here, Figueroa et al. (2021) present a global analysis of the distribution of 2937 native plants across the Andes, Sierras of Central America and mountain ranges of North America. They show that the diversity of alpine plants is highest in the Central Andes and western North America, and that assemblages with lower phylogenetic diversity contained species with a greater degree of alpine specialization. From a comparison of ecologically similar near-Arctic and Patagonian mountain ranges they conclude that abiotic filtering alone is unlikely to explain the structure of alpine species assemblages in the Americas. Their analysis also highlights that assemblages of alpine species mostly consist of phylogenetically related taxa, and that alpine specialists have mostly diversified from pre-adapted lower elevation taxa.

In their molecular phylogenetic study of *Oritrophium*, as it turned out a non-monophyletic group which diversified largely within and among species-rich Páramo communities of the Andes, Salomón et al. (2021) found that the group likely diversified with the emergence of the Páramo during the Late Pliocene and further dispersed mainly from South-to-North in the Pleistocene. This migration involved both long-distance dispersal from the Central Andes to Mexico and gradual migration of species along the Andes.

East Asian mountain ranges encompass the highest peaks on earth in the Himalayas, the high-elevation Tibetan plateau and the Hengduan Mountains. This enormous diversity of plant species has been subject to large numbers of phylogenetic and biogeographical studies in the recent past, highlighting the north–south-oriented Hengduan Mountain as a channel for plant migration and exchange. In their study of the region, Sun et al. (2021) review the influence of the geological changes in the course of major rivers on plant diversification. They conclude that the reorganization of drainage systems resulted, at different times, in distributional

Table 1 Key components of a model of alpine plant evolution, highlighting spatial and temporal data that need to be integrated for biogeographical interpretations and for guidelines to conservation

Mountain ranges	Plant lineages
Geological history	Adequate sampling of both inter- and intraspecific diversity
Edaphic heterogeneity	Ecological characterization of taxa (biotic and abiotic)
Climatic history (ideally beyond the last glacial maximum)	History of relationships based on high-resolution molecular markers (ideally plastid vs nuclear loci)
Connectivity to other mountain ranges	Knowledge of other properties (e.g., life-history traits, dispersal, chromosome numbers)
Environmental data at relevant resolution in space and time	Patterns and processes of variation and diversification in space and time

discontinuity preventing East–West migration and leading to both the origin of new taxa and increased North–South genetic exchange.

In their phylogeographic study of (mainly) two species of *Acanthocalyx* across the Himalaya-Hengduan mountains, Mu et al. (2021) illustrate how geomorphological features of the region influenced the diversification of its alpine flora and resulted in the origin of important floristic boundaries.

Although all the above contributions add much to our understanding of alpine plant diversity, they collectively also reflect general and specific gaps in our understanding of the origin and distribution of plant diversity in mountain regions. As generally is the case, we remain rather ignorant of the relative impact of stochastic vs. adaptive drivers of the distribution of plant variation within and among species (Vellend 2016). Beyond necessary discussions about the definition of mountains (Körner et al. 2021 and references therein), we still do not know much about the role of specific regions within and among mountain ranges as regards the origin, expansion and demise of plant species. The roles of either orogeny or climate-induced range shifts for speciation and extinction have yet to be comprehensively investigated. For instance, we still hardly understand how to plant diversification is affected by the orientation of mountain chains (e.g. Wallis et al. 2016, Roquet et al. 2021 in this issue). These gaps in knowledge, among others, illustrate that not only additional detailed case studies but also global analyses will be necessary to integrate multidisciplinary knowledge and advance the field. As outlined in Table 1, key components of a model of alpine plant evolution will have to build on the accurate reconstruction of the physical history of mountain ranges and biologically relevant information on taxa under scrutiny. This calls for further coordination of networks and databases across plant phylogeny and phylogeography, geosciences and ecology to promote a satisfactory synthesis in the years to come. Seeking to integrate such multidisciplinary data in space and time, the field of alpine biogeography would greatly benefit from the development of robust methodologies for phylogenetic and phylogeographic analyses as well as appropriate methods to test specific hypotheses. The currently vivid community

of alpine botanists is tackling such stimulating challenges towards a better understanding of biodiversity in mountainous areas, which eventually must result in measures for its effective conservation.

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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